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Paternity and inheritance of wealth

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One of the oldest conjectures in anthropology is that men transfer wealth to their sister's son when the biological paternity of their 'own' children is in doubt[1–12]. Because maternity is certain, a man is necessarily related to his sister's son and his brother (see Fig. 1). It is argued here that relatedness to male heirs can be assured by passing wealth to sister's sons or down a line of brothers, whether the prevailing kinship system reckons those brothers matrilineally or patrilineally. It is also argued that when several transfers of wealth are considered, a man's likelihood of being cuckolded need not be unrealistically high[13] for his successive matrilineal heirs to be more related to him than his successive patrilineal heirs (see Fig. 2). Cross-cultural data on sister's son/brother inheritance[14] and frequency of extramarital sex for females[15] support the hypothesis that men tend to transmit wealth to their sister's son and/or brother when the probability that their putative children are their genetic children is relatively low.

In matrilineal inheritance a man's primary heir is his sister's son. This cross-generation transfer can be direct (25 societies) but more often occurs after wealth has been sequentially inherited by younger brothers ($\simeq 47$ societies), the last of whom leaves it to their mutual sister's son. Although matrilineal inheritance does not prevent a man from distributing significant benefits to his own children[16,17], and is thereby not a mirror image of patrilineal inheritance[18] ($\simeq 500$ societies), it is unique in designating major cross-generation heirs related to a male benefactor through an unbroken line of females (counts are of a composite inheritance score derived from ref. 14, as described below).

In 1771, after characterizing traditional societies as patrilineal with regard to inheritance of wealth, status and family membership, John Millar[1] noted an exception: "We read of several nations, among whom it [marriage] is either unknown, or takes place in a very imperfect and limited manner. To a people in this situation it will appear that children have much more connection with their mother than with their father. If a woman has no notion of attachment and fidelity to any particular person, if notwithstanding her occasional intercourse with different individuals . . . the child which she has born is regarded as a member of her own family . . . so that if any person was desired to give an account of the family to which he belonged, he was naturally led to recount his maternal genealogy in the female line. [In such nations] females, indeed, are held incapable of enjoying the office of chief, but through them the succession to that dignity is continued; and therefore, upon the death of a chief, he is succeeded not by his own son, but by that of his sister." In 1865 McLennan[3] renewed the hypothesis with enthusiasm (indeed, over-enthusiasm): "The connection between these two things—uncertain paternity and kinship through females only, seems so necessary—that of cause and effect—that we may confidently infer the one where we find the other."

In 1961 the first empirical study of matrilineality[19] found that it is distributed independently around the world and is associated with fishing, while patrilineality is associated with pastoralism—an intriguing finding in light of another of Millar's observations[1]: "Among the inhabitants of the eastern coast of Tartary it is said, that those tribes which are accustomed to the pasturing of cattle discover some sort of jealousy with regard to the chastity of their women, a circumstance which is looked upon as a matter of perfect indifference by those families in that country who procure their subsistence merely by fishing."

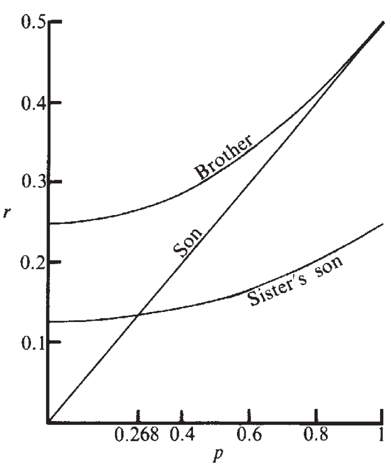

Fig. 1 p = Probability of paternity = the probability that a man's putative offspring by his wife are, in fact, his biological offspring; r = probabilistic degree of relatedness. If p is below 0.268, a man is more related to his sister's son than his 'own' son—see ref. 9 and Fig. 2. A man is more related to his brother whenever p is <1. r to son $= \frac{1}{2}p$; r to sister's son equals r through mother to sister to sister's son $= (\frac{1}{2})(\frac{1}{2})(\frac{1}{2})$, plus r through father to sister to sister's son $= (\frac{1}{2}p)(\frac{1}{2}p)(\frac{1}{2})$, which together $= (\frac{1}{2})(\frac{1}{4})(1+p^2)$; r to brother equals r through mother $= \frac{1}{4}$, plus r through father $= \frac{1}{4}p^2$, which together $= \frac{1}{4} + \frac{1}{4}p^2$.

In 1974 Alexander[7] made the hypothesis explicit with regard to modern evolutionary theory, and in 1978 Greene[9] calculated the probability of paternity (p) below which husbands must fall if they are to be, on average, more related to their sister's sons than their 'own' sons: $p < 0·268$ (Fig. 1). This threshold is so low because a man's probable relatedness to his sister's son must be reduced by his probable relatedness to his sister through their father, that is, the probability that he is his father's son and she his father's daughter. Unfortunately (for the hypothesis), if a society-wide p were < 0.268, the average man would have more than twice as much reproductive success by other men's wives as he would by his own wife—a circumstance which, in addition to straining the imagination, could render marriage a maladaptive male strategy (probably better to remain single and expend all of one's efforts on other men's wives).

Fortunately, a less extreme p can fit the paternity hypothesis if more than one generation is considered when contrasting ideal matrilineality against ideal patrilineality (father to son, to son's son, to son's son's son, etc.). The key here is that while a man with a p of 0.8 is probabilistically related to his son by $0.8 \times r$ where r is the degree of relatedness, he is related to his son's son by $0.8^2 \times r$ and to his son's son's son by $0.8^3 \times r$ (where $r = 0.5$, 0.5^2 and 0.5^3, respectively). That is, the exponent of p increases by a factor of 1 for each transfer to an heir related through a male. In contrast, p affects only the first cross-generation matrilineal transfer. A man's sister's son's sister's son is related to him by half as much as his sister's son, with no additional effect from p. This means, for example, that if p is < 0.725, a man is more related to his matrilineal heir than his patrilineal heir at three generations (Fig. 2).

Assuming that the paternity hypothesis is viable for reasonable values of p, assessing it would seem a matter of cross-tabulating matrilineal inheritance versus patrilineal inheritance by high versus low extramarital sex for females. However, there is a form of 'delayed' patrilineal inheritance, patrilineal brother inheritance, which can be seen as an alternative adaptation to low p. Given any $p < 1$, a man is more related to his brother than to any other potential male heir (Fig. 1). Because p cannot be 1, one might expect all patrilineal benefactors to follow the pattern

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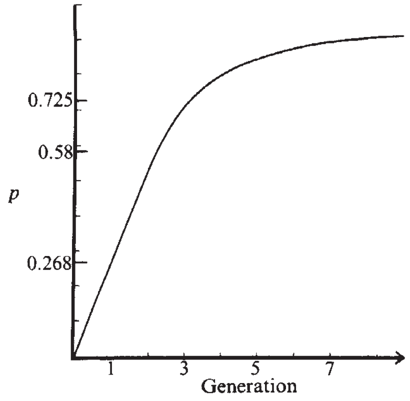

Generation	r to sister's son$_i$	r to son$_i$	Threshold at $p=$
1	$(\frac{1}{2})(\frac{1}{4})(1+p^2)$	$\frac{p}{2}$	0.268
2	$(\frac{1}{2})^2(\frac{1}{4})(1+p^2)$	$\left(\frac{p}{2}\right)^2$	0.58
3	$(\frac{1}{2})^3(\frac{1}{4})(1+p^2)$	$\left(\frac{p}{2}\right)^3$	0.725
i	$(\frac{1}{2})^i(\frac{1}{4})(1+p^2)$	$\left(\frac{p}{2}\right)^i$	$4p^i-p^2-1=0$

Fig. 2 Solving for p given i, $4p^i-p^2-1=0$, where $i=i$th generation, derives the probability of paternity below which a man is more related to his cross-generation matrilineal heir (sister's son$_i$) than his cross-generation patrilineal heir (son$_i$) at successive generations. For example, if p is <0.725, a man is likely to be more related to his third generation matrilineal heir than to his son's son's son. (I thank P. Greene for deriving this formula.)

of giving to their younger brother(s) with the stipulation that the wealth subsequently return to their son(s). However, at an average father's age of death, his son is near his reproductive prime while his brother is past that stage. Accordingly, a son's higher reproductive value[20] will compensate, in terms of effect on benefactor's inclusive fitness[21], when p is <1 but not $\ll 1$.

Why adaptation to low p should be patrilineally reckoned brother inheritance in some societies ($\simeq 70$ cases) and matrilineal inheritance in other societies ($\simeq 72$ cases) is unclear. The absolute relatedness of a brother is higher than that of a sister's son, but in patrilineal brother inheritance wealth eventually reverts to a man's own child. There seems to be a trade-off between absolute relatedness to heir and the number of transfers for which relatedness is assured (with matrilineal inheritance assuring some relatedness indefinitely). Perhaps the two strategies reflect a difference in p, or economic differences which affect the duration of effectiveness of inherited wealth, or perhaps patrilineal brother inheritance is simply as 'matrilineal' as an otherwise patrilineal society can get. Whatever the reason, given brother inheritance, whether in a matrilineal or patrilineal context, any inclusive fitness enhancing effect of wealth[8,22–24] resides for the longest possible time amongst most highly related males (for emphasis on males see refs 8, 22, 25, 26). The key here is that, for present purposes, patrilineal brother inheritance has more in common with matrilineal inheritance than with patrilineal inheritance. Thus, one should group patrilineal brother inheritance with matrilineal inheritance when testing the hypothesis that men stipulate an heir whose relatedness is less affected by low p in societies where p is relatively low.

Murdock and White have selected 'The Standard Cross-Cultural Sample'[27] by taking one society from each of the world's 186 major culture areas, giving a sample which maximizes independence and minimizes effects from cultural diffusion. Separate codes for inheritance of real property (land, house) and movable property (such as livestock, money) are as follows[14,28,29]:

0: No information.
1: No land rights/no inherited movable property/no rule governing the transmission of same.
2: Matrilineal inheritance by a sister's son or sons.
3: Matrilineal inheritance by heirs who take precedence over sisters' sons (such as younger brother).
4: Inheritance by children, but with daughters receiving less than sons.
5: Inheritance by children of either sex or both.
6: Inheritance by patrilineal heirs who take precedence over sons (such as younger brother).
7: Patrilineal inheritance by son or sons.

For present purposes code 3 is functionally the same as code 2—though brother is not stipulated as the only possibility, he is the most likely heir[16,18]. Where this is not the case, the pattern still qualifies as having heirs unaffected by low p, because any matrilineal heir must be related through the mother and because

PRIMARY HEIR(S)

FEMALE EXTRAMARITAL SEX	Brother/sister's son		Own children
high	*A* 6 Nyakyusa Nkundo Lesu Trobrianders Saramacca Crow	Huichol?	*B* 5 Romans Vietnamese Kwoma Trukese Aymara
low	1 Siuai *C*		10 Kikuyu Egyptians Turks Irish Lapps Lepcha Lakher Vedda Javanese Iban *D*

Fig. 3 Inheritance by probability of paternity. $N=22$; Fisher exact probabililty $=0.0298$; $\gamma=0.846$ (considering the two inheritance forms as 'high' and 'low' with regard to effect of p on relatedness to heir); $\phi=0.488$. The Huichol (see text) are rated 'high' on female extramarital sex and would go in cell *A* or *B* if included—either way the figure would retain significance below 0.05. This significance depends on grouping patrilineal brother inheritance with matrilineal inheritance. If the contrast were matrilineal versus own children/patrilineal brother, the Nyakyusa, Nkundo and Huichol would fall in cell *B*; giving cell $A=4$, cell $B=8$, cell $C=1$, cell $D=10$: Fisher exact probability $=0.162$. If the contrast were simply matrilineal versus own children, the Nyakyusa, Nkundo and Huichol would drop out, giving cell $A=4$, cell $B=5$, cell $C=1$, cell $D=10$: Fisher exact probability $=0.0893$. Murdock expressed doubt about his inheritance codes[14]. In response to an inquiry he wrote that he did not have reservations about the accuracy of the data, but felt that the codes were 'too crude' (personal communication). Future research would profit from refining the inheritance codes. For example, a man could extend considerable assistance to his brother, both during his lifetime and through inheritance and still follow the norms of a society coded in inheritance category 'own children'. According to the paternity hypothesis as presented here, societies in cell *B* would be expected to follow that pattern more than societies in cell *D*, and some cell *B* societies may have sufficient 'brother investment' to qualify for cell *A*.

wealth eventually goes to sister's son. Societies with code 6, however, must be checked to see whether brother is the heir. Of the 23 cases with usable codes for inheritance (see below) and frequency of female extramarital sex, three contain a 6 in their composite inheritance score: the Nyakyusa (6 and 6), the Nkundo (6 and 6) and the Huichol (5 and 6). These were checked in the Human Relations Area Files[28] to see whether brother is the preferred heir. The major ethnographer for the Nyakyusa puts the case succinctly[30]: "A man's heir is his full brother next to him in age, and only when all the full brothers of a family have died does the property pass to the eldest son of the eldest brother." For the Nkundo, cases were reported of brother taking precedence over son, of sister's son taking precedence over son, and of brother taking precedence over sister's son[31]. As put by Murdock[32], the Nkundo "lie wedged between the matrilineal Central Bantu in the south and the patrilineal Equatorial Bantu in the north. Being unusually well described, they shed considerable illumination on the process whereby the transition from the one to the other form of social organization has occurred in this general region." Perhaps the Nkundo would have to be coded 'none of the above', but it is clear that their system provides substantial brother, if not matrilineal, inheritance. The case for the Huichol is not as clear. Movable property goes to children, but real property goes communally to a group of family members that probably, but not necessarily, contains brother(s)[33]. Accordingly, the Huicol were left out of the analysis.

To maximize sample size and variable dichotomy, the contrast for inheritance norms was made between: (1) societies that stipulate heirs necessarily related to male benefactors through females (heirs whose r to benefactor is relatively unaffected by low p), and (2) societies that exclude such heirs and stipulate only those heirs whose r to benefactor is highly affected by low p. Accordingly, societies were grouped into: (1) those with brother/matrilineal inheritance for either type of property (code 2, 3 or 6, where 6 has been checked—see above), or (2) those for which benefactor's own children are the only stipulated heirs for both types of property (code 4, 5 or 7).

Broude and Greene[15] have coded frequency of extramarital sex for females as: (1) universal, moderate, and (2) rare, not common[34]. As would be predicted by the paternity hypothesis, the appropriate cross-tabulation (Fig. 3) indicates an association between relatively frequent female extramarital sex and a cultural norm that allows men to designate heirs whose relatedness is relatively unaffected by low probability of paternity.

It is assumed that the behaviours relevant to this analysis have little heritability across same-sex individuals within a society, and negligible heritability by sex across societies—that is, it is presumed that differences in individual behaviour are phenotypic responses to different conditions, that the behaviours in question have been too important for too long for there to be much genetic variance left, and that extant within-sex genetic variance is an irrelevant variable (compare refs 26, 35 with 36).

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Sustained potentiation of transmitter release by adrenaline and dibutyryl cyclic AMP in sympathetic ganglia

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Cyclic AMP[1] is known to mediate actions of various hormones and neurotransmitters in a variety of cells[2–5]. Its physiological role, however, in the transmitter release mechanism of vertebrate synapses is still controversial[6–9]. We report here evidence for the sustained, acceleratory effects of adrenaline and dibutyryl cyclic AMP on transmitter release in bullfrog sympathetic ganglia. The amplitude and quantal content of the fast excitatory postsynaptic potential (e.p.s.p.) and the frequency of miniature excitatory postsynaptic potential (m.e.p.s.p.) increased markedly for a long time after pretreatment with adrenaline or dibutyryl cyclic AMP. These results suggest a significant modulatory role for adrenaline, presumably linked with a cyclic AMP system, in the transmitter release mechanism, which may serve as a mechanism for neuronal plasticity in the peripheral autonomic nervous system.

The ninth or tenth paravertebral sympathetic ganglia of the bullfrog (*Rana catesbeiana*) were isolated. B-type neurones were studied using a conventional intracellular recording technique[10]. Microelectrodes were filled with 3 M KCl or 1 M K_3-citrate (tip resistance 25–100 MΩ). The fast e.p.s.p. generated by the nicotinic action of acetylcholine (see ref. 11) was recorded in a low Ca^{2+}–high Mg^{2+} solution (Ca^{2+} 0.7–0.9 mM, Mg^{2+} 5.4–6.5 mM). The quantal content of the fast e.p.s.p. was calculated by both the variance and failure methods[12] and the average taken; m.e.p.s.ps were recorded in a high-K^+ (10 mM) solution. The composition of normal Ringer was described previously[10] and experiments were done at 20–24 °C.

Figure 1 shows the effects of adrenaline on the fast e.p.s.p. Perfusion of the sympathetic ganglion with a solution containing adrenaline (100 μM) decreased the amplitude of the fast e.p.s.p. ($65 \pm 7\%$ (s.e.) of the control, $n = 5$) and its quantal content