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Cuckolded Fathers Rare in Human Populations

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Contemporary data of extra-pair paternity (EPP) in human populations may be biased by the use of modern contraceptives. Studies have now estimated historical EPP rates in several human populations. The observed low EPP rates challenge the idea that women routinely 'shop around' for good genes by engaging in extra-pair copulations.

Cuckoldry in Human Societies: Myth or Reality?

A common urban myth is that many fathers are cuckolded into raising children that genetically are not their own. This fear is fuelled not just by the paternity tests that have become a standard staple of gossip magazines, talk shows, and TV series but also by the biological fact that in many socially monogamous species, females appear to regularly engage in mating outside the long-term pair bond. In many songbirds, for example, approximately one in 10 of all chicks has been shown to be the result of so-called extra-pair copulations (EPCs). In addition, evolutionary theory has shown that seeking out EPCs can be a viable reproductive strategy not just for males but also for females in many pair-bonding species. For males, EPCs are expected whenever they can be acquired at low cost [1]. More paradoxically, however, females may also be selected to actively seek EPCs, for example, as a way to improve the genetic diversity and quality of offspring, as an insurance against male infertility or to obtain additional material resources and increased protection by the extra-pair mate [1]. If these theories are right, the question arises to what extent these factors could also drive extra-pair paternity in our own species. Indeed, given that female adultery is common, occurring in an estimated 5–27% for people younger than 30 years old, the fear of fathers being cuckolded into raising someone else's child may well be justified [2].

After many years of speculation, reliable data on extra-pair paternity (EPP) frequencies in contemporary human populations have only become available over the past decade. Although popular scientific literature still often reports highly upward-biased EPP estimates of 10–30% (e.g., [3]), which were mainly based on data from paternity testing laboratories where paternity was disputed, recent work shows that the EPP rate in contemporary populations is in the range of just 1–2% [4,5]. If true, this would be reassuring news for many fathers. Critics, however, point out that in historical times, EPP rates might well have been much higher due to the lack of reliable contraceptive methods and limited knowledge about sexually transmitted diseases. Indeed, in one study, a slight but significant decrease in EPP events was reported following the introduction of the birth control pill [6]. To test this theory in more detail, several recent studies have developed genetic genealogical approaches that enable EPP rates to be estimated as they would have been several hundred years ago, before the introduction of modern contraceptive methods [7–9].

Rates of Cuckoldry in Historical Times

To be able to reconstruct the sex lives of our ancestors and infer EPP rates as they would have been in historical times, one method compares family specific Y chromosomal variation between men that, based on genealogical evidence, were patrilineally related [7,8]. In this 'genealogical pair' method, EPP events then simply show up in mismatches in the paternally inherited Y chromosomal genotypes (Figure 1A). In addition, two further indirect approaches were developed that provide estimates of past EPP rates by analysing the association between Y chromosomal variation and patrilineally inherited surnames [7,9] (the 'surname' and 'admixture' methods; Figure 1B,C). In the first study employing the genealogical pair method [8], historical EPP rates were estimated at 1.8% in a Dogon population in Mali. This low estimate was surprising, given that the study employed oral genealogies, which by themselves could have introduced a small amount of Y chromosomal mismatches. Subsequently, another study further perfected the genealogical pair method, employing written genealogical evidence, and also introduced the admixture method to provide an independent estimate, and applied it to a Western population in Flanders, Belgium [7]. This study arrived at a similarly low EPP estimate of 0.9% per generation over the past 500 years [7]. Finally, three further studies appeared that all confirmed the low occurrence of human EPP among several other Western populations: 0.9% per generation over the past 300 years in a (Western) Afrikaner population in South Africa [10] and 1.2% per generation over the past 400 years in a north Italian population [11] (both estimated using the genealogical pair method), and 0.6–1.7% per generation over the past few centuries in Catalonia [12] (estimated based on the surname method and taking into account the historical rate of surname adoption and matrilineal surname transmission of 0.9% per generation).

Trends

Contemporary extra-pair paternity rates in humans may be biased.

Genetic approaches are now developed to estimate historical cuckoldry rates.

Rate of cuckolded fathers stayed low in the past across human societies.

Extra-pair children may be rare in humans because of high potential costs.

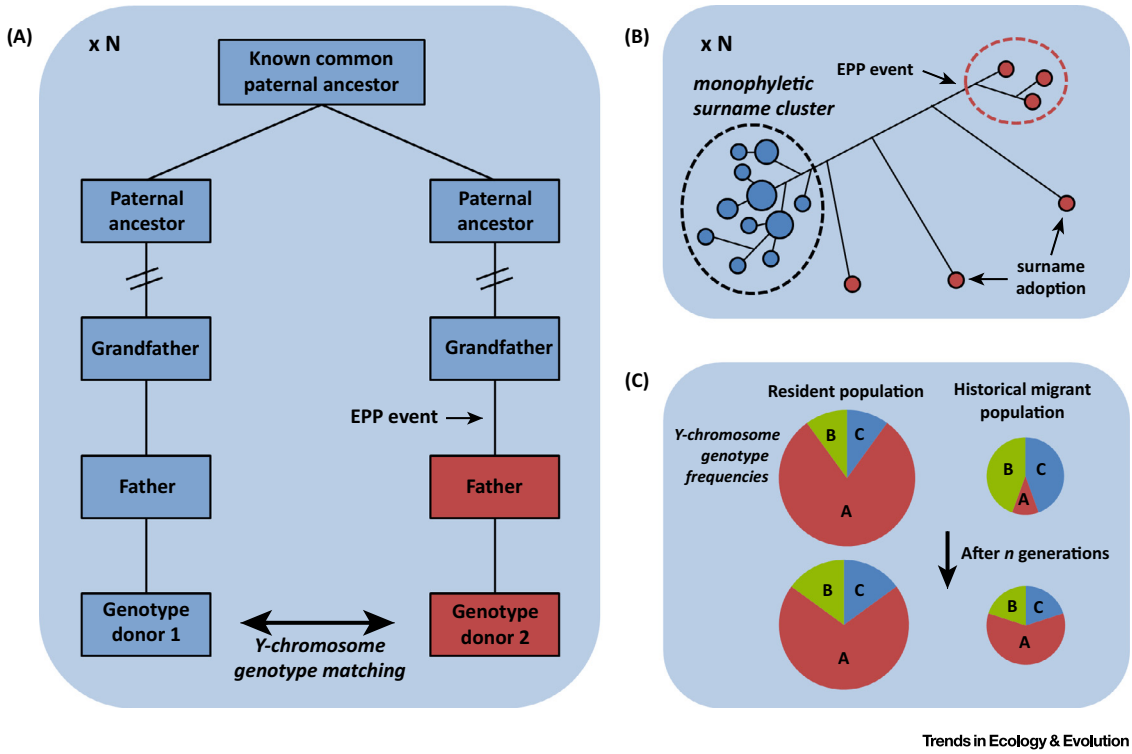

Figure 1. Three Genetic Genealogical Approaches that Allow Calculation of Past Extra-Pair Paternity (EPP) Rates in Human Populations. (A) In the 'genealogical pair' method [7,8], the EPP rate is estimated directly from mismatches in Y chromosomal genotypes between pairs of individuals that based on genealogical evidence share a common paternal ancestor (*N* = number of genealogically related pairs analysed). First developed by Strassmann *et al.* [8], this method was later extended by Larmuseau *et al.* [7] to take into account the occurrence of multiple non-paternity events within one genealogy. (B) In the 'surname' method [9], the EPP rate is estimated indirectly from mismatches in Y chromosomal genotypes across individuals that share the same surname. For this method to work, surnames must be patrilineally inherited and each surname must have only one single origin. EPP rates are estimated based on the proportion of individuals whose Y chromosome maps outside (red) the monophyletic surname cluster (broken line) in a median-joining phylogenetic network, taking into account the historical age of the surname, the rate of surname adoption (caused, e.g., by adopting a stepfather's name), and occasional matrilineal surname transmission (size of circles = incidence of particular genotype, *N* = number of surnames analysed). (C) In the 'admixture' method [7], the EPP rate is estimated from the change in the distribution of Y chromosomal genotypes (pie charts) in a historical migrant population (right) and a resident population (left) before (top) and after (bottom) *n* generations of admixture. High EPP would result in the disappearance of any differences in genotype frequencies between both sets of individuals. Residents and historical migrants are distinguished on the basis of authentic surnames typical for each region. Genotype frequencies before admixture are for the resident population estimated from a part of the population where no immigration took place, whereas for the historical migrants it is that of the present-day source population.

The surprising result of these new studies is that human EPP rates have stayed near-constant at around 1% across several human societies over the past several hundred years. This poses an immediate puzzle for behavioural scientists, who estimated that 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 and observed kin investments of matri- and patrilineal family members, which are known to be inversely related to EPP [13]. Hence, 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 relatively greater number of extra-marital affairs, but in EPP rates that have remained as low as they were before. Alternatively, it could be that traditional methods to avoid pregnancy, for example, breastfeeding infertility or fertility awareness, were more effective than they are usually given credit for, allowing for adultery without it being expressed in high EPP rates. Either way, these data pose a major challenge to the idea that women routinely 'shop around' for good genes by engaging in EPCs to obtain genetic benefits for their children [14]. There may be several reasons for the low incidence of EPP, including the fear of attracting sexually transmitted diseases, the risk of spousal aggression ('crime passionnel'), divorce, or reduced paternal investment by the social partner or his close relatives if the infidelity was discovered [1]. Therefore, the (potential) genetic benefits of extra-pair children are unlikely to be offset by

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the (potential) costs of being caught, particularly in such a long-lived species as humans with heavy offspring dependence and massive parental investment. Moreover, in other socially monogamous species, offspring of extra-pair mating have in some cases been shown to have lower lifetime fitness and genetic quality than offspring of within-pair mating (e.g., [15]). Finally, anti-cuckoldry tactics, such as male sexual jealousy, religious practices that regulate female sexuality, and strongly negative reactions towards female adultery, may also have played a role in limiting EPP [1,8]. Indeed, higher rates of EPP have so far only been documented in human populations with very specific characteristics, such as in a Mexican population where EPP rates were up to 20% higher among families of low-socioeconomic status, or in some societies with a belief in partible paternity in South America, such as the Yanomami, where EPP rates of approximately 10% have been reported, and multiple (often genetically related) social fathers may contribute resources to a woman and children [4]. Future studies on historical EPP rates in human populations will enable us to look in more detail at the evolutionary, cultural, and sociodemographic factors that shape variation in EPP rates among various ethnic and socioeconomic backgrounds. Such detailed knowledge on historical EPP rates is not just of interest to evolutionary biologists but will also benefit an array of other applications, including pedigree-based inferences in medicine, forensics, and human demography, the formulation of epidemiological models of the spread of sexually transmitted diseases, and derived applications in human behavioural ecology and population genetics [7].

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Book Review

Forty Years of Wildlife Conservation in a Nutshell

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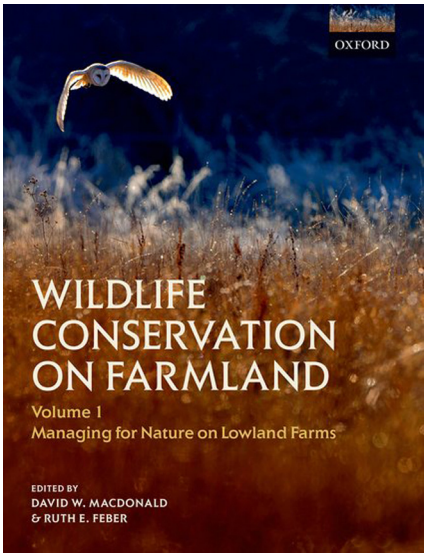

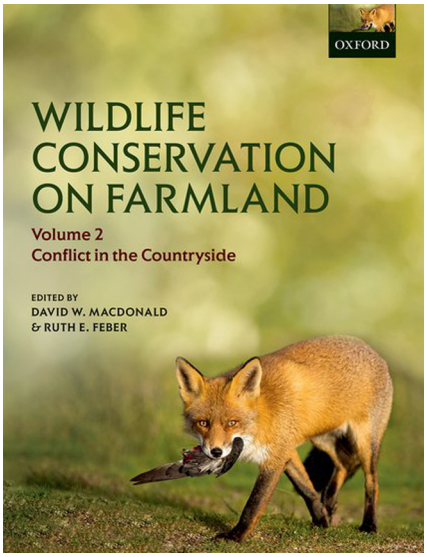

Europe is peculiar in that a large proportion of the myriad species that occur on