Evolution of monogamous marriage

by maximization of inclusive fitness

(supporting information)

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Theoretical framework

Male and female strategies

We consider a population with n males and n females, in which individuals marry either monogamously (M) or polygamously (P). We use $w \geq 1$ to denote the number of wives for males and $h \geq 1$ the number of husbands for females; males and females marry with probabilities Ω and Φ, respectively, which are derived below.

Each female produces one male and one female offspring. Unmarried females transfer their resources, denoted δ_{f}, to their own offspring, whereas unmarried males transfer their resources, denoted δ_{m}, to their sister's offspring. The resources of married females are controlled by their husbands, i.e. a male controls his own δ_{m} and a share $1/h$ of the δ_{f} of each of his w wives. Males transfer resources "vertically" to their wife's (or wives') offspring (V), with probability m_{V}, or "diagonally" to their sister's offspring (D), with probability m_{D}; each male transfers either vertically or diagonally, i.e. m_{V} and m_{D} take values 0 or 1, and $m_{\mathrm{V}} = 1 - m_{\mathrm{D}}$. To simplify the notation, we assume that individuals in the parent generation transfer resources to sibling pairs rather than to individuals in the offspring generation. Each sibling pair inherits resources

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δ, with $\delta = \delta_m + \delta_f = 1$ for the offspring of a monogamous couple in a monogamous population in which all males transfer vertically. The fitness of each sibling pair is given by δ^z, with $z > 0$. $\delta_{\mathbb{B}'}$ and $\delta_{\mathbb{F}'}$ denote the resources inherited by sibling pairs $\mathbb{B}'$ and $\mathbb{F}'$, respectively (Figure 1 in the text).

The probability p that a male is the biological father of his wife's offspring depends on the behaviour of females. Females give their husbands either "high" paternity p_H (H) or "low" paternity p_L (L), with $0 < p_L < p_H \leq 1$. Females obtain an additional generic advantage α from mating with other males beyond their husbands; for example, α may represent genetic benefits which lead to increased offspring survival or resource benefits such as nuptial gifts (Reynolds 1996; Kokko 1999). We assume that $\alpha_L > \alpha_H$, and $\alpha_H = 0$ for $p_H = 1$. For simplicity, we further assume that $0 < \alpha < 1/2$, such that its fitness value is small relative to the value of the resources transferred to the offspring generation, and does not affect the amount of resources males transfer to their wives' or sister's offspring.

Both males and females know their spouses' marriage strategy. The transfer strategy of males may be conditional upon the marriage and paternity strategies of females. A "suspicious" male (S) transfers vertically if his wives are monogamous and provide paternity p_H, diagonally otherwise. An "ingenuous" male (I) transfers diagonally if his wives are monogamous and provide paternity p_H, vertically otherwise. These strategies require that males have cues about paternity (e.g. Kokko 1999): in humans, these include direct phenotypic cues or indirect behavioural cues (e.g. the conformity of females to cultural norms regulating their sexual behaviour). The paternity strategy of females may be conditional only upon the marriage strategy of males. An "astute" female (A) provides paternity p_H if her husbands marry monogamously, p_L otherwise. A "naive" female (N) provides paternity p_L if her husbands marry monogamously, p_H otherwise.

Table S1 presents a summary of the strategies included in the game. We use XY to denote the marriage strategy X and transfer strategy Y for a male, XZ to denote the marriage strategy X and paternity strategy Z for a female, and (XY, XZ) to denote a pair of male and female strategies. For example, (MV, MH) represents the interaction of a monogamous male who transfers vertically, MV, with a monogamous female who always provides "high" paternity, MH. Table S2 presents a summary of all the symbols used in the model.

Table S1: Summary of the possible strategies

(a) Male strategies

Strategy			
Attribute	Symbol	Behaviour	Description
Marriage (X)	M	Monogamous	Male marries one female only ($w = 1$)
	P	Polygynous	Male marries more than one female ($w > 1$)
Transfer (Y)	V	Vertical	Married male transfers resources to wives' offspring
	D	Diagonal	Married male transfers resources to sister's offspring
	S	Suspicious	Married male is V if wife is M and provides p_H, D otherwise
	I	Ingenuous	Married male is D if wife is M and provides p_H, V otherwise

(b) Female strategies

Strategy			
Attribute	Symbol	Behaviour	Description
Marriage (X)	M	Monogamous	Female marries one male only ($h = 1$)
	P	Polyandrous	Female marries more than one male ($h > 1$)
Paternity (Z)	H	High	Married female provides "high" paternity ($0 < p_H \leq 1$, α_H)
	L	Low	Married female provides "low" paternity ($0 < p_L < 1$, α_L)
	A	Astute	Married female provides p_H if husband is M, p_L otherwise
	N	Naive	Married female provides p_L if husband is M, p_H otherwise

Table S2: Symbols used in the model

Notation	Description
X: M, P	marriage strategy (of males and females)
Y: V, D, S, I	transfer strategy (of males)
Z: H, L, A, N	paternity strategy (of females)
n	number of individuals of each sex in the population
Ω, Φ	marriage probability for a male and for a female
m_{M}, m_{P}	frequency of monogamous and of polygynous males in the population
f_{M}, f_{P}	frequency of monogamous and of polyandrous females in the population
w, w_{P}	number of wives for a male (generic and for a polygynous male)
h	number of husbands for a female (generic)
δ, $\delta_{\mathbb{B}'}$, $\delta_{\mathbb{F}'}$	resources inherited by a sibling pair in the offspring generation (generic, by sibling pair $\mathbb{B}'$, and by sibling pair $\mathbb{F}'$)
δ_{m}, δ_{f}	relative male and female contribution to δ
z	describes the relationship between inherited resources and fitness, given by δ^z
m_{V}, m_{D}	probability that a male transfers vertically and diagonally
p, p_{H}, p_{L}	probability that a female's husband is the biological father of her offspring (generic, for a female who provides "high" paternity, and for a female who provides "low" paternity)
α, α_{H}, α_{L}	advantage to a female of mating with other males beyond her husbands (generic, for a female who provides "high" paternity, and for a female who provides "low" paternity)
$\mathbb{M}$, $\mathbb{F}$	focal male and female (or sibling to the focal individual)
$\mathbb{A}$	$\mathbb{F}$'s husband
$\mathbb{B}$	$\mathbb{M}$'s wife
$\mathbb{C}$	$\mathbb{B}$'s brother
$\mathbb{B}'$	$\mathbb{B}$'s offspring
$\mathbb{F}'$	$\mathbb{F}$'s offspring
$E_{\mathbb{M}}$, $E_{\mathbb{F}}$	inclusive fitness for a focal male and for a focal female
β_i, ϕ_i	resources transferred to $\mathbb{B}'$ and to $\mathbb{F}'$
r_{xy}	coefficient of relatedness of focal individual x ($\mathbb{M}$ or $\mathbb{F}$) to heir y ($\mathbb{B}'$ or $\mathbb{F}'$)
$^\circ$	denotes any attribute that may depend on the relevant strategy for the focal individual

Marriage probabilities

For simplicity, we assume that polygamous individuals either marry w or h spouses, or do not marry at all. Denoting m_M and m_P the frequencies of monogamous and polygynous males in the population, and f_M and f_P the frequencies of monogamous and polyandrous females, a focal monogamous male marries with probability

$$\Omega_M = \begin{cases} f_M\left[m_M \cdot 1 + m_P\dfrac{n}{(n-1)w+1}\right] + f_P\left[m_M \cdot 1 + m_P\dfrac{nh}{(n-1)w+1}\right] & \text{if} \quad \dfrac{nh}{(n-1)w+1} \leq 1 \\[4ex] f_M\left[m_M \cdot 1 + m_P\dfrac{n}{(n-1)w+1}\right] + f_P[m_M \cdot 1 + m_P \cdot 1] & \text{if} \quad \dfrac{nh}{(n-1)w+1} \geq 1 \end{cases}.$$

This is derived as follows:

- in a population of monogamous females and monogamous males there are n females, each requiring one husband, and n males, each requiring one wife; thus, the focal male marries with probability $\Omega_M = 1$;

- in a population of monogamous females and polygynous males there are n females, each requiring one husband, $n-1$ resident polygynous males, each requiring w wives, and the focal monogamous male, requiring one wife; thus, the focal male marries with probability $\Omega_M = n/[(n-1)w+1]$;

- in a population of polyandrous females and monogamous males there are n females, each requiring h husbands, and n males, each requiring one wife; thus, the focal male marries with probability $\Omega_M = 1$;

- in a population of polyandrous females and polygynous males there are n females, each requiring h husbands, $n-1$ resident polygynous males, each requiring w wives, and the focal monogamous male, requiring one wife; thus, the focal male marries with probability $\Omega_M = nh/[(n-1)w+1]$ if the number of potential wives is smaller than the number of wives required, i.e. if $nh/[(n-1)w+1] \leq 1$, or with probability $\Omega_M = 1$ if the number of potential wives is greater than the number of wives required, i.e. if $nh/[(n-1)w+1] \geq 1$.

By similar reasoning, a focal polygynous male marries with probability

$$
\Omega_{\mathrm{P}} = \begin{cases} f_{\mathrm{M}}\left[m_{\mathrm{M}}\dfrac{n}{(n-1)+w} + m_{\mathrm{P}}\dfrac{1}{w}\right] + f_{\mathrm{P}}\left[m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\dfrac{h}{w}\right] & \text{if} \ \ \dfrac{h}{w} \leq 1 \\[3em] f_{\mathrm{M}}\left[m_{\mathrm{M}}\dfrac{n}{(n-1)+w} + m_{\mathrm{P}}\dfrac{1}{w}\right] + f_{\mathrm{P}}\left[m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\cdot 1\right] & \text{if} \ \ \dfrac{h}{w} \geq 1 \end{cases}.
$$

Assuming that n is large relative to h and w, Ω_{M} and Ω_{P} simplify to

$$
\Omega = \begin{cases} f_{\mathrm{M}}\left(m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\dfrac{1}{w}\right) + f_{\mathrm{P}}\left(m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\dfrac{h}{w}\right) & \text{if} \ \ \dfrac{h}{w} \leq 1 \\[3em] f_{\mathrm{M}}\left(m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\dfrac{1}{w}\right) + f_{\mathrm{P}}\left(m_{\mathrm{M}}\cdot 1 + m_{\mathrm{P}}\cdot 1\right) & \text{if} \ \ \dfrac{h}{w} \geq 1 \end{cases},
$$

which, assuming that $h = w$, simplifies to

$$
\Omega = f_{\mathrm{M}}\left(m_{\mathrm{M}} + \frac{m_{\mathrm{P}}}{w}\right) + f_{\mathrm{P}}.
$$

The probability of marrying for females is derived by analogous reasoning. Assuming that n is large relative to h and w, a focal female marries with probability

$$
\Phi = \begin{cases} m_{\mathrm{M}}\left(f_{\mathrm{M}}\cdot 1 + f_{\mathrm{P}}\dfrac{1}{h}\right) + m_{\mathrm{P}}\left(f_{\mathrm{M}}\cdot 1 + f_{\mathrm{P}}\dfrac{w}{h}\right) & \text{if} \ \ \dfrac{w}{h} \leq 1 \\[3em] m_{\mathrm{M}}\left(f_{\mathrm{M}}\cdot 1 + f_{\mathrm{P}}\dfrac{1}{h}\right) + m_{\mathrm{P}}\left(f_{\mathrm{M}}\cdot 1 + f_{\mathrm{P}}\cdot 1\right) & \text{if} \ \ \dfrac{w}{h} \geq 1 \end{cases},
$$

which, assuming that $h = w$, simplifies to

$$
\Phi = m_{\mathrm{M}}\left(f_{\mathrm{M}} + \frac{f_{\mathrm{P}}}{h}\right) + m_{\mathrm{P}}.
$$

Inclusive fitness payoffs

We use ˚ to indicate any attribute that may depend on the relevant strategy for the focal individual, such that its value may differ from the corresponding value for the resident population. For example, $\mathring{w}$ denotes the number of wives for a focal male $\mathbb{M}$, with $\mathring{w} \neq w$ for a mutant focal male whose marriage strategy differs from the strategy of resident males, and $\mathring{w} = w$ in all other cases. With reference to Figure 1 in the text, the inclusive fitness payoff for a focal male $\mathbb{M}$ can

be written as

$$
\begin{aligned}
E_{\mathbb{M}} = \mathring{w}\Bigg\{ \Bigg[&\underbrace{\Omega\,\mathring{m}_{\mathrm{V}}\left(\delta_{\mathrm{m}} + \mathring{w}\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_1} + \underbrace{\Omega\,\mathring{w}\,m_{\mathrm{V}}(h-1)\left(\frac{\delta_{\mathrm{m}}}{w} + \frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_2} \\
&+ \underbrace{\Omega\,\mathring{w}\,(1-\Omega)\delta_{\mathrm{m}}}_{\beta_3} + \underbrace{\Omega\,\mathring{w}\,\Omega\,m_{\mathrm{D}}\left(\delta_{\mathrm{m}} + w\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_4} \Bigg] \Big/ \mathring{w} \Bigg\}^{z} r_{\mathbb{MB}'} \\
&+ \Bigg[\underbrace{(1-\Omega)\delta_{\mathrm{m}}}_{\phi_1} + \underbrace{\Omega\,\mathring{m}_{\mathrm{D}}\left(\delta_{\mathrm{m}} + \mathring{w}\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\phi_2} + \underbrace{(1-\Phi)\delta_{\mathrm{f}}}_{\phi_3} + \underbrace{\Phi\,h\,m_{\mathrm{V}}\left(\frac{\delta_{\mathrm{m}}}{w} + \frac{\delta_{\mathrm{f}}}{h}\right)}_{\phi_4} \Bigg]^{z} r_{\mathbb{MF}'},
\end{aligned}
$$

where β_i represents resources inherited by the offspring $\mathbb{B}'$ of his $\mathring{w} \geq 1$ wives and ϕ_i represents resources inherited by his sister's offspring $\mathbb{F}'$; the subscript $i = 1, \ldots, 4$ denotes the pathway through which resources are transferred to the heir. $r_{\mathbb{MB}'}$ and $r_{\mathbb{MF}'}$ represent the coefficients of relatedness between $\mathbb{M}$ and, respectively, $\mathbb{B}'$ and $\mathbb{F}'$, as derived below.

β_1, β_2, β_3, and β_4 are only relevant if $\mathbb{M}$ marries, while ϕ_4 is only relevant if $\mathbb{F}$ marries. Specifically:

β_1 represents the resources $\mathbb{M}$ transfers to $\mathbb{B}'$ if his transfer strategy is V; this includes his δ_{m} and a share $1/h$ of the δ_{f} of each $\mathbb{B}$;

β_2 represents the resources transferred to $\mathbb{B}'$ by the other $h-1$ husbands of each $\mathbb{B}$, excluding $\mathbb{M}$, if the transfer strategy of resident males is V; for each husband, this includes a share $1/w$ of his δ_{m} and a share $1/h$ of $\mathbb{B}$'s δ_{f};

β_3 represents the resources each $\mathbb{C}$ transfers to $\mathbb{B}'$ if he does not marry;

β_4 represents the resources each $\mathbb{C}$ transfers to $\mathbb{B}'$ if he marries and his transfer strategy is D; this includes his δ_{m} and a share $1/h$ of the δ_{f} of each of his w wives;

ϕ_1 represents the resources $\mathbb{M}$ transfers to $\mathbb{F}'$ if he does not marry;

ϕ_2 represents the resources $\mathbb{M}$ transfers to $\mathbb{F}'$ if he marries and his transfer strategy is D; this includes his δ_{m} and a share $1/h$ of the δ_{f} of each $\mathbb{B}$;

ϕ_3 represents the resources $\mathbb{F}$ transfers to $\mathbb{F}'$ if she does not marry;

ϕ_4 represents the resources each $\mathbb{A}$ transfers to $\mathbb{F}'$ if the transfer strategy of resident males is V; this includes a share $1/w$ of his δ_{m} and a share $1/h$ of $\mathbb{F}$'s δ_{f}.

The inclusive fitness payoff for a focal female $\mathbb{F}$ is derived by analogous reasoning, and can be written as

$$
\begin{aligned}
E_{\mathbb{F}} = {} & w\Bigg\{\Bigg[\underbrace{\Omega\, m_{\mathrm{V}}\left(\delta_{\mathrm{m}} + w\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_1} + \underbrace{\Omega\, w\, m_{\mathrm{V}}(h-1)\left(\frac{\delta_{\mathrm{m}}}{w} + \frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_2} \\
& + \underbrace{\Omega\, w\,(1-\Omega)\delta_{\mathrm{m}}}_{\beta_3} + \underbrace{\Omega\, w\, \Omega\, m_{\mathrm{D}}\left(\delta_{\mathrm{m}} + w\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\beta_4}\Bigg]\Big/w\Bigg\}^z r_{\mathbb{F}\mathbb{B}'} \\
& + \Bigg[\underbrace{(1-\Omega)\delta_{\mathrm{m}}}_{\phi_1} + \underbrace{\Omega\, m_{\mathrm{D}}\left(\delta_{\mathrm{m}} + w\,\frac{\delta_{\mathrm{f}}}{h}\right)}_{\phi_2} + \underbrace{(1-\Phi)\delta_{\mathrm{f}}}_{\phi_3} + \underbrace{\Phi\,\mathring{h}\,\mathring{m}_{\mathrm{V}}\left(\frac{\delta_{\mathrm{m}}}{w} + \frac{\delta_{\mathrm{f}}}{\mathring{h}}\right)}_{\phi_4}\Bigg]^z r_{\mathbb{F}\mathbb{F}'} + \mathring{\alpha},
\end{aligned}
$$

where β_i represents resources inherited by the offspring $\mathbb{B}'$ of her brother's $w \geq 1$ wives and ϕ_i represents resources inherited by her offspring $\mathbb{F}'$; as in the previous case, the subscript $i = 1, \ldots, 4$ denotes the pathway through which resources are transferred to the heir. $r_{\mathbb{F}\mathbb{B}'}$ and $r_{\mathbb{F}\mathbb{F}'}$ represent the coefficients of relatedness between $\mathbb{F}$ and, respectively, $\mathbb{B}'$ and $\mathbb{F}'$, as derived below. $\mathring{\alpha} \neq \alpha$ for a mutant focal female whose paternity strategy differs from the strategy of resident females, and $\mathring{\alpha} = \alpha$ in all other cases.

As in the previous case, β_1, β_2, β_3, and β_4 are only relevant if $\mathbb{M}$ marries, while ϕ_4 is only relevant if $\mathbb{F}$ marries. In this case, $\mathbb{F}$'s husbands transfer vertically with probability $\mathring{m}_{\mathrm{V}}$ because the transfer strategy of males may depend on the marriage and paternity strategies of females (males XS and XI, Table S1). If this is the case, $\mathring{m}_{\mathrm{V}} \neq m_{\mathrm{V}}$ for a mutant focal female whose marriage and/or paternity strategy differs from the strategy of resident females. $\mathring{m}_{\mathrm{V}} = m_{\mathrm{V}}$ in all other cases.

Coefficients of relatedness

For simplicity, we assume that the biological fathers of the offspring of a promiscuous female are not related, and that the h husbands of a polyandrous female are not related and have equal probability of fathering her offspring. Under these assumptions, and assuming that p in the parent generation is equal to p in the previous generation, a female is related to her offspring by $1/2$, a male to his wife's offspring by an average of $p/2h$, and siblings by an average of $(1 + p^2/h)/4$. Thus, $r_{\mathbb{F}\mathbb{F}'} = 1/2$, $r_{\mathbb{F}\mathbb{B}'} = (p/2h)[(1 + p^2/h)/4]$, and $r_{\mathbb{M}\mathbb{F}'} = (1/2)[(1 + p^2/h)/4]$.

$r_{\mathbb{M}\mathbb{B}'}$ must accommodate the fact that the paternity strategy of females may depend on the marriage strategy of males (females XA and XN, Table S1). If this is the case, $\mathring{p} \neq p$ for a

mutant focal male whose marriage strategy differs from the strategy of resident males. $\mathring{p} = p$ in all other cases. Because a female's h husbands have equal probability of fathering her offspring, the coefficient of relatedness between a focal male $\mathbb{M}$ and his wife's offspring $\mathbb{B}'$ is affected both by the paternity strategy his wife plays against him, and by the paternity strategy she plays against her other $h - 1$ husbands. This can be written as

$$r_{\mathbb{M}\mathbb{B}'} = \frac{(1/h)\mathring{p} + [(h-1)/h]p}{2h} = \frac{\mathring{p} + (h-1)p}{2h^2},$$

which reduces to $p/2h$ for $\mathring{p} = p$.

Stability of social monogamy

The possible combinations of male and female strategies differ in inclusive fitness payoffs; given these payoffs, we can derive evolutionarily stable equilibria consisting of pairs of male and female strategies that cannot be invaded by rare mutants playing alternative strategies (Maynard Smith 1982). The software Mathematica (Wolfram Research, Inc. 2007) was used to perform the numerical analysis and to produce the stability plots.

Only two pairs of pure stable strategies result in social monogamy: (MS, MH) and (MS, MA). Because the model does not yield simple analytical solutions, we describe in detail the analytical results for the simplest case, $p_H = 1$; these are plotted in Figure 2 in the text. Figure S1 shows graphical results obtained with numerical methods for $p_H = 0.5$.
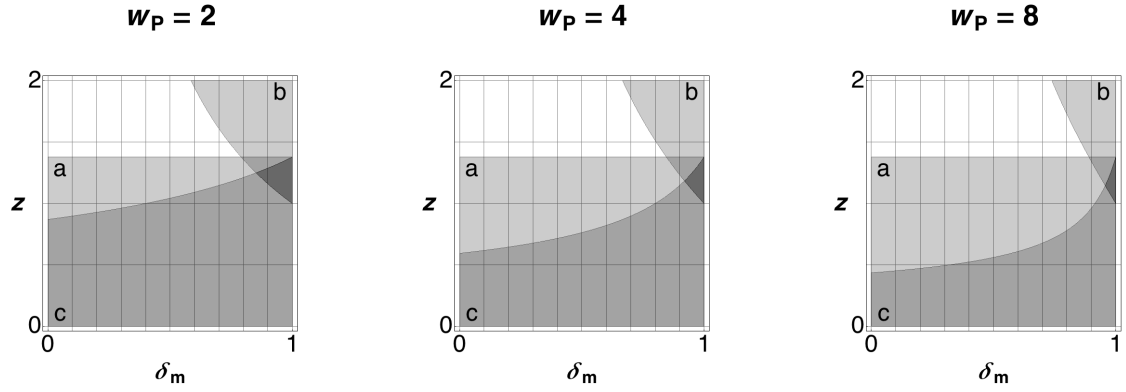
Stability of (MS, MH)

In the first scenario, (MS, MH), resident males are monogamous and suspicious, that is, they transfer vertically if females are monogamous and provide "high" paternity, diagonally otherwise. Resident females are monogamous and always provide "high" paternity. This combination of male and female strategies results in monogamous marriage, vertical transfer, and "high" paternity (Table S1).

(MS, MH) is a weak equilibrium, because resident males MS are neutral with males MV, and resident females MH are neutral with females MA. For $p_H = 1$, males MS are stable for

$$z < \frac{\log 3}{\log 2} \quad \text{against males MD and MI,} \tag{1a}$$

$$w_P \left(\frac{\delta_m}{w_P} + \delta_f \right)^z < 1 \quad \text{against males PV and PS, and} \tag{1b}$$
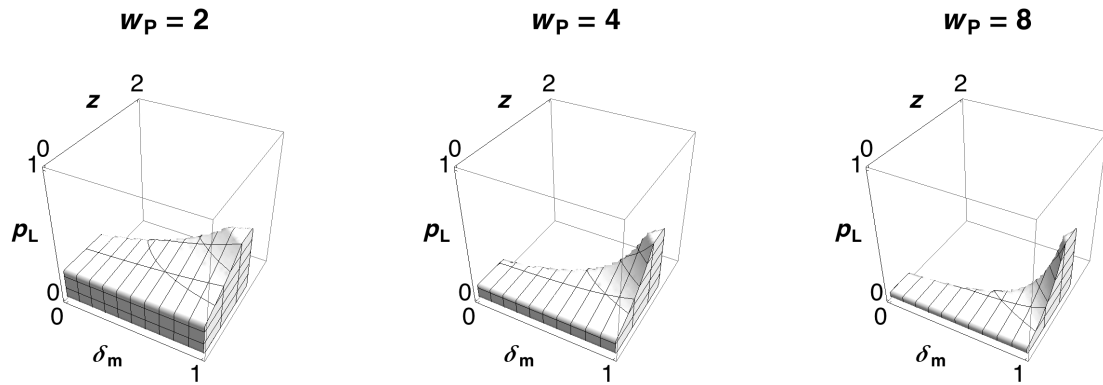
(a)

(b)

Figure S1: Stability of "suspicious" monogamous males against mutant males with $w_P = 2$, $w_P = 4$, or $w_P = 8$, for $p_H = 0.5$; w_P denotes the number of wives for polygynous males, and p_H the paternity level of males with females who always provide "high" paternity and of monogamous males with "astute" females. δ_m represents the relative male contribution to the resources transferred to the offspring generation; z describes the relationship between resources and individual fitness; p_L represents the paternity level of polygynous males with "astute" females. See text for details. (a), with monogamous females who always provide "high" paternity. **a** is the condition for stability against monogamous males who transfer diagonally, **b** against polygynous males who transfer vertically, **c** against polygynous males who transfer diagonally. Social monogamy is stable in the darker area, where all conditions are met. (b), with "astute" monogamous females. Monogamy is stable throughout the volume shown.

$$(2\delta_{\mathrm{m}} + \delta_{\mathrm{f}} + w_{\mathrm{P}}\delta_{\mathrm{f}})^z < 3 \quad \text{against males PD and PI,} \tag{1c}$$

where $w_{\mathrm{P}} > 1$ denotes the number of wives for a polygynous male.

These conditions are derived by comparing the inclusive fitness payoff for a resident male to the payoff for mutant males. The payoff for a resident focal male $\mathbb{M}$ is given by the resources $\beta_1 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ he transfers to $\mathbb{B}'$, and by the resources $\phi_4 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ his sister's husband $\mathbb{A}$ transfers to $\mathbb{F}'$ (Figure 1 in the text). Thus, $\delta_{\mathbb{B}'} = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ and $\delta_{\mathbb{F}'} = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$, with inclusive fitness value for $\mathbb{M}$ $(\delta_{\mathrm{m}} + \delta_{\mathrm{f}})^z(1/2)$ and $(\delta_{\mathrm{m}} + \delta_{\mathrm{f}})^z(1/4)$, respectively. Because $\delta_{\mathbb{B}'} = 1$ and $\delta_{\mathbb{F}'} = 1$, the inclusive fitness value of these resources is not affected by z (i.e. $\delta_{\mathbb{B}'}^z = 1$ and $\delta_{\mathbb{F}'}^z = 1$).

The payoff for a mutant focal male $\mathbb{M}$ who is monogamous and transfers diagonally (males MD and MI in this population, Table S1) is given by the resources $\phi_1 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ he transfers to $\mathbb{F}'$, and by the resources $\phi_4 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ male $\mathbb{A}$ transfers to $\mathbb{F}'$ (Figure 1 in the text). Thus, $\delta_{\mathbb{B}'} = 0$, while $\delta_{\mathbb{F}'} = 2\delta_{\mathrm{m}} + 2\delta_{\mathrm{f}} = 2$, with inclusive fitness value for $\mathbb{M}$ $(2\delta_{\mathrm{m}} + 2\delta_{\mathrm{f}})^z(1/4)$. Note that $\delta_{\mathbb{F}'}^z > 2$ for $z > 1$, that is, values of $z > 1$ result in a greater than twofold increase in fitness for $\mathbb{F}'$. Condition (1a) specifies that vertical transfer can be advantageous where the benefit to a mutant male of providing extra resources to his sister's offspring is offset by their lower relatedness relative to wife's offspring (i.e. for $z < \log 3 / \log 2$).

The payoff for a mutant focal male $\mathbb{M}$ who is polygynous and transfers vertically (males PV and PS in this population, Table S1) is given by the resources $\beta_1 = (\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}$ he transfers to each $\mathbb{B}'$, and by the resources $\phi_4 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ male $\mathbb{A}$ transfers to $\mathbb{F}'$ (Figure 1 in the text). Thus, $\delta_{\mathbb{B}'} = (\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}$ and $\delta_{\mathbb{F}'} = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$, with inclusive fitness value for $\mathbb{M}$ $w_{\mathrm{P}}[(\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}]^z(1/2)$ and $(\delta_{\mathrm{m}} + \delta_{\mathrm{f}})^z(1/4)$, respectively. Note that $\delta_{\mathbb{B}'} < 1$ if $\mathbb{M}$ contributes at least part of the resources transferred to the next generation (i.e. if $\delta_{\mathrm{m}} > 0$), thus $\delta_{\mathbb{B}'}^z < 1$ for $z > 1$, that is, values of $z > 1$ result in a reduction of the fitness value of the resources. Condition (1b) specifies that monogamous marriage can be advantageous if the fitness value of resources is depleted through division (i.e. for $\delta_{\mathrm{m}} > 0$ if $z > 1$), and becomes increasingly advantageous as each female provides a relatively smaller share of the resources inherited by her offspring (i.e. as δ_{m} increases and/or w_{P} decreases).

Finally, the payoff for a mutant focal male $\mathbb{M}$ who is polygynous and transfers diagonally (males PD and PI in this population, Table S1) is given by the resources $\phi_1 = \delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}} \geq 1$ he transfers to $\mathbb{F}'$, and by the resources $\phi_4 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ male $\mathbb{A}$ transfers to $\mathbb{F}'$ (Figure 1 in

the text). Thus, $\delta_{\mathbb{B}'} = 0$, while $\delta_{\mathbb{F}'} = 2\delta_{\mathrm{m}} + \delta_{\mathrm{f}}(w_{\mathrm{P}} + 1) \geq 2$, with inclusive fitness value for $\mathbb{M}$ $[2\delta_{\mathrm{m}} + \delta_{\mathrm{f}}(w_{\mathrm{P}} + 1)]^z(1/4)$. Note that, as for (1a), $\delta_{\mathbb{F}'}^z > 2$ for $z > 1$, that is, values of $z > 1$ result in a greater than twofold increase in fitness for $\mathbb{F}'$. Condition (1c) specifies that vertical transfer can be advantageous where the benefit to a mutant male of providing extra resources to his sister's offspring is offset by their lower relatedness relative to wife's offspring; additionally, it becomes increasingly advantageous as each female provides a relatively smaller share of the resources inherited by her offspring (i.e. as δ_{m} increases and/or w_{P} decreases). Condition (1c) reduces to (1a) for $\delta_{\mathrm{m}} = 1$.

For $p_{\mathrm{H}} = 1$, the payoff for females MH includes the fitness contribution by their offspring and the fitness contribution by their brother's wife's offspring. Because resident males are suspicious, this is always greater than the payoff for mutant females who are polyandrous and/or provide "low" paternity (females XL, XN, PH, and PA in this population, Table S1), which is limited to the fitness contribution by their brother's wife's offspring (and possibly α_{L}).

Thus, (MS, MH) is stable for values of δ_{m} and z for which conditions (1a) to (1c) are satisfied simultaneously (Figure 2a in the text). The upper limit to the range of values of z is given by condition (1c), marked **c** in Figure 2a, and the lower limit by condition (1b), marked **b** in Figure 2a; condition (1a), marked **a** in Figure 2a, is always satisfied where (1c) is satisfied.

Stability of (MS, MA)

In the second scenario, (MS, MA), resident males are monogamous and suspicious, that is, they transfer vertically if females are monogamous and provide "high" paternity, diagonally otherwise. Resident females are monogamous and astute, that is, they provide "high" paternity if males are monogamous, "low" paternity otherwise. As for (MS, MH), this combination of male and female strategies results in monogamous marriage, vertical transfer, and "high" paternity (Table S1).

(MS, MA) is a weak equilibrium, because resident males MS are neutral with males MV, and resident females MA are neutral with females MH. For $p_{\mathrm{H}} = 1$, males MS are stable for

$$z < \frac{\log 3}{\log 2} \quad \text{against males MD and MI,} \tag{2a}$$

$$w_{\mathrm{P}}\left(\frac{\delta_{\mathrm{m}}}{w_{\mathrm{P}}} + \delta_{\mathrm{f}}\right)^z p_{\mathrm{L}} < 1 \quad \text{against males PV and PI, and} \tag{2b}$$

$$(2\delta_{\mathrm{m}} + \delta_{\mathrm{f}} + w_{\mathrm{P}}\delta_{\mathrm{f}})^z < 3 \quad \text{against males PD and PS,} \tag{2c}$$

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As in the previous case, these conditions are derived by comparing the inclusive fitness payoff for a resident male to the payoff for mutant males. The inclusive fitness payoff for a resident focal male $\mathbb{M}$ is identical to the payoff derived for the previous scenario.

Condition (2a) is the condition for the stability of resident males MS against invasion by mutant males who are monogamous and transfer diagonally (males MD and MI in this population, Table S1), and is identical to (1a).

As for (1b), the payoff for a mutant focal male $\mathbb{M}$ who is polygynous and transfers vertically (males PV and PI in this population, Table S1) is given by the resources $\beta_1 = (\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}$ he transfers to each $\mathbb{B}'$, and by the resources $\phi_4 = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$ male $\mathbb{A}$ transfers to $\mathbb{F}'$ (Figure 1 in the text). Thus, $\delta_{\mathbb{B}'} = (\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}$ and $\delta_{\mathbb{F}'} = \delta_{\mathrm{m}} + \delta_{\mathrm{f}} = 1$; because in this case resident females give polygynous males paternity p_{L}, these resources have inclusive fitness value for $\mathbb{M}$ $w_{\mathrm{P}}[(\delta_{\mathrm{m}} + w_{\mathrm{P}}\delta_{\mathrm{f}})/w_{\mathrm{P}}]^z(p_{\mathrm{L}}/2)$ and $(\delta_{\mathrm{m}} + \delta_{\mathrm{f}})^z(1/4)$, respectively. As for (1b), $\delta_{\mathbb{B}'} < 1$ if $\mathbb{M}$ contributes at least part of the resources transferred to the next generation (i.e. if $\delta_{\mathrm{m}} > 0$), thus $\delta_{\mathbb{B}'}^z < 1$ for $z > 1$, that is, values of $z > 1$ result in a reduction of the fitness value of the resources. However, because of the reduction in relatedness between polygynous males and their wives' offspring, condition (2b) specifies that monogamy can be advantageous irrespective of whether the fitness value of resources is depleted through division (i.e. for $z > 0$). As for (1b), monogamy becomes increasingly advantageous as each female provides a relatively smaller share of the resources inherited by her offspring (i.e. as δ_{m} increases and/or w_{P} decreases). Additionally, monogamy becomes increasingly advantageous as the relatedness between a polygynous male and his wives' offspring decreases (i.e. as p_{L} decreases); for $p_{\mathrm{L}} < 1/w_{\mathrm{P}}$, any potential fitness benefit to polygyny is offset by the reduction in relatedness to wives' offspring, such that monogamy is stable for all values of δ_{m}.

Finally, condition (2c) is the condition for stability against mutant males who are polygynous and transfer diagonally (males PD and PS in this population, Table S1), and is identical to (1c).

For $p_{\mathrm{H}} = 1$, the payoff for females MA is always greater than the payoff for mutant females who are polyandrous and/or provide "low" paternity (females XL, XN, PH, and PA in this population, Table S1): as in the previous scenario, the former includes the fitness contribution by own offspring and brother's wife's offspring, while the latter is limited to the fitness contribution by brother's wife's offspring (and possibly α_{L}).

Thus, (MS, MA) is stable for values of δ_{m}, z, and p_{L} for which conditions (2a) to (2c) are

satisfied simultaneously (Figure 2b in the text). The upper limit to the range of values of z is given by condition (2c) and the lower limit by condition (2b); condition (2a) is always satisfied where (2c) is satisfied.

References

Kokko, H. 1999 Cuckoldry and the stability of biparental care. *Ecol. Lett.* **2**, 247–255.

Maynard Smith, J. 1982 *Evolution and the theory of games.* Cambridge: Cambridge University Press.

Reynolds, J. D. 1996 Animal breeding systems. *Trends Ecol. Evol.* **11**, 68–72.

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