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Evolution of monogamous marriage

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by maximization of inclusive fitness

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1 **Abstract**

2 The majority of human societies allow polygynous marriage, and the prevalence of this
3 practice is readily understood in evolutionary terms. Why some societies prescribe monogamous
4 marriage is however not clear: current evolutionary explanations — that social
5 monogamy increases within-group co-operation, giving societies an advantage in competition
6 with other groups — conflict with the historical and ethnographic evidence. We show
7 that, within the framework of inclusive fitness theory, monogamous marriage can be viewed
8 as the outcome of the strategic behaviour of males and females in the allocation of resources
9 to the next generation. Where resources are transferred across generations, social monogamy
10 can be advantageous if partitioning of resources among the offspring of multiple wives causes
11 a depletion of their fitness value and/or if females grant husbands higher fidelity in exchange
12 for exclusive investment of resources in their offspring. This may explain why monogamous
13 marriage prevailed among the historical societies of Eurasia: here, intensive agriculture led
14 to scarcity of land, with depletion in the value of estates through partitioning among multiple
15 heirs. Norms promoting high paternity were common among ancient societies in the region,
16 and may have further facilitated the establishment of social monogamy. In line with the
17 historical and ethnographic evidence, this suggests that monogamous marriage emerged in
18 Eurasia following the adoption of intensive agriculture, as ownership of land became critical
19 to productive and reproductive success.

20 **Keywords** marriage, wealth inheritance, monogamy, polygyny, paternity, human social behaviour,
21 kin selection, inclusive fitness, strategic behaviour, social norms, human behavioural ecology

1 Introduction

2 Background

3 Eighty-three percent of human societies allow polygynous marriage (Murdock & White 1969; Murdock &
4 Wilson 1972). In humans, as in other sexually reproducing species, the lower investment in gametes by
5 males leads to the higher potential rate of reproduction of individual males relative to individual females.
6 This, coupled with proximate constraints such as internal gestation and lactation, produces the typical
7 mammalian pattern of polygynous breeding, characterized by high male investment in mating effort and
8 high female investment in parental effort (Trivers 1972; Clutton-Brock & Vincent 1991). Extension of
9 this paradigm to human social systems is used to explain the cross-cultural prevalence of polygynous
10 marriage (e.g. Low 2003, 2007; Marlowe 2003). In some societies that allow polygynous marriage the
11 majority of men may be each married to a single wife, because few command sufficient skill or resources
12 to marry polygynously (White 1988). This marriage pattern, sometimes referred to as “monogamy” (e.g.
13 Marlowe 2003), is common among foragers and likely evolved because of the benefits of biparental care
14 to offspring survival (Low 2003, 2007).

15 This is distinct from the system of social monogamy found in the remaining 17% of societies, in
16 which polygynous marriage is forbidden or disapproved (Murdock & White 1969; Murdock & Wilson
17 1972). Current evolutionary explanations view this marriage strategy as a mechanism of reproductive
18 levelling (e.g. Alexander et al. 1979; Alexander 1987; Bowles et al. 2003). A system of “socially imposed
19 monogamy” (Alexander et al. 1979, p. 420) would reduce within-group competition by suppressing
20 differences in reproductive success among men. Because of the attendant increase in within-group co-
21 operation, societies adopting this strategy would have an advantage in competition with other groups.
22 This would enable the cohesion of increasingly larger societies, ultimately leading to the formation
23 of large nations (Alexander et al. 1979; Alexander 1987). However, social monogamy long predates the
24 establishment of large nation states (Herlihy 1995): while the diffusion of norms prescribing monogamous
25 marriage is commonly attributed to the spread of Christianity, restrictions on polygynous marriage
26 appear in the earliest historical records (Westermarck 1921). For instance, Babylonian men were legally
27 entitled to an additional wife only under special circumstances, such as illness or infertility of the first (as
28 documented by the *Codex Hammurabi*, early second millennium BCE); strict monogamy is the only legally
29 recognized form of marriage documented for ancient Greece and Rome (Herlihy 1995; Scheidel 2009).
30 More importantly, the “socially imposed monogamy” model rests on the assumption that monogamous
31 marriage significantly reduces the variance in male reproductive success (Alexander et al. 1979). However,
32 the historical and ethnographic evidence show that dominant individuals invariably attain extraordinary
33 reproductive success even where marriage is strictly monogamous (Herlihy 1995; Low 2003; Scheidel
34 2009). Ancient Rome is a case in point: despite the fanatical prescription of monogamous marriage,

1 wealthy men fathered children by large numbers of slave women (Betzig 1992b,a; Herlihy 1995; Scheidel
2 2009). Consistently, across data for 18 modern populations collated by Brown et al. (2009) we found no
3 significant difference in variance in male reproductive success between societies practising monogamous
4 marriage ($n = 6$, median: 10.0, range: 2.3 – 23.6) and societies practising polygynous marriage ($n = 12$,
5 median: 10.4, range: 8.1 – 24.4) [Mann-Whitney $U = 27.00$, $z = -0.84$, n.s., $r = -0.20$. We coded
6 societies on marriage strategy based on information in the original references in Brown et al. (2009), or
7 references therein; our coding corresponds to the mating system coding in Brown et al. (2009), except for
8 the Pimbwe, Dobe !Kung, and Ache, which we coded as practising polygynous marriage]. This evidence
9 suggests that monogamous marriage may have evolved as a form of “monogamous transfer” of a man’s
10 resources rather than as a form of monogamous mating.

11 **Objectives and rationale**

12 Here we address the question of the function of marriage strategies, that is, of their adaptive value in terms
13 of differential reproduction, and show that the evolution of monogamous marriage can be understood
14 within the framework of inclusive fitness theory (Hamilton 1964a,b). At this ultimate level of explanation,
15 we can ask evolutionary questions about cultural behaviours — that is, behaviours that are acquired
16 through social transmission (Richerson & Boyd 2005) — without reference to the underlying mechanism
17 of transmission (Dunbar & Barrett 2007). How a given behaviour is transmitted, whether genetically
18 or through social learning, is a proximate question (West et al. 2007). We proceed in three steps. In
19 the remainder of this section, we identify two candidate factors that can make social monogamy, as a
20 form of “monogamous transfer” of resources, advantageous over alternative marriage strategies. Next,
21 we develop a game-theoretic model of the strategic behaviour of males and females in the allocation of
22 resources to the next generation to show that these factors can indeed result in monogamous marriage as
23 a stable evolutionary strategy. Finally, we discuss previous anthropological observations on the history
24 and cross-cultural distribution of marriage strategies in the context of the model, and briefly outline
25 specific predictions to be tested against the archaeological, historical, and ethnographic data.

26 Evolutionary accounts of marriage strategies typically assume that male reproductive success is
27 constrained by access to females. However, in traditional human societies where individuals hold rights
28 to property, inherited wealth is a key determinant of reproductive success, and reproductive opportunities
29 may be constrained more by ownership of resources than by access to mates. In these societies, individuals
30 are expected to transfer resources across generations in ways that maximize the effect of the resources
31 on their inclusive fitness (Rogers 1990; Hrdy & Judge 1993). To the extent that there is a trade-off
32 between transmitting genes and transmitting wealth to the next generation (Rogers 1990), in some cases
33 the optimal strategy may be to concentrate resources in a limited number of heirs. By definition, social
34 monogamy channels a man’s property to the offspring of a single wife; additionally, unigeniture (e.g.

1 primo- or ultimogeniture) may be used to avoid partitioning resources among them. In contrast, the
2 property of a polygynous man is typically divided among his wives' offspring (although unigeniture may
3 apply *within* sets of siblings by the same mother) (Gray 1964; Mair 1971; Goody 1976). This suggests
4 that social monogamy may be advantageous where partitioning of resources causes a depletion of their
5 fitness value.

6 But in humans, as in other sexually reproducing species, the reproductive interests of individuals in
7 a socially monogamous pair only coincide if the male is the biological father of the female's offspring
8 (Alexander 1987). Therefore, males need to balance the benefit of investing in closely related heirs with
9 the risk of investing in someone else's offspring. If a man has a low probability of being the biological
10 father of his wife's children, he may be better off investing in his sister's: relatedness to a sister is always
11 certain (through one's mother), as is relatedness to her offspring (Alexander 1974; Greene 1978). In
12 fact, the transfer of a man's property to his sister's sons is common in societies with frequent female
13 extramarital sex (Flinn 1981; Hartung 1981). We extend this reasoning to incorporate the strategic
14 behaviour of females: if natural selection favours males who allocate resources based on their level of
15 paternity, in turn it may favour females who allocate paternity based on the degree of male investment
16 in their offspring. The resulting trade-off between paternity and investment of resources may lead to
17 social monogamy: males would benefit from increased paternity in their wife's offspring, and females
18 from exclusive investment of their husband's resources. Of course, this mechanism can only operate if
19 males have cues about paternity. In humans, in addition to direct phenotypic cues (see discussion in
20 Geary 2006), indirect behavioural cues may include the conformity of females to norms regulating their
21 sexual behaviour; such norms are found in the vast majority of societies (Broude & Greene 1976).

22 **Theoretical framework**

23 We capture these intuitive arguments with a game-theoretic model, described in detail in the supporting
24 information (SI). We focus on a population in which both males and females marry either monogamously
25 or polygamously, with $w \geq 1$ wives for males and $h \geq 1$ husbands for females. Males transfer resources
26 to the next generation "vertically" to their wives' offspring or "diagonally" to their sister's offspring
27 (Figure 1). Females produce one male and one female offspring; each sibling pair inherits resources δ
28 from the parent generation, with $\delta = \delta_m + \delta_f = 1$ in a monogamous population in which all males transfer
29 vertically, and $0 \leq \delta_m \leq 1$ and $0 \leq \delta_f \leq 1$ the male and female contributions to δ . The fitness of each
30 sibling pair is given by δ^z , with $z > 0$; for $z > 1$, the fitness value of δ is depleted when δ is partitioned
31 among the offspring of multiple wives.

32 The probability p that a male is the biological father of his wife's offspring depends on the behaviour of
33 females, who give their husbands either "high" paternity p_H or "low" paternity p_L , with $0 < p_L < p_H \leq 1$.

1 Females obtain an additional generic advantage α from mating with other males beyond their husbands,
 2 with $\alpha_L > \alpha_H$, and $\alpha_H = 0$ for $p_H = 1$. Males can infer their level of paternity from the behaviour of
 3 females.

4 [[Figure 1 approximately here]]

5 Schematically, the inclusive fitness payoff for a focal male \mathbb{M} in the parent generation is given by the
 6 fitness value of resources β_i , inherited by the offspring \mathbb{B}' of his $\hat{w} \geq 1$ wives, plus the fitness value of
 7 resources ϕ_i , inherited by his sister's offspring \mathbb{F}' , each scaled by the respective coefficient of relatedness
 8 ($r_{\mathbb{M}\mathbb{B}'}$ or $r_{\mathbb{M}\mathbb{F}'}$) (Figure 1; Table 1; SI Text). The subscript $i = 1, \dots, 4$ denotes the pathway through
 9 which resources are transferred to the heir, as per Figure 1; $\hat{w} \neq w$ for a mutant focal male whose
 10 marriage strategy differs from the strategy of resident males, and $\hat{w} = w$ in all other cases. Resources
 11 are divided equally among the male's wives' offspring. This can be written as

$$12 \quad E_{\mathbb{M}} = \hat{w} \left(\frac{\beta_1 + \beta_2 + \beta_3 + \beta_4}{\hat{w}} \right)^z r_{\mathbb{M}\mathbb{B}'} + (\phi_1 + \phi_2 + \phi_3 + \phi_4)^z r_{\mathbb{M}\mathbb{F}'}$$

13 Similarly, the inclusive fitness payoff for a focal female \mathbb{F} is given by the fitness value of resources
 14 β_i , inherited by the offspring \mathbb{B}' of her brother's $w \geq 1$ wives, plus the fitness value of resources ϕ_i ,
 15 inherited by her offspring \mathbb{F}' , each scaled by the respective coefficient of relatedness ($r_{\mathbb{F}\mathbb{B}'}$ or $r_{\mathbb{F}\mathbb{F}'}$), plus
 16 any advantage $\hat{\alpha}$ she obtains from mating with other males beyond her husbands (Figure 1; Table 1; SI
 17 Text). As in the previous case, the subscript $i = 1, \dots, 4$ denotes the pathway through which resources
 18 are transferred to the heir, as per Figure 1; $\hat{\alpha} \neq \alpha$ for a mutant focal female whose paternity strategy
 19 differs from the strategy of resident females, and $\hat{\alpha} = \alpha$ in all other cases. This can be written as

$$20 \quad E_{\mathbb{F}} = w \left(\frac{\beta_1 + \beta_2 + \beta_3 + \beta_4}{w} \right)^z r_{\mathbb{F}\mathbb{B}'} + (\phi_1 + \phi_2 + \phi_3 + \phi_4)^z r_{\mathbb{F}\mathbb{F}'} + \hat{\alpha}$$

21 [[Table 1 approximately here]]

22 The possible combinations of male and female strategies differ in inclusive fitness payoffs; given these
 23 payoffs, we can derive evolutionarily stable equilibria consisting of a pair of male and female strategies
 24 that cannot be invaded by rare mutants playing alternative strategies (Maynard Smith 1982) (SI Text).

25 Results

26 Social monogamy is a stable evolutionary outcome under two scenarios (SI Text and Table S1); both
 27 require “suspicious” males, that is, males who transfer vertically if females are monogamous and provide
 28 “high” paternity, diagonally otherwise. In the first scenario females always provide “high” paternity. In
 29 the second scenario females are “astute”, that is, they provide “high” paternity if males are monogamous,
 30 “low” paternity otherwise. Both combinations of male and female strategies result in monogamous
 31 marriage, vertical transfer, and “high” paternity.

1 [[Table 2 approximately here]]

2 [[Figure 2 approximately here]]

3 Figure 2 illustrates the two scenarios for $p_H = 1$. In the first case, monogamy can be advantageous
4 where there is a fitness cost to dividing resources among the offspring of multiple wives (i.e. for $z > 1$;
5 condition **b** in Table 2; Figure 2a). In the second case, because of the strategic behaviour of females,
6 polygynous males suffer a reduction in relatedness to wives' offspring; consequently, monogamy can be
7 advantageous irrespective of whether the fitness value of resources is depleted through division (i.e. for
8 $z > 0$; condition **b** in Table 2; Figure 2b). Vertical transfer can be advantageous where the benefit to
9 a man of providing extra resources to his sister's offspring is offset by their lower relatedness relative to
10 wife's offspring (i.e. for z below the threshold specified by condition **c** in Table 2; Figures 2a and 2b).
11 Monogamy and vertical transfer become increasingly advantageous as each wife provides a relatively
12 smaller share of the resources inherited by her offspring (i.e. as δ_m increases and/or w_P decreases;
13 conditions **b** and **c** in Table 2; Figures 2a and 2b). Additionally, in the second case the benefit to
14 monogamy increases as the relatedness between a polygynous male and his wives' offspring decreases
15 (i.e. as p_L decreases; for $p_L < 1/w_P$, any potential fitness benefit to polygyny is offset by the reduction
16 in relatedness to wives' offspring, such that monogamy is stable for all values of δ_m ; condition **b** in Table
17 2; Figure 2b).

18 SI Figure S1 shows that these results hold for values of $p_H < 1$. Here $p_H = 0.5$, which is likely an
19 extremely low value of p_H : men would attain on average as much reproductive success by other men's
20 wives as by their own in a society with a paternity level of $p < 0.5$ (Hartung 1981). For comparison, in
21 contemporary populations men are the biological fathers of their putative children, on average, in 98.3%
22 of cases if they have high confidence of paternity, and in 70.2% of cases if they have low confidence of
23 paternity; actual paternity levels must fall between these values for most societies (Anderson 2006). As-
24 suming that comparable paternity levels characterized our species' recent evolutionary past, this suggests
25 that social monogamy represented a stable outcome in the evolution of human social systems.

26 Discussion

27 We developed a game-theoretic model to investigate whether monogamous marriage can be viewed
28 as the outcome of the strategic behaviour of males and females in the allocation of resources to the
29 next generation. The model showed that where resources are linked to fitness and are transferred
30 across generations, social monogamy is a stable evolutionary outcome (i) if dividing resources among the
31 offspring of multiple wives causes a depletion of their fitness value and/or (ii) if females grant husbands
32 higher fidelity in exchange for exclusive investment of resources in their offspring. In both cases, the

1 benefit to monogamy increases as the relative contribution of resources by females decreases.

2 These findings suggest that monogamous marriage can be understood as an individual-level adapta-
3 tion by males and females to maximize their inclusive fitness. In turn, this challenges previous evolution-
4 ary explanations for the emergence of monogamous marriage, and for variation in marriage strategies
5 across societies more generally: the former assume the implication of group-level processes, while both
6 assume that male reproductive success is always maximized by polygynous marriage or, equivalently,
7 that variance in male reproductive success is always greater under polygynous than under monogamous
8 marriage (Low 2003, 2007). The framework we develop makes both assumptions unnecessary. Rather, it
9 shows that where resources are transferred across generations and are linked to fitness, whether monog-
10 amous or polygynous marriage represents the optimal strategy for males depends on whether the value
11 of the resources they provide is depleted through division among multiple heirs; some form of division is
12 inevitable if multiple wives are involved.

13 Further, this framework extends current evolutionary explanations for transfer strategies, which rely
14 on the notion of strategic male behaviour (e.g. Alexander 1974; Greene 1978; Kurland 1979), to incor-
15 porate the strategic behaviour of females: if selection favours males who allocate resources strategically,
16 based on their level of paternity, it is also likely to favour females who allocate paternity strategically,
17 based on the level of male investment in their offspring. This simple extension has important implica-
18 tions for analysis of the evolution of marriage strategies, leading to a situation where both males and
19 females stand to gain from monogamous marriage: males benefit from investing resources “safely” in
20 the individuals in the next generation that provide the greatest potential fitness returns, that is, their
21 wife’s offspring; females, in turn, benefit from exclusive investment of their husband’s resources in their
22 own offspring. In a similar way, this extension is likely to have important implications for analysis of
23 the evolution of other aspects of human social organization that are linked to transfer strategies: for
24 example, the notion of strategic male behaviour in this context underlies current explanations for the
25 evolution of descent systems (see review in Cronk & Gerkey 2007).

26 The historical and ethnographic evidence suggest that these mechanisms likely operated in shaping
27 the evolution of human social systems. In the Old World, polygyny prevails among African societies with
28 subsistence economies based on pastoralism or extensive agriculture (Goody 1976). The relationship
29 between resources and fitness documented for the Gabbra pastoralists of Kenya (Mace 1996) and for the
30 Chewa horticulturalists of Malawi (Holden et al. 2003) indicates that in pastoralism and horticulture
31 the fitness value of resources is not depleted through division. Among the Gabbra, for example, parents
32 provide on average ten camels to marry off a son: three as bridewealth to the bride’s kin, and seven
33 to the groom for starting an independent household (Mace 1996). If the division of resources depleted
34 their fitness value, the reproductive success of men owning five camels would be less than half the
35 reproductive success of men owning ten. Conversely, men with five camels have more than half the

1 reproductive success of men with ten (Mace 1996). This is likely because in both subsistence systems
2 productivity is constrained more by availability of labour than by ownership of the primary productive
3 resources (Goody 1976): in pastoralist societies holdings of livestock can easily be increased through
4 husbandry; in horticultural societies the low productivity afforded by extensive agricultural techniques
5 means that land is rarely a scarce resource (Gray 1964; Goody 1976).

6 This is in stark contrast with the intensive agriculture practised in the historical societies of Eurasia,
7 where irrigation and ploughing led to increased productivity, which in turn sustained continued popu-
8 lation growth. Combined, increased productivity and population growth caused shortages of land. As
9 land scarcity increased, so did the pressure to keep holdings above the minimum size required to set up
10 a viable productive and reproductive unit (Goody 1976; Hrdy & Judge 1993). Under these conditions
11 of habitat saturation, the partitioning of estates depleted their value; in extreme cases the reduction in
12 value was so great that parents commonly designated a single heir, at the expense of all other offspring,
13 through systems of unigeniture (Hrdy & Judge 1993; e.g. Boone 1986, 1988; Volland & Dunbar 1995).

14 Consistent with our finding that social monogamy can be advantageous where the value of resources
15 is depleted through division, marriage was typically monogamous in the agrarian societies of Eurasia
16 with economies based on intensive agriculture (Goody 1976). In line with our expectations, the relative
17 contribution of women to production is lower in these societies compared to other subsistence systems
18 (Murdock & Provost 1973; Goody 1976). Indeed, across societies access to new land for expansion is
19 a key ecological determinant of polygyny (White & Burton 1988), and within societies the incidence
20 of polygyny declines with increasing scarcity of land (White 1988). This raises the possibility that
21 restrictions on polygynous marriage emerged in the ancient societies of Eurasia following the adoption of
22 intensive agriculture, as ownership of land became increasingly critical to economic success, and growing
23 shortages of land imposed greater costs on partibility. Cultural norms promoting high paternity, such as
24 ideologies of honour, virginity, and sexual fidelity, were common in these societies (Mair 1971; Scheidel
25 2009). To the extent that these norms resulted in an increase in average relatedness between a man
26 and his wife's offspring, our findings suggest that they may have facilitated the establishment of social
27 monogamy in this region.

28 The model generates the following predictions about the cross-cultural distribution and history of
29 marriage strategies, to be tested against the ethnographic, archaeological, and historical data. First, the
30 stability of monogamous marriage requires that men transfer resources vertically, that is, to their wife's
31 offspring. Therefore, we predict the cross-cultural data to reveal an association between monogamous
32 marriage and the transfer of a man's property to his wife's offspring. Second, we expect the archaeo-
33 logical evidence to show that the emergence of monogamous marriage was linked to the development
34 of intensive agricultural techniques, possibly coupled with the establishment of social norms promoting
35 high paternity. Analogous property considerations may help explain historically attested transitions be-

1 tween marriage strategies within societies, such as the recent shift from polygyny to monogamy in several
2 Muslim countries, or the shift from monogamy to polygyny among the Mormons during the nineteenth
3 century (Cairncross 1974).

4 Of course, any model can capture but a small fraction of variation in human social systems, and
5 must overlook the many historical contingencies, such as the diffusion of religious beliefs (e.g. Goody
6 1983), that may have influenced their development. Yet placing this variation within an inclusive fitness
7 framework allows us to conceptualize general evolutionary mechanisms shaping the organization of hu-
8 man societies. This finally resolves the crux of anthropological discussions about whether the primary
9 function of marriage is “economic and productive” or “sexual and reproductive” (Goody 1973, p. 189). In
10 evolutionary terms, the proximate economic determinants of marriage underlie its ultimate reproductive
11 function.

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1 Tables

Table 1: Symbols used in the inclusive fitness payoffs

Symbol*	Focal individual	
	\mathbb{M}	\mathbb{F}
Resource transfers to \mathbb{B}' (β_i)		
β_1	$\Omega \mathring{m}_V[\delta_m + \mathring{w}(\delta_f/h)]$	$\Omega m_V[\delta_m + w(\delta_f/h)]$
β_2	$\Omega \mathring{w} m_V(h-1)(\delta_m/w + \delta_f/h)$	$\Omega w m_V(h-1)(\delta_m/w + \delta_f/h)$
β_3	$\Omega \mathring{w} (1-\Omega)\delta_m$	$\Omega w (1-\Omega)\delta_m$
β_4	$\Omega \mathring{w} \Omega m_D[\delta_m + w(\delta_f/h)]$	$\Omega w \Omega m_D[\delta_m + w(\delta_f/h)]$
Resource transfers to \mathbb{F}' (ϕ_i)		
ϕ_1	$(1-\Omega)\delta_m$	$(1-\Omega)\delta_m$
ϕ_2	$\Omega \mathring{m}_D[\delta_m + \mathring{w}(\delta_f/h)]$	$\Omega m_D[\delta_m + w(\delta_f/h)]$
ϕ_3	$(1-\Phi)\delta_f$	$(1-\Phi)\delta_f$
ϕ_4	$\Phi h m_V(\delta_m/w + \delta_f/h)$	$\Phi \mathring{h} \mathring{m}_V(\delta_m/w + \delta_f/\mathring{h})$
Coefficients of relatedness (r_{xy})		
to \mathbb{B}'	$[\mathring{p} + (h-1)p]/2h^2$	$(p/2h)[(1+p^2/h)/4]$
to \mathbb{F}'	$(1/2)[(1+p^2/h)/4]$	$1/2$

* The subscript $i = 1, \dots, 4$ to β and ϕ denotes the pathway through which resources are transferred to the heir, while the subscripts to r denote the focal individual x (\mathbb{M} or \mathbb{F}) and heir y (\mathbb{B}' or \mathbb{F}'), as per Figure 1. Ω denotes the marriage probability for males, Φ the marriage probability for females. m_V denotes the probability that a male transfers vertically, $m_D = 1 - m_V$ the probability that he transfers diagonally. $\mathring{\cdot}$ indicates 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. See SI Text for details.

Table 2: Conditions for the stability of “suspicious” monogamous males for $p_H = 1$

Notation [*]	Condition [†]	Strategy of mutant males
a	$z < \log 3 / \log 2$	Monogamous marriage with diagonal transfer
b[‡]	$w_P(\delta_m/w_P + \delta_f)^z p_L < 1$	Polygynous marriage with vertical transfer
c	$(2\delta_m + \delta_f + w_P\delta_f)^z < 3$	Polygynous marriage with diagonal transfer

^{*} Corresponds to the notation used in Figure 2a. See SI Text for details.

[†] $w_P > 1$ denotes the number of wives for a polygynous male.

[‡] $p_L = 1$ with females who always provide “high” paternity.

1 Figures

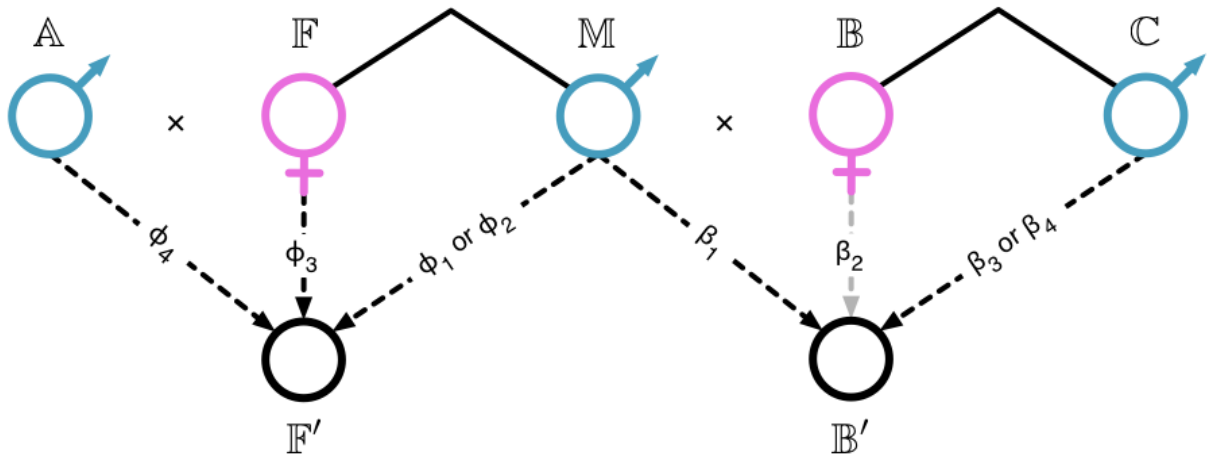
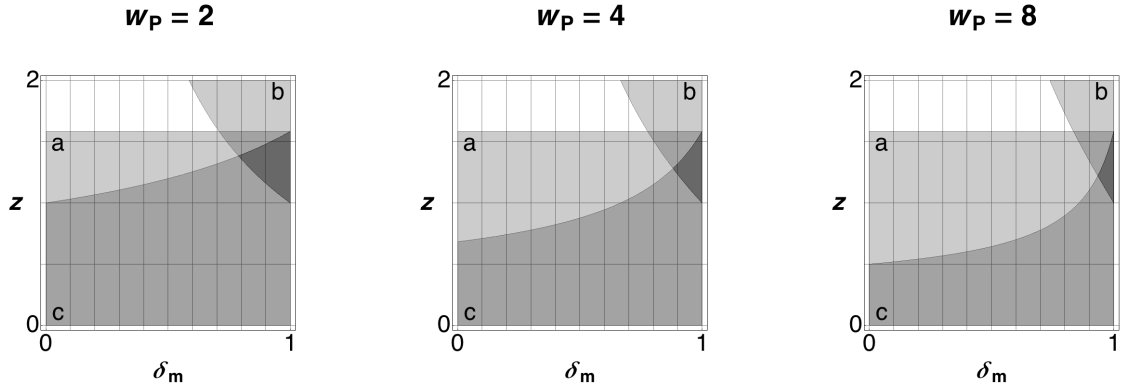


Figure 1: Inclusive fitness contributions for a focal male M and a focal female F . In the parent generation crosses represent marriages, solid lines represent brother–sister relationships (A : F 's husband; B : M 's wife; C : B 's brother). In the offspring generation B' and F' each represent a sibling pair (B' : B 's offspring; F' : F 's offspring). Dashed arrows represent resource transfers from parent to offspring generation. β_i represents resources transferred to B' (β_1 if M transfers vertically; β_2 if B is polyandrous and her other husbands, excluding M , transfer vertically; β_3 if C does not marry; β_4 if C marries and transfers diagonally); β_2 is grey to indicate that the resources are transferred by B 's husbands (other than M , not shown), rather than by B herself. ϕ_i represents resources transferred to F' (ϕ_1 if M does not marry; ϕ_2 if M marries and transfers diagonally; ϕ_3 if F does not marry; ϕ_4 if F marries and A transfers vertically). See text and SI Text for details.

(a)



(b)

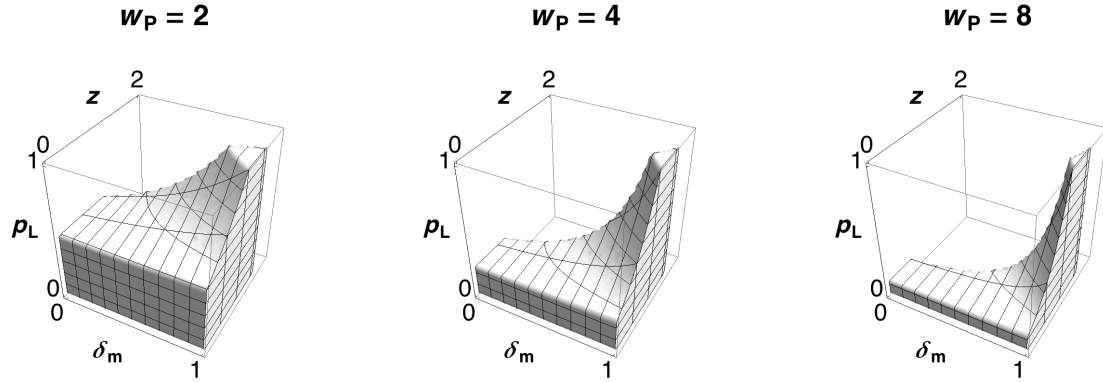


Figure 2: Stability of “suspicious” monogamous males against mutant males with $w_P = 2$, $w_P = 4$, or $w_P = 8$, for $p_H = 1$; w_P denotes the number of wives for polygynous males, and p_H the paternity level of males with females who always provide “high” paternity and of monogamous males with “astute” 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 and SI 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 (see Table 2). Monogamy is stable in the darker area, where all conditions are met. (b), with “astute” monogamous females. Monogamy is stable throughout the volume shown.