

Female choice and extra-pair paternity in a traditional human population

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Seeking out extra-pair paternity (EPP) is a viable reproductive strategy for females in many pair-bonded species. Across human societies, women commonly engage in extra-marital affairs, suggesting this strategy may also be an important part of women's reproductive decision-making. Here, I show that among the Himba 17 per cent of all recorded marital births are attributed by women to EPP, and EPP is associated with significant increases in women's reproductive success. In contrast, there are no cases of EPP among children born into 'love match' marriages. This rate of EPP is higher than has been recorded in any other small-scale society. These results illustrate the importance of seeking EPP as a mechanism of female choice in humans, while simultaneously showing it to be highly variable and context-dependent.

Keywords: extra-pair paternity; female choice; Himba; Namibia; life-history theory

1. INTRODUCTION

In many species, female choice plays an important role in females' mating decisions, and influences their reproductive success [1]. Early literature on this topic equated female choice with choosiness, depicting females as coy and discriminating [2]. This characterization was guided by the assumption that females had little to gain from additional partnerships, unlike males who could significantly improve their reproductive success by mating with multiple partners. This strict dichotomy has been criticized in recent years [3] and myriad studies, which demonstrate that females benefit from serial monogamy, polyandry and extra-pair partnerships, have reframed the concept of female choice, emphasizing the active and often assertive role that females have in mating decisions [4,5].

This revised vision of female choice led to a spate of research on monogamy and growing support for the contention that females exert active choice in mating decisions. For females, the potential reproductive benefits of extra-pair paternity (EPP) include improved genetic quality of offspring, insurance against male infertility, greater access to material resources and increased protection against infanticide [6]. In humans, these benefits have been shown in societies with partible paternity, where multiple

'social fathers' contribute resources to women and children [7,8].

Despite increased attention to this topic, cross-cultural evidence of EPP in humans remains limited. However, extra-marital relationships are well-studied and adultery is common. In Western societies, the rate of female adultery ranges from 20 to 50 per cent [9]. In the Standard Cross-Cultural Sample, female extra-marital affairs are common among foragers, horticulturalists and pastoralists [10], and in general infidelity is the most frequently cited reason for divorce among men and women [11]. These data are consistent with numerous ethnographic accounts describing female infidelity: e.g. the !Kung [12], Ache [13,14], Bari [7], Tsimane [15] and Tiwi [16].

Given the near ubiquity of adultery cross-culturally, studies of EPP are of paramount importance to understanding mating and parenting dynamics in humans. However, almost all of the data on EPP currently available come from Western, industrialized populations [17,18]. These studies indicate worldwide non-paternity rates ranging between 1 and 10 per cent, which are much lower than might be expected given the rates of infidelity reported across human societies. The only known study of genetic paternity from a small-scale natural fertility (non-contraceptive using) population is from research with the Yanomamo in the 1960s, showing a non-paternity rate of 9.1 per cent [19], the high end of global reported rates.

In addition to a dearth of data on EPP in natural fertility populations, we also lack quantitative data about when extra-pair unions occur. Among pair-bonded birds, the prevalence of EPP varies according to socioecological context [20,21]. Human females should also vary their behaviour according to circumstance. In particular, I predict that females will seek out more EPP when they are tied to mates they did not choose. Arranged marriages are often driven by familial concerns for strategic alliances or reciprocity, representing a form of parent-offspring conflict that daughters often lose [22,23]. In 'love matches' daughters' interests either coincide with or supersede those of their parents, and they should therefore have less impetus to seek extra-pair mates. Therefore, the proportion of EPP should be higher in arranged marriages than in 'love matches'.

2. MATERIAL AND METHODS

(a) Study population

The Himba are a semi-nomadic pastoral population living in the northwest corner of Namibia. The data for this study were collected from women living in 23 compounds in the Omuhonga basin. The Himba remain largely isolated from the market economy, relying mainly on livestock for daily subsistence and trade. Both men and women carry out duties related to caring for livestock, and this division of labour can cause long-term separation of spouses while one remains at the main homestead and the other is residing at a cattle post. In general, women have considerable autonomy of movement. All marriages are formally arranged by kin with a small brideprice paid, though couples exert partner choice in 'love matches'. Polygyny and divorce are both common, as are children born out of wedlock. This is a natural fertility population with little knowledge or use of contraceptives.

(b) Data collection and analysis

Reproductive histories were collected on 118 women, 110 of whom are included in this analysis. Eight were excluded because they had no children ($n = 5$) or because data on reported paternity were not collected ($n = 3$). This resulted in a record of 421 births, of which

329 occurred within marriage. Non-marital births were excluded from the analysis. Data were not collected on children who died as women were reticent to discuss details of these children's lives. For each birth, the respondent attributed paternity to her husband or a marital affair. The Himba word for an extra-pair birth is *omoka*. Each marriage was recorded as a 'love match' or a strictly arranged marriage. The author conducted all interviews, with a translator's assistance.

To ensure accuracy in women's EPP reports, several conditions were met. First, women had to be willing to discuss EPP. Among the Himba, infidelity is not a taboo topic and is regularly discussed. However, special care was taken to ensure complete confidentiality and privacy. Second, women must be able to reliably report paternity, requiring reasonable knowledge about conception timing and a lack of partner overlap within ovulatory cycles. While the data presented here cannot substitute for genetic paternity data, women reported great confidence in their paternity assertions, stating that they counted back upon becoming visibly pregnant and determined paternity. These assertions are supported by ethnographic accounts of husbands and wives spending significant periods apart. Third, women must be able to remember paternity attributions for births that occurred long ago. To determine whether memory difficulties are affecting the data, women's age is included as a control in these analyses. However, memory loss is likely to underreport EPP.

Data were coded in two ways. First, each woman was recorded as an independent datapoint and the number of births attributed to her husband and affairs were recorded. Second, each birth was used as a datapoint and was recorded as *omoka* or not. The distribution of *omoka* births in arranged marriages and 'love matches' was compared using a resampling analysis. The 58 *omoka* births were randomly assigned across marriage types. The simulation was repeated 1000 times to obtain the expected distribution of *omoka* births in 'love matches'. The observed distribution was compared against the simulated distribution to obtain the significance level.

Women's reproductive success was analysed to look for effects of EPP using Poisson regressions. This analysis was limited to post-menopausal women (older than 50 years). The measure of reproductive success used is the number of offspring surviving to age five. Primary predictors were whether a woman had any *omoka* children and the number of *omoka* children she had. Both regressions controlled for mother's year of birth. A separate test for cohort effects showed no effect of mother's year of birth on the likelihood of an extra-pair birth.

3. RESULTS

In this sample, 31.8 per cent of Himba women had at least one extra-pair (*omoka*) birth during their lifetime. This accounts for 17.6 per cent of all marital births. Of the 36 women who had at least one extra-pair birth, 20 had one, nine had two and six had three or more. This is a conservative estimate of EPP in this population due to reporting bias and the exclusion of children who died.

Women in 'love matches' were significantly more faithful to their husbands than women in arranged marriages. There were no *omoka* children born within love matches (0 of 79), compared with 23.2 per cent *omoka* children from arranged marriages (table 1). This is highly unlikely to be due to chance ($p < 0.001$; figure 1). It is possible that sampling bias affects these results. Women may be more likely to report extra-pair paternity in failed marriages, and arranged marriages may be more likely to fail. However, 21 per cent of 'love matches' resulted in divorce, yet there were no reports of EPP in this group.

Extra-pair liaisons are tied to reproductive benefits. Post-reproductive women who had at least one extra-pair birth have significantly higher reproductive success than women with none (coefficient = 0.562 ± 0.18 , $p = 0.002$). When EPP is recorded as an ordinal variable, the effect is similar. Increasing numbers of

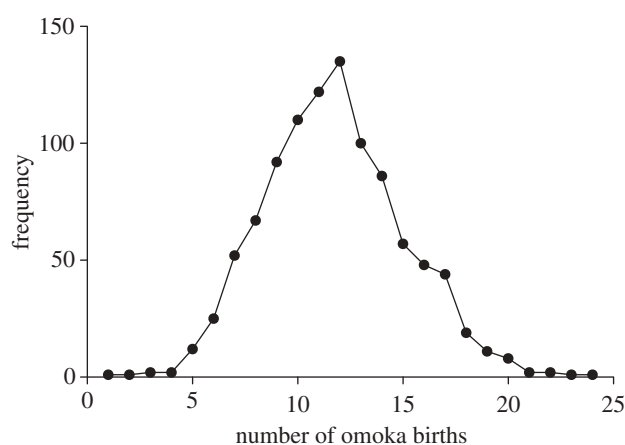


Figure 1. Number of *omoka* births expected to occur in 'love match' marriages. The observed sample of births is used to approximate the expected distribution of *omoka* children born into 'love matches'. Resampling with replacement was performed 1000 times (range 3–26, mean = 17.34, s.d. = 3.3).

Table 1. Summary statistics ($n = 110$ women).

| | all marriages | arranged marriages | love matches |
|---------------------------------------|------------------|--------------------|--------------|
| average number of marriages per woman | 1.41 | 1.08 (76.6%) | 0.33 (23.4%) |
| number of children | 329 ^a | 250 | 79 |
| number of <i>omoka</i> children | 58 (17.6%) | 58 (23.2%) | 0 |

^aExcludes 92 out-of-wedlock births.

omoka children are associated with increased overall reproductive success (coefficient = 0.284 ± 0.08 , $p = 0.001$; figure 2).

4. DISCUSSION

These data represent some of the first evidence linking extra-pair paternity to improved reproductive success in a natural fertility population. This finding is congruent with ethnographic data from other small-scale populations. Among the Ache and Bari, children who had 'secondary fathers' had increased survivorship over those with only one father [7,13]. Similarly, among the Pimbwe, serial monogamy is correlated with increased reproductive success [5]. These data further indicate that Himba women's decisions about extra-pair relationships are highly context-dependent. Women who had choice in their marital partner were more likely to remain faithful. For women in arranged marriages, having an affair may be a viable option for exerting choice while still obliging one's parents. I do not propose that EPP is always a viable strategy, or that it is one that comes without risk. I only suggest there is variation in these risks that should be considered when studying female choice. The Himba appear to represent one end of a spectrum, where female adultery is common and may counterbalance parental influence and subsequent parent-offspring conflict over marriage arrangements.

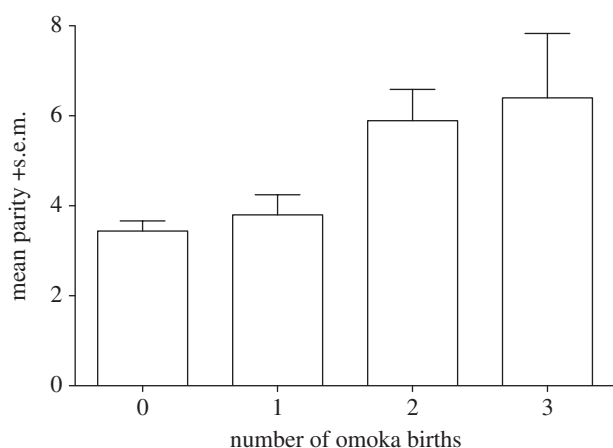


Figure 2. Increasing numbers of omoka births are associated with an increase in the total number of children women have who survive to adulthood. Sample is limited to post-menopausal women. Error bars s.e.m. ($n = 33$).

This study demonstrates some benefit of EPP to women, but why would husbands tolerate this behaviour? One explanation is that the costs of mate guarding are too high to maintain. Among the Himba, where division of labour often leads to spouses being separated for substantial periods, husbands may do better seeking EPCs themselves rather than risking economic loss to monitor their wives. Himba men also provide little paternal investment. Wealth inheritance is matrilineal and brideprice is low. Finally, Himba children are important sources of labour. From a young age they participate in herding and domestic labour and where children more quickly become net producers, paternity uncertainty may be more tolerable to men because they can reap the benefits of child labour.

Together these data posit active reproductive decision-making in women and the use of EPP as a method of exerting choice in the face of constraints. Just as divorce and serial monogamy allow women some control over paternity decisions, EPP can be used within marriages to counter parental interests that may dominate marriage arrangements, particularly early in a woman's reproductive career. The benefits of EPP are particularly striking because we might expect EPP to be correlated with increased child mortality and therefore lower overall reproductive success. The opposite pattern is shown here, indicating that in this social context extra-pair mating may be an adaptive strategy.

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