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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  $\delta$   
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  $\delta$ . The fitness of each  
30 sibling pair is given by  $\delta^z$ , with  $z > 0$ ; for  $z > 1$ , the fitness value of  $\delta$  is depleted when  $\delta$  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  $\alpha$  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  $\beta_i$ , inherited by the offspring  $\mathbb{B}'$  of his  $\hat{w} \geq 1$  wives, plus the fitness value of  
 7 resources  $\phi_i$ , 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  $\beta_i$ , inherited by the offspring  $\mathbb{B}'$  of her brother's  $w \geq 1$  wives, plus the fitness value of resources  $\phi_i$ ,  
 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  $\delta_m$  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  $\delta_m$ ; 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; Voland & 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 $\mathbb{B}'$ ( $\beta_i$ )		
$\beta_1$	$\Omega \mathring{m}_V[\delta_m + \mathring{w}(\delta_f/h)]$	$\Omega m_V[\delta_m + w(\delta_f/h)]$
$\beta_2$	$\Omega \mathring{w} m_V(h-1)(\delta_m/w + \delta_f/h)$	$\Omega w m_V(h-1)(\delta_m/w + \delta_f/h)$
$\beta_3$	$\Omega \mathring{w} (1-\Omega)\delta_m$	$\Omega w (1-\Omega)\delta_m$
$\beta_4$	$\Omega \mathring{w} \Omega m_D[\delta_m + w(\delta_f/h)]$	$\Omega w \Omega m_D[\delta_m + w(\delta_f/h)]$
Resource transfers to $\mathbb{F}'$ ( $\phi_i$ )		
$\phi_1$	$(1-\Omega)\delta_m$	$(1-\Omega)\delta_m$
$\phi_2$	$\Omega \mathring{m}_D[\delta_m + \mathring{w}(\delta_f/h)]$	$\Omega m_D[\delta_m + w(\delta_f/h)]$
$\phi_3$	$(1-\Phi)\delta_f$	$(1-\Phi)\delta_f$
$\phi_4$	$\Phi h m_V(\delta_m/w + \delta_f/h)$	$\Phi \mathring{h} \mathring{m}_V(\delta_m/w + \delta_f/\mathring{h})$
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  $\beta$  and  $\phi$  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.  $\Omega$  denotes the marriage probability for males,  $\Phi$  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  $p_H = 1$

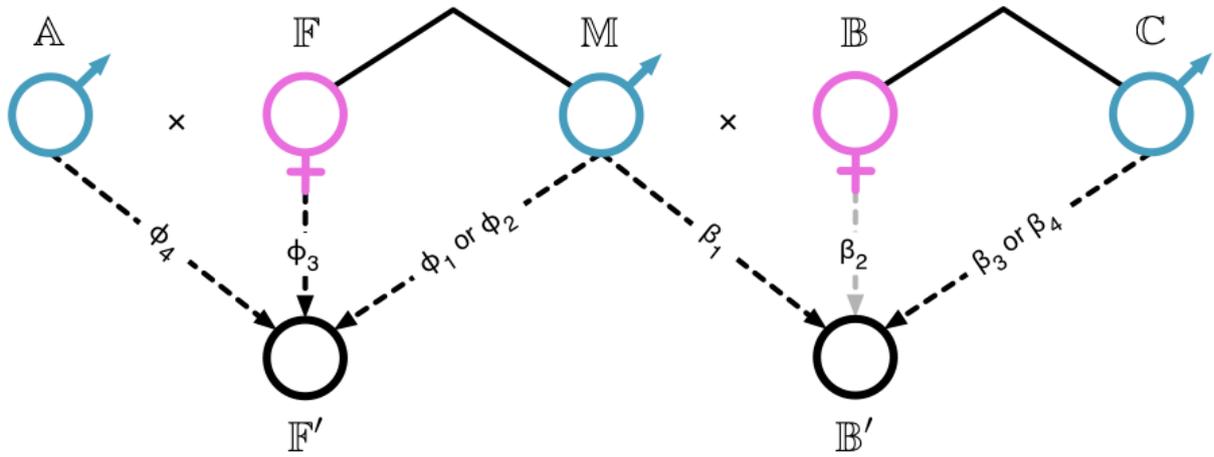
Notation <sup>*</sup>	Condition <sup>†</sup>	Strategy of mutant males
<b>a</b>	$z < \log 3 / \log 2$	Monogamous marriage with diagonal transfer
<b>b<sup>‡</sup></b>	$w_P(\delta_m/w_P + \delta_f)^z p_L < 1$	Polygynous marriage with vertical transfer
<b>c</b>	$(2\delta_m + \delta_f + w_P\delta_f)^z < 3$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

<sup>\*</sup> Corresponds to the notation used in Figure 2a. See SI Text for details.

<sup>†</sup>  $w_P > 1$  denotes the number of wives for a polygynous male.

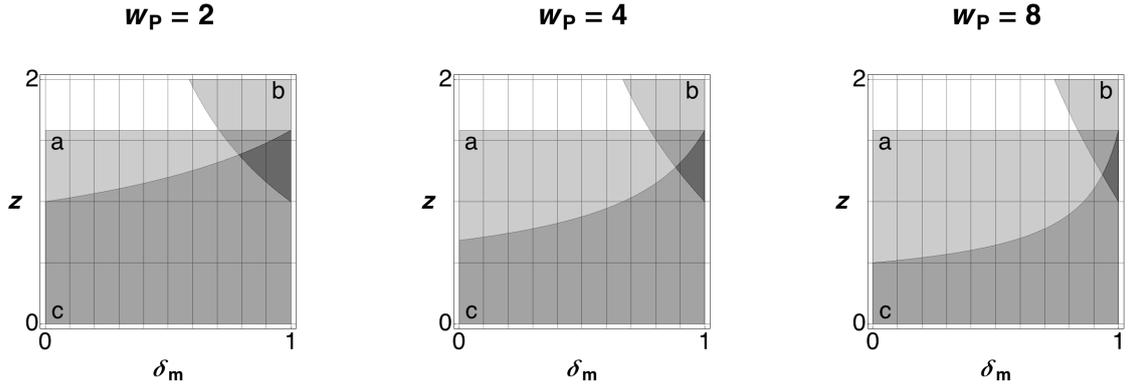
<sup>‡</sup>  $p_L = 1$  with females who always provide “high” paternity.

# 1 Figures

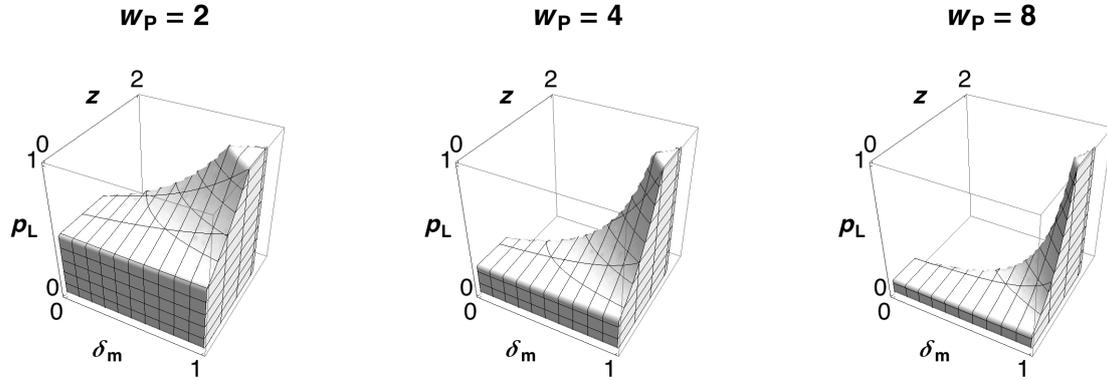


**Figure 1:** Inclusive fitness contributions for a focal male  $M$  and a focal female  $F$ . In the parent generation crosses represent marriages, solid lines represent brother–sister relationships ( $A$ :  $F$ 's husband;  $B$ :  $M$ 's wife;  $C$ :  $B$ 's brother). In the offspring generation  $B'$  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.  $\beta_i$  represents resources transferred to  $B'$  ( $\beta_1$  if  $M$  transfers vertically;  $\beta_2$  if  $B$  is polyandrous and her other husbands, excluding  $M$ , transfer vertically;  $\beta_3$  if  $C$  does not marry;  $\beta_4$  if  $C$  marries and transfers diagonally);  $\beta_2$  is grey to indicate that the resources are transferred by  $B$ 's husbands (other than  $M$ , not shown), rather than by  $B$  herself.  $\phi_i$  represents resources transferred to  $F'$  ( $\phi_1$  if  $M$  does not marry;  $\phi_2$  if  $M$  marries and transfers diagonally;  $\phi_3$  if  $F$  does not marry;  $\phi_4$  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.  $\delta_m$  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.