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Culturally transmitted paternity beliefs and the evolution of human mating behaviour

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Recent anthropological findings document how certain lowland South American societies hold beliefs in 'partible paternity', which allow children to have more than one 'biological' father. This contrasts with Western beliefs in 'singular paternity', and biological reality, where children have just one father. Here, mathematical models are used to explore the coevolution of paternity beliefs and the genetic variation underlying human mating behaviour. A gene–culture coevolutionary model found that populations exposed to a range of selection regimes typically converge on one of two simultaneously stable equilibria; one where the population is monogamous and believes in singular paternity, and the other where the population is polygamous and believes in partible paternity. A second agent-based model, with alternative assumptions regarding the formation of mating consortships, broadly replicated this finding in populations with a strongly female-biased sex ratio, consistent with evidence for high adult male mortality in the region. This supports an evolutionary scenario in which ancestral South American populations with differing paternity beliefs were subject to divergent selection on genetically influenced mating behaviour, facilitated by a female-biased sex ratio, leading to the present-day associations of female control, partible paternity and polygamy in some societies, and male control, singular paternity and monogamy in others.

Keywords: cultural transmission; gene–culture coevolution; infanticide; mating behaviour; paternity beliefs; polygamy

1. INTRODUCTION

Recent anthropological work (Beckerman *et al.* 1998; Beckerman & Valentine 2002) has shown that a number of societies in lowland South America hold beliefs in 'partible paternity', the idea that children can have more than one 'biological' father. Conception and foetal growth are seen to result from the accumulation or other combined action of more than one man's semen, and consequently a significant proportion of children in these populations acknowledge 'secondary fathers', i.e. men who slept with the children's mothers around conception or during pregnancy. Consequently, children with two fathers have a significantly greater chance of survival to reproductive age than children with only one father (Hill & Hurtado 1996; Beckerman *et al.* 1998). This benefit may result from additional provisioning of the child with extra food by multiple fathers (accentuated by the sexual division of labour practiced by these societies wherein males' hunting provides valuable animal proteins and fats), either to the child itself or indirectly to the child's mother when the child is *in utero* (Beckerman *et al.* 1998), and/or greater protection (e.g. from infanticide) afforded to children with two fathers (Hill & Hurtado 1996). These studies find no ecological, demographic or linguistic differences between partible societies and neighbouring singular paternity societies (where 'singular paternity' is the biologically accurate belief that children can have only one father), hence these survivorship differences appear to be directly related to the different paternity beliefs.

The existence of partible paternity societies highlights the potential dissociation between culturally transmitted folk beliefs and biological reality. This relationship is frequently taken for granted in Western societies where singular paternity beliefs are prevalent. The existence of partible paternity societies potentially challenges several assumptions of Western science regarding human mating behaviour. In particular, many evolutionary biologists and psychologists have argued that men universally strive to ensure exclusive paternity of offspring (Symons 1979; Pinker 1997; Wilson 1998). Partible paternity beliefs, in contrast, seem to explicitly increase paternity uncertainty, benefiting females who receive extra provisioning and conferring a greater chance of survival on their offspring. It is of considerable theoretical interest, therefore, whether such beliefs have the potential to affect the evolution of human mating behaviour, favouring genetic differences between human populations expressed in traits such as promiscuity, jealousy and faithfulness. The following two mathematical models explore the coevolution of culturally inherited paternity beliefs and the genetic variation underlying human mating behaviour. Model 1 uses population-based 'gene–culture coevolution' methods, while Model 2 uses an agent-based modelling technique.

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Table 1. Genotypes and fitnesses associated with each mating behaviour.

genotypes of mating individuals				mating behaviour	model 1: cluster fitness		model 2: probabilities of reproduction	
male 1	female 1	male 2	female 2		B_p	B_s	B_p	B_s
M	M			monogamy	$1+s$	$1+s$	$0.5+s$	$0.5+s$
m	M		M	polygyny	$2(1+s/2)$	$2(1+s/2)$	$0.5+s/2$	$0.5+s/2$
M	m	M		polyandry	$1+2s$	$1+(1+a)s-r$	$0.5+2s$	$0.5+(1+a)s-r$
M	m	m	M	polygynandry	$2(1+s)$	$2(1+s-r)$	$0.5+s$	$0.5+s-r$
M	m	m	m	polygynandry	$2(1+s)$	$2(1+s-r)$	$0.5+s$	$0.5+s-r$
m	M	M	m	polygynandry	$2(1+s)$	$2(1+s-r)$	$0.5+s$	$0.5+s-r$
m	M	m	m	polygynandry	$2(1+s)$	$2(1+s-r)$	$0.5+s$	$0.5+s-r$
m	m	M	M	polygynandry	$2(1+s)$	$2(1+s-r)$	$0.5+s$	$0.5+s-r$
m	m	M	m	polygynandry	$2(1+s)$	$2(1+s-r)$	$0.5+s$	$0.5+s-r$
m	m	m	M	polygynandry	$2(1+s)$	$2(1+s-r)$	$0.5+s$	$0.5+s-r$
m	m	m	m	polygynandry	$2(1+s)$	$2(1+s-r)$	$0.5+s$	$0.5+s-r$

2. POPULATION-BASED MODEL (MODEL 1)

(a) *Methods*

Gene–culture coevolution models (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Feldman & Cavalli-Sforza 1976) simultaneously track changes in allele frequencies in the gene pool and changes in cultural traits in the cultural pool, exploring the interaction between these two systems of inheritance. Each individual is commonly described in terms of their 'phenogenotype' (the combined package of their genes and cultural traits; Feldman & Cavalli-Sforza 1976) and transmission rules for both genes and culture are specified.

Model 1 employed gene–culture coevolution methods to explore the interaction between genetic bases of mating behaviour and culturally transmitted paternity beliefs. We assume that genetic variation, either now or in the past, and acting via hormonal influences on behaviour, to some degree underlies human mating behaviour, consistent with animal (Pitkow *et al.* 2001) and human (Cherkas *et al.* 2004) data. Mating is affected by variation at a single haploid genetic locus (**M**), with two alleles, M and m. While humans are not haploid, diploid models gave broadly equivalent results (see methods in electronic supplementary material), and haploid models offer greater tractability. M individuals behave 'monogamously' and only mate with a single partner, while m individuals behave 'polygamously' and always mate with two partners. These assumptions generate different 'mating clusters' (see figure S3 in electronic supplementary material), classed as *monogamous* (one male and one female), *polygynous* (one male and two females), *polyandrous* (two males and one female) or *polygynandrous* (two males and two females). Note that M individuals may be part of polygamous clusters if their mate is m. Ethnographic data suggest that polygamous individuals typically restrict themselves to a maximum of two mates (possibly due to constraints on availability of food for provisioning; Beckerman & Valentine 2002), justifying our corresponding assumption in the model.

Individuals hold one of two mutually exclusive beliefs concerning paternity, either B_p (belief in partible paternity) or B_s (belief in singular paternity). We modelled both vertical (from biological parents) and oblique (from unrelated members of the parental generation) cultural transmission of paternity beliefs. Note that oblique transmission is generalizable to unbiased horizontal cultural transmission, with biological generations redefined as transmission episodes (Boyd & Richerson 1985). No differences were found between the vertical and the oblique/horizontal models, so the latter, simpler, model is presented here. Hence, we assume offspring adopt B_p with a probability equal to the frequency of B_p in the parental generation, and B_s with a probability equal to the frequency of B_s in the parental generation. Residential patterns in lowland South American societies are strongly kin-based, and paternity beliefs persist across multiple generations (Beckerman & Valentine 2002), both consistent with vertical/oblique cultural transmission. Other ethnographic studies suggest that cultural transmission of beliefs, skills and knowledge (including mating beliefs) in traditional societies is predominantly vertical, both at the population level (Guglielmino *et al.* 1995; Hewlett *et al.* 2002) and the individual level (Hewlett & Cavalli-Sforza 1986; Ohmagari & Berkes 1997; Aunger 2000), although it is frequently difficult to distinguish vertical from horizontal transmission. There is some debate over the prevalence of vertical and horizontal cultural transmission in traditional societies (R. Boyd 2004, personal communication), hence we stress that the different modes of cultural transmission here generate equivalent results.

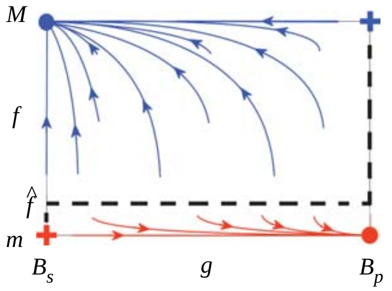

Figure 1. Illustrative behaviour of model 1 for biologically realistic parameter values (s, b_1, $b_2=0.1$, $r=0.01$, SR$=0.5$), with f and g the frequencies of M and B_p, respectively. Circles, stable equilibria; crosses, unstable equilibria; thick dashed lines, lines of unstable equilibria; and thin solid lines, trajectories of test populations within the phenogenotype space in the direction of the arrows. Colour indicates mating behaviour: blue lines end at entirely monogamous equilibria; red lines end at entirely polygynandrous equilibria. Here $\hat{f}=0.12$.

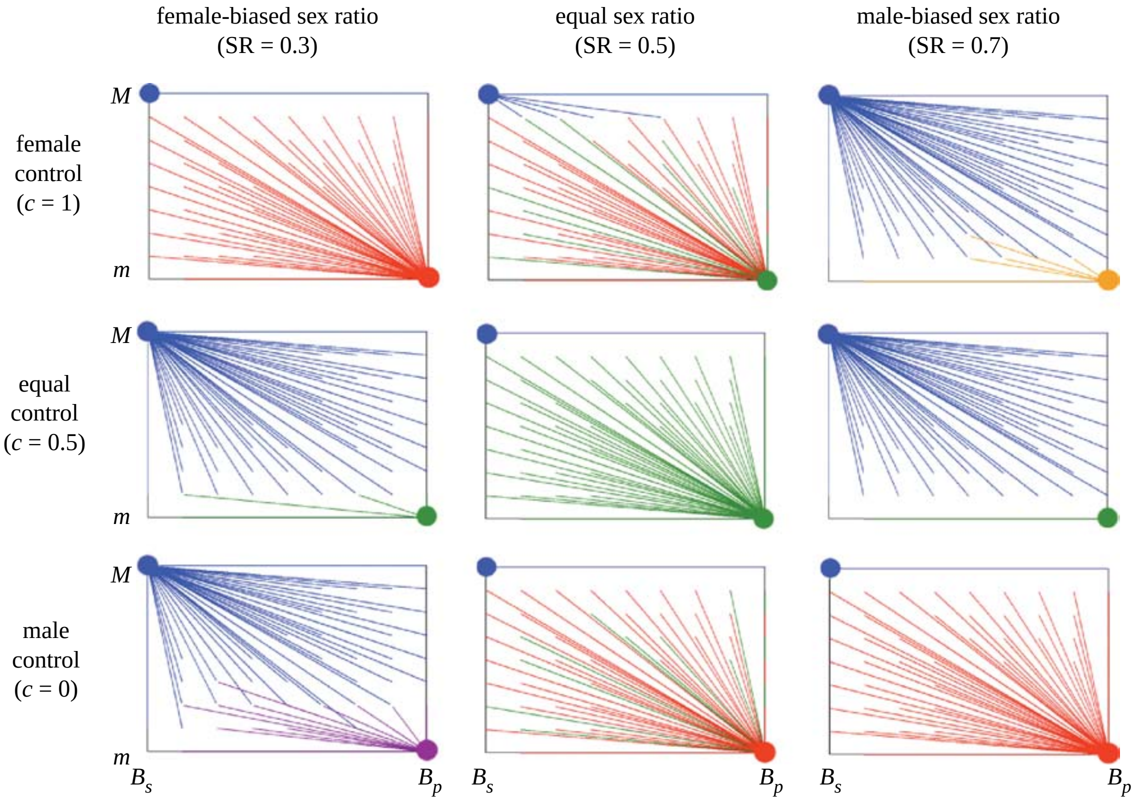

Figure 2. Interaction between sex ratio (SR) and control over mating (c) in model 2 ($s=0.2$, $r=0.25$, $b_1=0.1$, $b_2=0.1$). Circles indicate stable equilibria and lines indicate the start point and final equilibrium of test populations. Colour denotes mating behaviour of the population at the final equilibrium: blue, monogamy; purple, polygyny; orange, polyandry; red, polygynandry; green, stable mix of more than one mating behaviour.

Individuals possess one of four phenogenotypes: MB_p, MB_s, mB_p or mB_s. These phenogenotypes are allotted frequencies of x_1, x_2, x_3 and x_4 and y_1, y_2, y_3 and y_4 in males and females, respectively. Table 1 shows how mating is affected by genotypes, together with the fitness associated with each mating cluster, expressed as deviations from a baseline of 1. To minimize the number of parameters to be tracked, table 1 specifies the combined fitness of all females in each mating cluster, rather than fitness terms for individual males and females. The parameter s $(0<s<1)$ quantifies the fitness benefit to clusters associated with the help of one male. Monogamous females receive help from a single male, giving a fitness of $(1+s)$. Polygynous females share a male with another female, giving an average fitness of $(1+s/2)$, which is doubled as there are two females in polygynous clusters, giving $2(1+s/2)$. Polyandrous B_p females receive help from two males, giving $(1+2s)$. Polygynandrous B_p females receive help from two males, which is shared with another female, giving an average of $(1+s)$, doubled owing to the two females, giving $2(1+s)$. Polyandrous and polygynandrous B_s females are similar but feature two additional parameters, a and r. The parameter a $(0<a<1)$ represents 'paternity confusion' and determines how cooperative the polyandry is in B_s clusters. Hence, rather than both males helping fully to give $2s$ units of help, the amount of help received varies with a. The parameter r $(0<r<1)$ represents the fitness cost to polyandrous and polygynandrous B_s clusters of infanticide and/or injury from male aggression, specifically motivated by emotional states such as jealousy related to sharing females. A significant effect of jealousy-based aggression has been observed in both B_s human societies and non-human species engaged in polyandrous and polygynandrous behaviours (Daly & Wilson 1988; Davies 1992). It is assumed that this fitness cost does not apply to B_p males who believe that paternity is shared and have less cause for jealousy-based aggression (Beckerman & Valentine 2002). This parameterization is broadly consistent with observed patterns of help and its associated fitness benefits in animal and human societies (Davies 1992; Hill & Hurtado 1996; Beckerman *et al.* 1998; Beckerman & Valentine 2002).

Mating is random apart from the restrictions imposed by the mating rules (e.g. two m individuals cannot be monogamous) and the operation of cultural biases b_1 and b_2. (Actual human mating is unlikely to be random; assortative mating is considered in model 2.) We assume that B_s beliefs are more compatible with predispositions towards monogamy than polygamy, so offspring of $MB_p \times MB_s$ matings are biased towards increased adoption of B_s with probability b_1 $(0<b_1<0.25)$. Similarly, offspring of $mB_p \times mB_s$ matings are predisposed towards B_p with probability b_2 $(0<b_2<0.25)$. No bias operates for $M \times m$ matings or where both parents hold the same beliefs. The biases b_1 and b_2 and standard haploid rules of inheritance were used to generate a system of phenogenotype recursions, which were iterated for 500 000 generations or until equilibrium was reached from each of 121 systematically varied starting frequencies of M/m and B_s/B_p (see methods in electronic supplementary material).

(b) *Results and discussion*

Analyses of model 1 found that, for all biologically realistic, non-zero parameter values (s, r, b_1,$b_2 > 0$), populations converge on one of two stable equilibria, one in which B_s and M are fixed, and the other in which B_p and m are fixed (figure 1). These two regions of attraction are isolated by a linear separatrix, the position of which is a complex function of the fitness terms and the sex ratio (SR), which affect the frequencies of the mating clusters. Selection for M predominates above the separatrix because clusters comprising fewer individuals are more likely to occur than larger clusters. Hence, monogamy (two individuals) is more likely to occur than polygyny or polyandry (three individuals) and polygynandry (four individuals). M is selected owing to its association with monogamy, and B_s because the cultural bias b_1 promotes B_s in the offspring of $M \times M$ matings. Below the separatrix, selection for m occurs from starting populations with a large majority of m because the fitness advantage of polygynandrous over monogamous clusters (table 1) outweighs the aforementioned advantage to monogamy. Selection for B_p occurs here because r imposes a fitness cost on polygamous B_s clusters, further enhanced by the cultural bias b_2.

These two factors—increased probability of smaller clusters (selecting for M) and polygynandrous matings having double the fitness of monogamous matings (selecting for m)—outweighed any effect of varying the parameter s, which did not affect the final equilibria, and had little influence on the model dynamics. The parameter a also had no effect, as populations rapidly became either monogamous or polygynandrous, and a only affects polyandrous matings. The SR, when strongly skewed (where $0.25 > \mathrm{SR} > 0.75$), caused selection for M and removed the separatrix. Any deviation less than 0.25 from an equal SR had no observable effect.

The two stable equilibria observed in figure 1 are reminiscent of the relatively polygamous partible paternity and the relatively monogamous singular paternity societies documented in lowland South America (Beckerman & Valentine 2002), although no evidence yet exists for genetic differences in mating behaviour in these societies. Although standard gene-culture coevolution models usually incorporate genetic inheritance, note that model 1 is also consistent with an alternate non-genetic scenario in which M and m are vertically transmitted cultural beliefs regarding mating behaviour rather than vertically inherited alleles, with identical results in both cases. However, before drawing further conclusions, we first highlight two potential concerns regarding the population-genetic methods of model 1: the assumption of random mating, which may have disproportionately favoured monogamy; and the lack of demographic constraints, with individuals choosing from an infinite pool of mates. These are addressed in model 2.

3. AGENT-BASED MODEL (MODEL 2)

(a) *Methods*

Model 2 used an agent-based modelling technique (Epstein & Axtell 1996; Kohler & Gumerman 2000). A finite population of agents select mates according to two mating rules: (i) M agents accept only one mate, while m agents accept up to two mates and (ii) agents prefer to mate with M agents, as they provide exclusive reproductive access or exclusive provisioning, whereas m agents might be shared with another mate (although m mates are accepted if no M agents are left in the population). Such rules were impractical to implement in the population-genetic model. Mating proceeds until no unmated agents of at least one sex are left in the population, at which point reproduction begins. Here, each mated female is randomly selected and reproduces with a probability determined by her belief and number of mates (table 1). These probabilities resemble the fitnesses of model 1 except that the baseline is 0.5 (as they are probabilities) and the parameters for polygyny and polygynandry are not doubled, as they concern individual females rather than entire mating clusters. Note that with an s of around 0.1 or 0.2, these probabilities roughly correspond to survivorship probabilities observed in the Barí (Beckerman *et al.* 1998) of 0.8 for children with two fathers (polyandry: $0.5+2s$) and 0.65 for children with one father (monogamy: $0.5+s$), and similar probabilities in the Aché (Hill & Hurtado 1996) of 0.85 for children with two fathers and 0.7 for children with one father.

If, depending on this probability, the female reproduces, her offspring inherits the mating behaviour of its parents according to standard haploid genetic inheritance (or vertical cultural transmission if mating behaviour is assumed to be cultural) and inherits paternity beliefs from the parental generation according to oblique/horizontal cultural transmission (as in model 1, vertical transmission of paternity beliefs gave qualitatively identical results). Offspring sex is determined probabilistically according to the SR (the probability that the offspring is male; $1-\mathrm{SR}$ for females), which was fixed. The cultural biases (b_1 and b_2) work as before to promote B_s in the offspring of $M \times M$ matings and B_p in the offspring of $m \times m$ matings. The parameter c ($0 < c < 1$) represents the control over mating afforded to each sex. Where $c = 1$ only females select mates; where $c = 0$ only males select mates; and where $c = 0.5$ agents chosen at random select mates. Control over mating has been informally noted to correlate with paternity belief and mating system; monogamous, singular paternity societies tend to exhibit male control over mating, and polyandrous, partible paternity societies tend to exhibit female control over mating (Beckerman & Valentine 2002). Once mating is complete, females reproduce according to the probabilities specified in table 1, resulting in a new population. This mating–reproduction cycle was repeated for 5000 generations. We also implemented assortative mating and conformist cultural transmission, although these had no qualitative effect on the results (see methods in electronic supplementary material).

(b) *Results and discussion*

Initially variable populations again typically converge on one of two stable equilibria with either MB_s or mB_p fixed. The parameters s, a, r, b_1 and b_2 had the same effects as in model 1. Figure 2 shows the relationship between sex ratio (SR) and control over mating (c), two parameters which had a large impact on the dynamics of model 2. Consider first the central cell, under an equal SR and equal control over mating. Whereas in model 1, the assumption of random mating generated, under these conditions, selection for M, the more realistic mating rules of model

2 generate selection for m. In other words, smaller clusters are no longer inherently more likely to occur and m agents potentially form more clusters than M agents (table 1; five of the eleven clusters feature a majority of m, only three feature a majority of M). With predominantly m matings, r and b_2 generate selection for B_p.

Considering the other cells of figure 2, where SR is female biased and there is equal or male control over mating, or where SR is male biased and there is equal or female control over mating, the majority of populations converge on stable equilibria where M is fixed. Selection for monogamy occurs because, where the SR is skewed, the majority sex can provide all (or most) of the minority sex with preferred M mates, promoting M. With an equal SR, or where the majority sex controls the mating, M mates are rapidly depleted and thereafter m mates are chosen, generating selection for m.

In lowland South America, partible paternity societies are frequently polygamous and feature female control over mating, while singular paternity societies are often monogamous and feature male control (Beckerman & Valentine 2002). High male mortality from warfare is another feature of South American societies (Beckerman & Lizarralde 1995), consistent with a female-biased SR. These ethnographic observations correspond well with the results of model 2 under a female-biased SR (e.g. SR$=$0.3, left column of figure 2), where male control (figure 2, bottom left) favours B_s, M and monogamy, and female control (figure 2, top left) favours B_p, m and polygamy. This analysis therefore supports an evolutionary scenario in which ancestral populations of lowland South American societies exhibited female-biased SRs, causing divergence into polygamous, female-oriented, partible paternity societies and monogamous, male-oriented, singular paternity societies. A highly skewed SR is not unreasonable if founder populations are small (the founder population of North America has been estimated at just 70 individuals; Hey 2005). Notably, another region that exhibits partible paternity is New Guinea (Counts & Counts 1983), the island geography of which may have favoured similarly small founder populations with skewed SRs. Conceivably, the rarity of males in such societies may also have favoured the *origination* of partible paternity beliefs; if males are rare they will be in high demand as resource-providing fathers, making beliefs in multiple fathers more attractive and likely to emerge. This scenario could be tested by seeking genetic evidence from existing lowland South American populations for a past population bottleneck and female-biased SR.

4. GENERAL DISCUSSION

Two different modelling techniques were used to explore the coevolution of culturally transmitted paternity beliefs and the genetic bases of human mating behaviour. Model 1, using population-based 'gene–culture coevolution' methods, found that populations typically converged on one of two stable equilibria, one in which all individuals were genetically predisposed towards monogamy and held singular paternity beliefs, and the other in which all individuals were genetically predisposed towards polygamy and held partible paternity beliefs. Model 2, which employed agent-based methods, broadly replicated the findings of model 1, although only under certain conditions with respect to the SR and which sex controls mating. Correspondences between ethnographic observations and both the results of model 1, and the results of model 2 under a female-biased SR, suggest the following evolutionary scenario: ancestral South American societies were subject to divergent selection, facilitated by a female-biased SR due to high male mortality, leading to the present-day distributions of mating systems and cultural beliefs in lowland South America (Beckerman & Valentine 2002), where some societies are relatively monogamous, hold singular paternity beliefs and feature male control over mating, and other societies are relatively polygamous, hold partible paternity beliefs and feature female control over mating.

The analyses raise the possibility that, in addition to conventional explanations for mixed mating strategies in humans, such as differential male resources or patrilineal inheritance of wealth (Hrdy 1981, 1999), there may be genetic differences between societies, expressed in variant predispositions to monogamy, jealousy and aggression, underpinning between-society variation in sex roles (although a purely cultural model in which mating behaviour is transmitted culturally is also plausible). In these respects, the findings support diverse and variable conceptions of 'human nature' (Ehrlich 2000; Ehrlich & Feldman 2003), and challenge the common assumption within evolutionary psychology that all men desire multiple mates.

In both models, the partible paternity (mB_p) equilibrium emerges in part due to the cost of infanticide (r) imposed on polygamous B_s individuals. Given that previous models (van Schaik & Dunbar 2000) and evidence (Palombit 1999) suggest that infanticide may have favoured the evolution of monogamy in some primate species, model 2 suggests that in some human populations partible paternity beliefs may have reversed selection back to favour polygamy by reducing infanticide.

These models are, of course, simplified versions of reality and there are many potentially important factors that have not been considered due to limitations imposed by the already complex nature of these models. Such factors include male resource holding potential, sex-linked genes, inbreeding and a heritable SR. Nonetheless, given the complexity of the present models, it is encouraging that the results were robust with regard to several factors, including genetics (haploid or diploid) and mode of cultural transmission (vertical, oblique or conformist), and tractable in the face of manipulation of other parameters, including the SR and control over mating.

More generally, the analyses presented here suggest that cultural processes have the potential to strongly affect the course of human evolution, consistent with previous gene–culture coevolutionary analyses (Laland *et al.* 1995; Henrich & McElreath 2003; Richerson & Boyd 2005; Mesoudi *et al.* 2006) and similar arguments against purely genetic conceptions of human behaviour and evolution (Ehrlich 2000; Ehrlich & Feldman 2003). The analyses are also consistent with a flexible characterization of human mating behaviour (Borgerhoff Mulder 1990, 1991; Hrdy 1981, 1999), in which humans collectively are not well-described as 'naturally' monogamous or 'naturally' polygamous since, if anything, they are 'naturally' variable in their mating behaviour.

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