



Offspring mortality was a determinant factor in the evolution of paternal investment in humans: An evolutionary game approach



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ABSTRACT

Some researchers support the belief that man evolved philandering behavior because of the greater reproductive success of promiscuous males. According to this idea, deserting behavior from the man should be expected along with null paternal involvement in offspring care. Paradoxically however, the average offspring investment in the human male is far higher than that of any other male mammal, including other primates. In our work, we have addressed this conundrum by employing evolutionary game theory, using objective payoffs instead of, as are commonly used, arbitrary payoffs. Payoffs were computed as reproductive successes by a model based on trivial probabilities, implemented within the Barreto's Population Dynamics Toolbox (2014). The evolution of the parent conflict was simulated by a game with two players (the woman and the man). First, a simple game was assayed with two strategies, 'desert-unfaithful' and 'care-faithful'. Then, the game was played with a third mixed strategy, 'care-unfaithful'. The two-strategy game results were mainly determined by the offspring survival rate (s) and the non-paternity rate (z), with remaining factors playing a secondary role. Starting from two empirical estimates for both rates ($s = 0.617$ and $z = 0.033$) and decreasing the offspring mortality from near 0.4 to 0.1, the results were consistent with a win for the 'care-faithful' strategy. The 'desert-unfaithful' strategy only won at unrealistically high non-paternity rates ($z > 0.2$). When three-strategy games were played, the mixed strategy of 'care-unfaithful' man could win the game in some less frequent cases. Regardless of the number of game strategies, 'care' fathers always won. These results strongly suggest that offspring mortality was the key factor in the evolution of paternal investment within the *Homo* branch. The 'care-faithful' strategy would have been the main strategy in human evolution but 'care-unfaithful' men did evolve at a lesser frequency. It can therefore be concluded that human populations, under most of the likely ecological situations, would arrive at a polymorphic state where alternative strategies might be present in significant quantity.

1. Introduction

In a classic paper on the fruit fly, *Drosophila melanogaster*, Bateman (1948) showed that the reproductive success (measured as fertility) of a male was directly related to the number of different mates he covered, whilst a female reached her fertility limit after the first or second copulation. More than 20 years later, Trivers (1972) further developed Bateman's ideas under a unifying single factor he named "parental investment". According to the theory, the less-investing sex (usually the male) is prone to desert as soon as he mates, looking for a new coupling and leaving his female mate having to rear the offspring alone. The heavily-investing sex (usually the female) has little or nothing to gain by mating promiscuously therefore her adaptive behavior should be to choose the most appropriate male.

Going from flies to humans, the first book on the evolutionary

origin of human sexuality (Symons, 1979) supported the view that a man, who can potentially initiate hundreds of pregnancies in his lifetime with little investment, would have evolved philandering behavior, and would have fathered a large number of children - many more than any committed and faithfully monogamous man (Buss and Schmitt, 1993; Buss, 1998). The man would have evolved a trend to desert his mate-pair looking for new mating opportunities and therefore investing nothing, or the minimum, in parental care. Meanwhile the woman would have evolved a trait to care for her offspring a great deal.

In the same vein, other works stated that human pair bonds were surreptitiously eroded by rampant sexual infidelity from both pair members (Goetz et al., 2008) making human monogamy nothing more than a romantic fiction. The sexual infidelity rate was estimated to be higher than 50%, with some estimates suggesting that more than 30%

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of children were the result of cuckoldry. This impressive increase in the reproductive success of unfaithful men would evolutionarily account for philanderers. Some extreme consequences linked to this behavior were posited, such as sperm competition (Baker and Bellis, 1993a, 1993b; Stockley, 2004), and marked sexual dimorphism (for both biological and psychological traits) (Shackelford et al., 2002), etc.

Conversely, others indicated that empirical evidence did not accommodate such a picture - that sperm competition was not supported by evidence (Dixon, 2009, 2012; Lovejoy, 2009), that differences between sexes are moderated (Hyde, 2005; Petersen and Hyde, 2011; Stewart-Williams and Thomas, 2013), and that cuckoldry rates are well below 30% (Anderson, 2006; Larmuseau et al., 2013). Moreover, further authors argued that the evolutionary trend for monogamy started very early along the human evolutionary branch (Lovejoy, 1981) as suggested by recent discoveries in the fossil record (Lovejoy, 2009). The fossil records have shown that, from the very beginning of the unique human evolutionary branch, around 6 million years ago, sexual dimorphism began to progressively diminish. While australopithecines were markedly sexually dimorphic, *Ardipithecus ramidus* was already showing a significant reduction in sexual differentiation, which continued in successive steps through to *Homo sapiens*, strongly suggesting a trend towards pair-bonding ever since the early evolution of the hominid branch (Lovejoy, 2009; Nakahashi and Horiuchi, 2012).

Indeed, it is widely accepted that, within the context of mammals and even primates, human mating behavior is quite special ('an evolutionary conundrum') (Dunbar, 2010) given the long-term relationship between pairs and the exceptional male commitment to offspring care. The role of the man is especially surprising, a 'mystery' (Conroy-Beam et al., 2015). This was clearly stated by the expert primatologist and feminist, Hrdy (1999: 54): "He [the man] has the capacity to inseminate a dozen or more females; why should he focus on one to the exclusion of others?"

The parental investment conflict has sometimes been addressed scientifically using evolutionary game theory, but encompassing a wide general approach for all animals (Dawkins, 1976; Maynard Smith, 1977) not specifically for humans. In our work, we have tried to gain new insight into the evolution of human mating behavior by using an evolutionary game approach. This approach is completely different to that usually proposed because we have run evolutionary games based on probabilistically-computed payoffs instead of starting with arbitrary payoff values. The payoffs were calculated using empirical values for the offspring survival rate and the non-paternity rate, thus simulating realistic situations. Many different ecological scenarios have been simulated by modifying these variables (offspring survival rate, non-paternity rate, initial frequencies, sex ratio, etc.) to determine the payoffs.

2. Material and methods

To proceed with an evolutionary game theory analysis, we have: (1) defined the populations of players, (2) developed a fitness function and (3) used different processes to govern the evolution of the populations. We evaluated two-player asymmetric games with continuous mixing and interaction between generations; to do this, we employed the appropriate continuous time dynamic equations (Rees, 2004).

2.1. Two strategy games

There are two players (the woman and the man) with two strategies ('desert-unfaithful' vs. 'care-faithful') available to each player. The 'desert-unfaithful' player provides no care to her/his progeny, gives no support to her/his mate, and is sexually unfaithful to her/his mate. Conversely, the 'care-faithful' player provides care to her/his progeny, gives support to her/his mate and is sexually faithful to her/his mate. Players were labelled as: Mdu, Mcf, Fdu, and Fcf; where 'M' stand for

male, 'F' for female, 'du' for 'desert-unfaithful', and 'cf' for 'care-faithful'. Therefore, there are four types of mating pairs (or 'families'): Mdu×Fdu (Pair 1), Mdu×Fcf (Pair 2), Mcf×Fdu (Pair 3) and Mcf×Fcf (Pair 4).

2.2. The model for computing payoffs

Payoffs were computed as the reproductive success (RS) of each strategy using a probabilistic estimation model of the progeny number for each individual in a population, using the following parameter set: population size (as the number of reproductive individuals, N), sex ratio (r), female fertility (f , modulated by a mating partner-dependent factor, v), minimum offspring survival rate (s), and the non-paternity or extra-pair paternity rate (z , as the proportion of genetically-unrelated children reared by a male parent).

In our model, N can take any positive integer value. Although N was used in intermediate calculations, RS and payoff values were fully independent of it. The sex ratio, r , can be shifted between near 0 (too few males) to near 1 (too many males). The maximum number of couples was limited by the number of women, $N(1-r)$. The initial proportions of Mcf and Fcf in the population were denoted by M_{cf0} and F_{cf0} (with $M_{du0} = 1 - M_{cf0}$ and $F_{du0} = 1 - F_{cf0}$). The 'care-faithful' male and female can have a certain preference towards some 'care-faithful' mates (i.e. mate choice). Here, mc denotes the deviation from random mating of Mcf towards Fcf and fc denotes the deviation of Fcf towards Mcf. Both deviations range from 0 (no preference) to near 1 (near exclusive choice).

Female fertility demonstrated an effect similar to N , i.e. it had no impact on the game because it did not affect payoffs. We fixed this at 10 for convenience and it was modulated by v (range 0–1), a parameter that has a positive effect (a fertility increase) on the female if the male partner is 'care' and a negative impact (a fertility decrease) if the partner is 'not care'. It is assumed that a caring man supports his female partner providing help and food to replenish her energy store; in turn, facilitating the resumption of ovulation and the shortening of the inter-birth period (thus increasing fertility).

The offspring survival rates were family-dependent, with the maximum value (1.0) being assigned to the mating pair where both partners were 'care' (Mcf×Fcf, Pair 4), the minimum (s_1) was assigned to the pair where both partners were 'not care' (Mdu×Fdu, Pair 1), and mixed pairs received scaled intermediate values, higher for Pair 2 with the female caring parent (Fcf; $s_2 = s_1 + 2(1 - s_1)/3$) than for the male caring parent (Mcf, Pair 3; $s_3 = s_1 + (1 - s_1)/3$).

Using these parameters, the probabilities for the four mating pair types in the population would be: $p_1 = (1 - M_{cf0})(1 - F_{cf0})$; $p_2 = (1 - M_{cf0})F_{cf0}(1 - fc)$; $p_3 = M_{cf0}(1 - F_{cf0})(1 - mc)$; and $p_4 = 1 - p_1 - p_2 - p_3$. It is noticeable that when there is mate choice ($mc > 0$ and/or $fc > 0$), the dissimilar pair probabilities (Pairs 2 and 3) decreased, and there was an identical increase in magnitude in Pair 4.

The number of children produced by mating pairs is $C_1 = f(1-v)p_1N(1-r)$, $C_2 = f(1-v)p_2N(1-r)$, $C_3 = f(1+v)p_3N(1-r)$ and $C_4 = f(1+v)p_4N(1-r)$, respectively. Differential fertility was taken in account. Children cared for by different parents have a different survival probability (s_i), so the number of surviving children will be $s_i C_i$, for mating Pair i .

The mean offspring size for an individual (man or woman) is:

$$\bar{O} = \frac{\sum_{i=1}^4 s_i C_i}{N(1-r)} = f[s_1(1-v)p_1 + s_2(1-v)p_2 + s_3(1+v)p_3 + s_4(1+v)p_4]$$

From the non-paternity rate, z , the illegitimate surviving children for each of the mating pair types (from 1 to 4) will be $zs_1 C_1$, 0, $zs_3 C_3$ and 0, respectively (assuming that 'care-faithful' women are strictly faithful to their partners and do not participate in extra-pair copulation). These figures only affect male RS, because of uncertain paternity, not female RS given that maternity is always certain.

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