

## Matriliny as daughter-biased investment

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### Abstract

From an evolutionary perspective, matriliney presents a puzzle because men in matrilineal societies transmit wealth to their sisters' sons, to whom they are only half as related as to their own sons. It has been argued that such systems would only maximise fitness under unrealistically high levels of paternity uncertainty. In this paper, we propose that matriliney can arise from daughter-biased investment by parents and/or grandparents. We show that daughter-biased investment is adaptive if the marginal benefit of wealth to sons (compared to daughters) does not outweigh the risk of nonpaternity in sons' offspring. We argue that such conditions will be rare where resource-holding polygyny is prevalent but could otherwise be widespread under even moderate levels of paternity uncertainty. The daughter-biased investment model explains two well-known characteristics of matrilineal descent: (a) matriliney's association with high levels of paternity uncertainty and (b) matriliney's ecological correlates, including its association with horticulture, its rarity in pastoralist and agro-pastoralist societies, and the tendency for matriliney to be replaced by son-biased inheritance during economic development. We present data on wealth, sex, and reproductive success (RS) in two African societies, the matrilineal Chewa in Malawi and patrilineal Gabbra in Kenya, which support the daughter-biased investment theory. © 2003 Elsevier Science Inc. All rights reserved.

*Keywords:* Matriliney; Parental investment; Sex-bias; Wealth inheritance

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## 1. Introduction

Matriliney is an uncommon but recurrent type of social organisation found in all regions of the world; in the Standard Cross-Cultural Sample, 31 of 186 societies (17%) are matrilineal (Murdock & White, 1969). In matrilineal societies, relatedness through females is treated as culturally more significant than relatedness through males. Most altruistic behaviour, including transfer of group membership, wealth, and political titles, is directed towards matrilineal kin (Schneider & Gough, 1961). Men transmit wealth and political rights to their sisters' sons. From an evolutionary perspective, matriliney presents a puzzle, because men are only half as related to their sisters' sons as to their own sons (Alexander, 1974; Greene, 1979; Hartung, 1981, 1985). This conflicts with the prediction of kin selection theory that, given equal costs and benefits, altruism will be directed towards relatives with the highest relatedness, usually offspring (Hamilton, 1964a, 1964b).

Matrilineal societies tend to be horticultural, i.e., farmers without plough agriculture or large domestic livestock. Aberle (1961) investigated the ecological correlates of matriliney in 565 societies worldwide. Of 84 matrilineal societies in his sample, 47 (56%) were horticultural compared to 19 (23%) that were pastoralist or agro-pastoralist. Forty-seven of 188 horticultural societies (30%) were matrilineal compared to 19 of 242 pastoralist or agro-pastoralist societies (8%). The association between horticulture and matriliney was highly significant. Aberle (p. 676) concluded that:

Although it would be unsafe to assume that horticulturally based societies lacking large domesticates or the plough are likely to be matrilineal, it would be reasonable to assume that matrilineal systems are likely to be 'dominantly horticultural.'

Foraging showed a less clear pattern; there was a slight tendency for foraging societies to be matrilineal rather than patrilineal but this effect may have been an artefact of Galton's problem (non-independence among several matrilineal Native American cultures). From these results, Aberle (1961, p. 680) argued that matriliney tends to be incompatible with subsistence types other than horticulture, especially with large domestic livestock. As he put it, "the cow is the enemy of matriliney." Although the results of Aberle may be questioned because cultures are not independent units for statistical purposes, Mace and Holden (1999) performed a phylogenetically controlled analysis testing for a negative correlation between matriliney and cattle in Africa, and replicated Aberle's results. The available cross-cultural data therefore indicate that a majority of matrilineal cultures are horticultural, and that a negative correlation between pastoralism and matriliney exists, even after controlling for phylogenetic effects.

A second characteristic of matrilineal societies is that they tend to have lower levels of paternity confidence than patrilineal societies. Using ethnographic evidence such as the reported frequency of adultery and divorce in 288 societies worldwide, Flinn (1981) found that matrilineal societies generally have low levels of paternity confidence compared to patrilineal societies. Other comparative studies have also found that matriliney is associated with low paternity confidence (Gaulin & Schlegel, 1980; Hartung, 1981, 1985). Quantitative genetic studies comparing levels of nonpaternity in patrilineal and matrilineal societies remain to be done.

In this article, we propose that matrilineal social structure can arise from daughter-biased wealth inheritance and other forms of altruism by parents and/or grandparents. We present data on wealth, sex, and reproductive success (RS) in two African societies, one patrilineal and one matrilineal, which support the daughter-biased investment theory. Daughter-biased parental investment has received little attention in the matrilineal literature, either in the classic ethnographic studies (Richards, 1950; Schneider & Gough, 1961) or in more recent evolutionary analyses (Flinn, 1981; Gaulin & Schlegel, 1980; Hartung, 1981, 1985), which focussed almost exclusively on male political rights and inheritance. The Ethnographic Atlas, a cross-cultural database of 1267 cultures, does not even include a code for wealth inheritance to daughters; only 4 societies (0.3%) are noted as having mother to daughter land inheritance, compared to 163 (13%) with matrilineal descent (Murdock, 1967). But despite its neglect in the anthropological literature, land inheritance by daughters is the norm in some matrilineal societies in Africa (Davison, 1997; personal observation by the authors) and in some Native American cultures (Murdock, 1967).

We suggest that daughter-biased grandparental or parental investment is an adaptive strategy when the risk of paternity uncertainty among sons' offspring outweighs the marginal benefits of wealth inheritance to sons. Daughter-biased investment is more likely to be adaptive when resources, such as livestock that increase sons' RS more than daughters' RS, are absent. The daughter-biased investment model may therefore explain matriliney's association with high levels of paternity uncertainty as well as the ecological correlates of matriliney, including its association with horticulture and its rarity in pastoralist and agropastoralist societies.

## 2. The paternity uncertainty hypothesis

One theory for matriliney is that, if paternity uncertainty is high, then men could have a higher probabilistic relatedness to their sister's children than to their own putative offspring, making it adaptive for men to invest in their sisters' children (Alexander, 1974). However, paternity uncertainty needs to be extremely high before a man is, on average, more related to his sister's children than to his wife's children. Greene (1979) showed that the probability of paternity,  $P$ , must be less than .268 before a man is more related to his sister's children than to his own putative children. This calculation takes into account the impact of  $P$  on the probability that a man and his sister have different fathers. Hartung (1985) suggested that matrilineal inheritance might be an adaptive long-term male strategy, because over several generations a man's probabilistic relationship to his patrilineal descendants decreases geometrically as  $P$  is multiplied each generation. If  $P < .725$ , then a man's probabilistic relationship to his great grandson is lower than his probabilistic relationship to his third generation matrilineal heir. If  $P < .46$ , then a man's cumulative relationship to six or more generations of his sister's sons is higher than his cumulative relationship to six or more generations of his own sons. However, it remains unclear why the short-term strategy of investing in sons, with higher short-term benefits, would not invade the population. Moreover, a probability of paternity less than .268 or even .46 is probably lower than the actual level in most matrilineal societies.

### 3. Daughter-biased grandparental and parental investment

As an alternative hypothesis, Hartung (1985) suggested that matriliney might be a grand-maternal strategy—investing in daughters' children. This is adaptive for grandmothers if there is any degree of paternity uncertainty (if  $P < 1.0$ , which is probably true in virtually all societies). However, this leaves open the question of how a strategy that is adaptive for grandmothers but has costs for men can persist, when men are politically dominant in most human societies.

The answer to this question may lie in the fact that, as grandfathers, men can also benefit from investing in their daughters' children (Flinn, 1981; Hartung, 1985). Both grandparents have a higher probabilistic relatedness to their daughters' children than their sons' children. For women, relatedness ( $R$ ) to daughters' offspring is  $.25$ , to sons' offspring  $R = .25P$ . For males, to daughters' offspring  $R = .25P$ , to sons' offspring  $R = .25P^2$ .

Female-biased investment may be directed by parents towards their daughters, or by grandparents towards their daughters' children. Direct inheritance of property to daughters occurs in some matrilineal societies, for example, daughters inherit land in matrilineal regions of south central Africa, including large parts of Malawi, Zambia, and Mozambique (Davison, 1997), and in Native American cultures including the Arikira, Hidatsa, Mandan, and Zuni (Murdock, 1967). In other matrilineal societies, property is transferred from the mother's brother to his sister's son (Schneider & Gough, 1961). For grandparents, this is equivalent to inheritance by their daughters' offspring. This type of inheritance allows sons to use inherited resources during their lifetime, while ensuring that those resources are ultimately transferred to the daughters' children.

Studies of general solicitude to kin by grandparents, aunts and uncles have shown a matrilineal bias in many societies (Euler & Weitzel, 1996; Gaulin, McBurney, & Brakewell-Wartell, 1997) although not universally (Pashos, 2000). However, wealth inheritance to daughters is rare, probably because of the additional benefits of wealth to sons compared to daughters. Wealth often has more effect on male RS than female RS; in such cases, parents will maximise their inclusive fitness by transmitting wealth to sons (Hartung, 1976, 1982; Mace, 1996; Trivers & Willard, 1973).

Sex bias in human wealth inheritance is often expected to follow the pattern predicted by the Trivers–Willard hypothesis, namely that high quality mothers will bias their parental investment towards sons, whereas low quality mothers will bias their parental investment towards daughters (Trivers & Willard, 1973); more recent models suggest that high quality mothers should also bias their investment towards daughters if offspring quality is highly heritable from the mother (Leimar, 1996). For nonhuman species, the Trivers–Willard hypothesis has mainly been studied in relation to sex ratio at birth (Clutton-Brock, Albon, & Guinness, 1984; Keller, Nesse, & Hofferth, 2001), but human studies testing for a Trivers–Willard effect have mainly investigated other types of parental investment such as breast-feeding or education (Bereczkei & Dunbar, 1997; Boone, 1989; Cronk, 1991; Keller et al., 2001). The Trivers–Willard hypothesis rests on the assumption that the relative return on investment in sons versus daughters differs between rich and poor parents (Hrdy & Judge, 1993). This is not always the case for inherited wealth in human societies. Where inherited

wealth increases sons' fitness more than daughters' among both rich and poor, all parents may maximise their fitness by transmitting wealth to sons (Hartung, 1997; Keller et al., 2001). This can be true even for poor parents whose daughters have higher average fitness than their sons, as illustrated by the case of the Gabbra (Mace, 1996), discussed below.

#### 4. A model predicting the direction of parental sex-bias

Son-biased wealth inheritance is usually an adaptive strategy for parents because inherited wealth has a stronger effect on the RS of sons than daughters (Hartung, 1982; Trivers & Willard, 1973). But parents need to balance the potential benefits of wealth to sons against the risk that a son might be cuckolded by his wife and that a nonrelative might then inherit their property. For property that is durable through the generations, inheritance to sons risks benefiting nonrelatives in subsequent generations.

We suggest that the direction of parental sex bias (whether to sons or daughters) therefore depends on two factors: the probability of paternity,  $P$ , and the additional benefits of inherited wealth to sons relative to daughters ( $B_S/B_D$ , where  $B_S$  is the benefit of a unit of wealth to a son,  $B_D$  the benefit to a daughter). These two factors are related as shown in Fig. 1. The benefits of wealth to sons and daughters are equal if:

$$B_S/B_D = 1/P.$$

If  $B_S/B_D > 1/P$  (above the curved line on the graph), then it is adaptive to give wealth to sons; if  $B_S/B_D < 1/P$ , then it is adaptive to give wealth to daughters. In other words, wealth inheritance to daughters is adaptive if the additional benefit of wealth to sons does not compensate for the risk of nonpaternity in sons' offspring.

This model can account for the association between matriliney and paternity uncertainty. High levels of paternity uncertainty will tend to push parents towards daughter-biased investment, to avoid the risk of their wealth being inherited by nonrelatives if their sons are cuckolded. This model can also account for the association between matriliney and horticulture and the negative correlation between matriliney and livestock. We predict that if the benefits of wealth to males and females are equal, daughter-biased inheritance will be preferred because of the risk of paternity uncertainty. However, any resource that benefits sons more than daughters will tend to increase parental bias towards sons. A heritable resource could benefit sons more than daughters for several reasons. There may be resource-based competition among males for women; this may be particularly strong in polygynous societies but in monogamous societies men may also use wealth to compete for high-quality wives or extra-marital partners. Sons may also be able to defend inherited resources better than daughters. Parents may also favour inheritance to sons if a woman's resources are liable to be used by her husband to further his own reproductive or political interests (Hrdy & Judge, 1993).

The negative correlation between matriliney and livestock probably arises because livestock benefit sons significantly more than daughters. Livestock are vulnerable to raiders, requiring male defence. In many African societies, livestock are also used for bridewealth, a marriage payment from the groom or his family to the bride's family that enables men to marry.

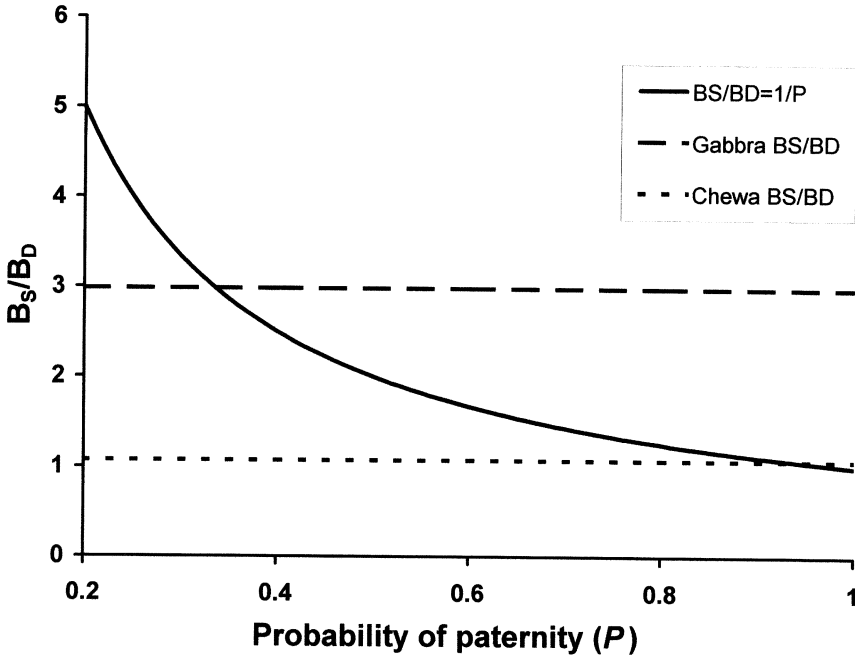


Fig. 1. Direction of parental sex-bias. The vertical axis shows the ratio of the benefit of inherited wealth to sons ( $B_S$ ) and daughters ( $B_D$ ). The horizontal axis shows the probability of paternity ( $P$ ). The solid black line  $B_S/B_D = 1/P$  shows when it is equally adaptive to invest in sons' and daughters' children. For values above this line, it is adaptive to invest in sons; for values below this line, it is adaptive to invest in daughters. Broken lines show empirically derived values of  $B_S/B_D$  for two African societies, the Gabbra (dotted line) and Chewa (dashed line). The point where these lines cross the solid line ( $B_S/B_D = 1/P$ ) shows the critical value of  $P$  needed to make daughter biased wealth inheritance adaptive in that society ( $P < .36$  in the Gabbra,  $P < .94$  in the Chewa).

Livestock can be highly productive, with low labour costs apart from the need for defence against raiders. Owning a herd of livestock enables men to support several wives, a human form of resource-holding polygyny (Hartung, 1982; Orians, 1969).

Although there is a negative cross-cultural correlation between matriliney and livestock (Aberle, 1961; Mace & Holden, 1999), livestock do not always lead to the loss of matriliney. We argue that it depends on whether livestock have marginal fitness benefits to sons. One exception to the rule that pastoralist societies are rarely matrilineal is the Tuareg in North Africa, who are highly pastoralist yet mainly matrilineal. Unusually among African societies, the Tuareg practice also monogamous marriage (Murdock, 1967), which may reduce the fitness benefits of wealth to sons. (We expect that resource-holding polygyny will tend to increase  $B_S/B_D$  and thus son-bias in wealth inheritance, although the marginal benefit of wealth to sons is probably still considerable in many monogamous societies that have son-biased wealth inheritance.) Flinn (1981) estimated that paternity confidence in the Tuareg was "moderate," i.e., below average in a worldwide sample. We hypothesise that matriliney may be an adaptive strategy for the Tuareg, even though they are pastoralists, because they practice monogamous marriage and have relatively high paternity uncertainty.

Land can also benefit sons if it is highly productive, enabling a man to support several wives, or scarce, so that a man without land would be at a disadvantage when attracting a wife. These conditions probably occur mostly in societies with intensive farming and plough agriculture. In many African horticultural societies with hoe agriculture, land was traditionally abundant but not very productive. Labour rather than land limited harvest sizes. Land may not have been worth the effort of male defence, or else men were unable to monopolize land, forcing women to marry them for access to it. Where land is poor, unproductive and abundant, its benefits for sons and daughters may be similar, in which case we would expect land inheritance to be biased towards daughters and daughters' children.

Matriliny tends to be replaced by son-biased inheritance under conditions of economic development. Economic development often brings an increase in inequality in wealth, which is likely to increase men's reproductive variance, especially in polygynous societies. This will increase the benefits of inherited wealth for sons relative to daughters. Conditions of increased scarcity and competition for resources may also increase the additional benefits of wealth to sons, as land becomes a valued resource (Douglas, 1969). Examples of transitions from matriliney to son-biased wealth inheritance under conditions of economic development include the Lodogaba in West Africa (Goody, 1962), Gold Coast cocoa-farmers (Hill, 1963), the Plateau Tonga in southeast Africa (Colson, 1958) and Mwinilunga cash-crop farmers (Turner, 1957) (all cited in Douglas, 1969). In some modern societies, more equal wealth inheritance to sons and daughters is also found (Judge & Hrdy, 1992). This may be because women are more able to defend their wealth in modern societies, and also because socially imposed monogamy reduces male reproductive variance and the marginal benefit of wealth to males (Hartung, 1997).

## 5. Testing the model in two African societies

We tested the predictions of the daughter-biased investment model (Fig. 1) in two African societies, the Gabbra and the Chewa. The Gabbra are nomadic camel herders who live in Northern Kenya. They are patrilineal with son-biased wealth inheritance. The Chewa are horticulturalists who live in Southern Malawi. They are matrilineal, with about 75% of land inherited from mother to daughter. The main productive resources in these societies (livestock and land respectively) are inherited rather than individually accumulated. From the model (Fig. 1), we predicted that the benefits of inherited wealth would be higher for males than females in the Gabbra, but similar for males and females in the Chewa. We tested this by comparing the effect of household wealth on male and female RS in the two societies.

### 5.1. Methods

Mace (1996) collected data on Gabbra men's and women's reproductive histories and household wealth during 1993 and 1994. The number of camels per household was the most important measure of wealth in this society. Residual fertility, a measure used to control for

the effect of age on fertility, was calculated for all men and women. Residual fertility was calculated by obtaining the average number of children born per individual in 5-year age groups, then subtracting this figure from the actual number of children born to each individual. Residual fertility of 0 indicates that the fertility of the individual is equal to the average fertility for his or her age group.

For each sex, residual fertility was regressed against the number of camels in the household. As the livestock data were skewed, with the majority of individuals having few camels, this variable was log transformed before performing the regression analysis, so individuals with no camels were excluded from the regression model. We have also performed the analysis without logging the data, with all individuals in the analysis, but this did not make a significant difference to the results.

During 1997, Sear collected data on men's and women's reproductive histories and household wealth in a Chewa lakeshore village in the Southern District of Malawi. Garden size was the most important determinant of wealth in this community. Residual fertility for each sex was calculated and regressed against the size of the garden farmed by the household. Again, the wealth variable was log transformed.

We tested whether the regression slopes for fertility on wealth were significantly different for men and women in the Gabbra and the Chewa by running a single equation that included terms for both sex and units of wealth (camels or garden size), as well as an interaction term between sex and wealth. A significant interaction between wealth and sex indicates that wealth has a different effect for men and women in a society.

To estimate the level of paternity confidence ( $P$ ) that would be necessary in each society to make wealth inheritance to sons or daughters adaptive, we calculated the relative benefit of wealth to sons ( $B_S/B_D$ ) by dividing the regression slopes for men and women for the Gabbra and Chewa.

## 6. Results

Data on wealth and residual fertility for the two sexes in the Gabbra and Chewa are summarised in Table 1. Regression slopes for residual fertility regressed against wealth are shown in Fig. 2. In the Gabbra, for both men and women, there was a significant positive relationship between number of camels and residual fertility, but the slope of the relationship was much steeper for men than for women [men: residual fertility =  $-0.556 + 1.118\log(\text{no. camels})$ ,  $P < .001$ ,  $n = 516$ ; women: residual fertility =  $-0.165 + 0.375\log(\text{no. camels})$ ,  $P < .023$ ,  $n = 1033$ ]. In the Chewa, there was a significant relationship between garden size and residual fertility for both sexes, but in contrast to the Gabbra, the shape of the relationship was virtually identical for men and women [men: residual fertility =  $-0.311 + 0.883\log(\text{garg}(\text{garden size}))$ ,  $P < .014$ ,  $n = 745$ ; women: residual fertility =  $-0.287 + 0.826\log(\text{garden size})$ ,  $P < .005$ ,  $n = 1070$ ].

Running a regression with an interaction term for sex and wealth shows that the slopes for males and females are significantly different in the Gabbra but not in the Chewa. For the Gabbra, there were significant main effects of both number of camels and sex on

Table 1  
Wealth and residual fertility of men and women in the Gabbra and Chewa

(a) Gabbra						
No. of camels	<i>n</i>	Men		<i>n</i>	Women	
		Mean residual fertility	S.D.		Mean residual fertility	S.D.
0	88	−0.53	1.54	174	−0.35	1.69
1	70	−0.26	1.94	134	−0.25	1.92
2	92	−0.3	1.84	184	0.05	1.7
3	54	−0.2	1.56	114	−0.07	1.8
4	77	−0.05	1.84	137	0.09	1.61
5	66	−0.06	1.75	138	−0.01	1.81
6	38	0.53	2.37	64	0.36	1.83
7	23	0.21	1.49	44	0.003	2.06
8–9	21	0.27	1.81	35	0.26	1.89
10–19	62	1.05	2.06	152	0.3	1.91
20+	13	0.97	3.24	31	0.003	2.42

(b) Chewa						
Garden size (acres)	<i>n</i>	Men		<i>n</i>	Women	
		Mean residual fertility	S.D.		Mean residual fertility	S.D.
<1	10	−0.44	2.26	13	−0.37	2.39
1–1.9	166	−0.17	2.26	257	−0.18	2
2–2.9	306	−0.06	2.14	451	−0.1	2.04
3–3.9	130	0.24	2.34	171	0.17	2.5
4–4.9	75	0.47	1.96	103	0.51	2.33
5–5.9	30	0.008	2.67	37	0.08	2.19
6+	28	0.47	2.34	38	0.11	1.92

For illustrative purposes, each population is divided into wealth categories, based on number of camels for the Gabbra and garden size for the Chewa (Column 1). The sample size (*n*), mean residual fertility and standard deviation (S.D.) for each wealth category are shown for men and women in each population.

fertility, as well as a significant interaction between the two variables. This indicates that, as predicted, in the Gabbra the relationship between wealth and fertility is different for the two sexes [residual fertility =  $-0.165 + 0.375 * \log(\text{camels}) - 0.390 * \text{sex} + 0.743 * \log(\text{camels}) * \text{sex}$ ,  $P = .026$  for camels,  $P = .049$  for sex,  $P = .012$  for interaction term]. For the Chewa, the single regression equation found that wealth was the only predictor of fertility in this population [residual fertility =  $-0.287 + 0.826 * \log(\text{garden}) - 0.024 * \text{sex} + 0.0564 * \log(\text{garden}) * \text{sex}$ ,  $P = .005$  for garden,  $P = .899$  for sex,  $P = .903$  for interaction]. Again as predicted, in the Chewa, the relationship between wealth and fertility is not significantly different for males and females.

The relative benefit of wealth for males compared to females ( $B_S/B_D$ ) in the Gabbra and Chewa is shown in Fig. 1. Although in our regression models (Fig. 2) the data were

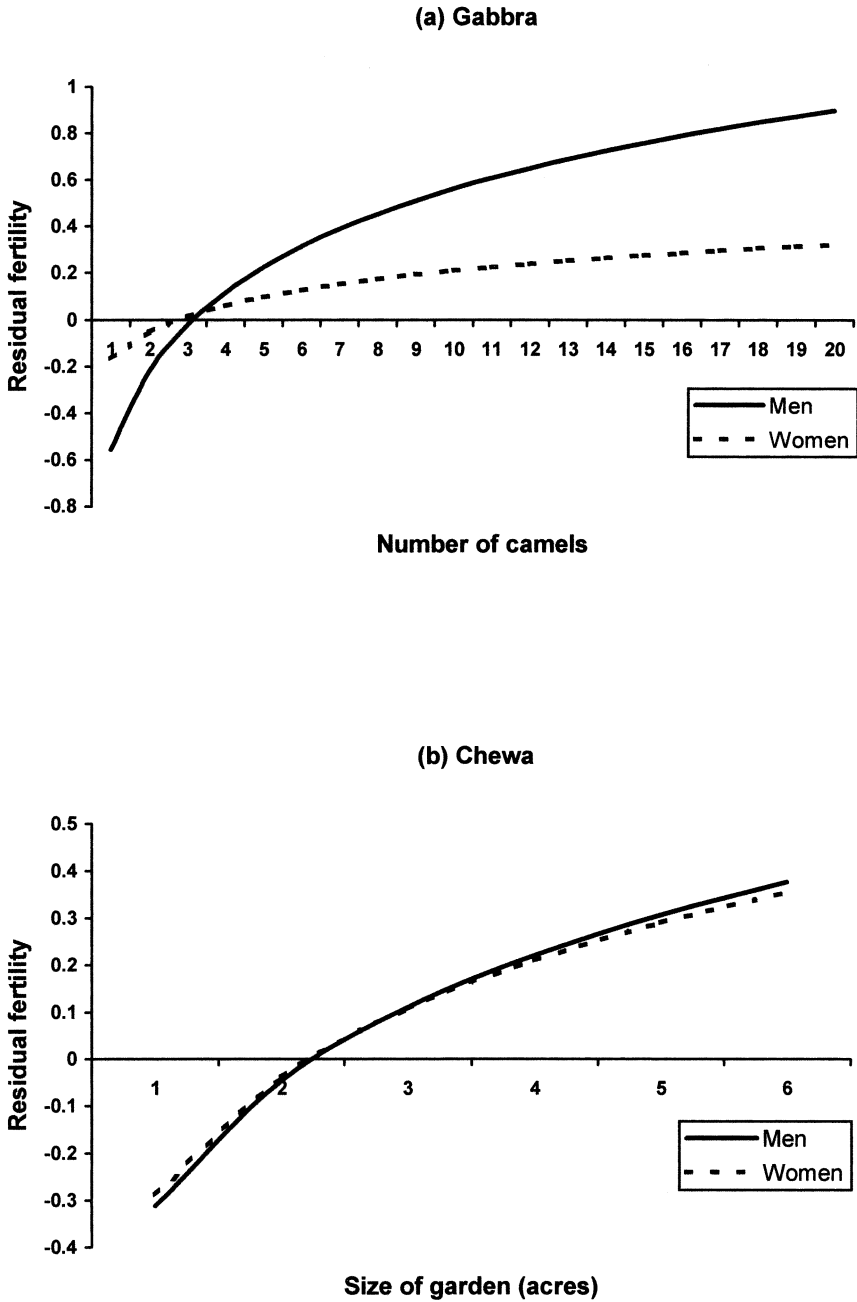


Fig. 2. Relationship between wealth and fertility for men and women in the patrilineal Gabbra in Northern Kenya and the matrilineal Chewa in Malawi. The graph for the Gabbra was re-drawn using data previously published in Mace (1996).

logged, the regression lines were straight so the ratio of the slopes ( $B_S/B_D$ ) is a constant. In the Gabbra, the benefit of wealth to sons is 2.98 times higher than to daughters, so the probability of paternity,  $P$ , would have to be less than .36 for daughter-biased investment to be adaptive ( $B_S/B_D = 1.118/0.375 = 2.98$ , critical value for  $P = 1/2.98 = .36$ ). In the Chewa, the benefit of wealth to sons is only 1.069 times higher than to daughters, so daughter-biased investment is adaptive if  $P$  is less than .94 ( $B_S/B_D = 0.883/0.826 = 1.069$ , critical value for  $P = 1/1.069 = .94$ ).

Relating to the previous discussion regarding the Trivers–Willard hypothesis, Fig. 2a shows that poorer Gabbra males, who live in households with only one or two camels, have lower RS than poor females. However, the positive effect of wealth on RS, shown by slope of the line, is stronger for males than females even in the poorest households. Therefore, even the poorest parents will increase their number of grandchildren more by transmitting their camels to sons. In societies like the Gabbra, it might be adaptive for a poor parent to bias the sex ratio of his offspring towards daughters if he could (Trivers & Willard, 1973), but still transfer any heritable wealth to his sons (Hartung, 1982, 1997; Keller et al., 2001; Mace, 1996).

## 7. Conclusion

We have argued that matriliney can arise from daughter-biased investment by parents or grandparents. To predict the direction of parental sex bias, both paternity uncertainty and the additional benefits of wealth to sons must be considered (Fig. 1). Daughter-biased investment is adaptive if the additional benefit of wealth to sons does not outweigh the risk of nonpaternity in sons' offspring. Direct daughter-biased wealth inheritance is rare but it does occur. More commonly in matrilineal societies, wealth is inherited from the mother's brother to the sister's son. This could be called grandparental daughter-biased investment. From the grandparents' point of view, this means their son benefits from the wealth during his lifetime, but it is then transferred to their daughter's children.

The daughter-biased investment model (Fig. 1) accounts for two well-known characteristics of matrilineal descent: first, matriliney's association with high levels of paternity uncertainty (Flinn, 1981; Gaulin & Schlegel, 1980; Hartung, 1981, 1985) and second, matriliney's ecological correlates, which include its association with horticulture, its rarity in pastoralist and agro-pastoralist societies, and its tendency to be replaced by son-biased inheritance under conditions of economic development (Aberle, 1961; Douglas, 1969; Mace & Holden, 1999). The level of paternity uncertainty in matrilineal societies is probably not high enough to make it adaptive for men to invest in their sisters' offspring (Greene, 1979; Hartung, 1985), but it is high enough to make grandparents favour their daughter's offspring (Euler & Weitzel, 1996; Gaulin et al., 1997; Hartung, 1985). Relatively low paternity confidence is probably also a consequence as well as a cause of matriliney.

Why has daughter-biased parental investment previously been absent as a possible explanation for matriliney (e.g. Flinn, 1981; Gaulin & Schlegel, 1980; Hartung, 1981, 1985)? The answer is probably that most classic ethnographies of matrilineal societies

focussed on men, and political rights such as succession to the status of Headman (Richards, 1950; Schneider & Gough, 1961). Wealth inheritance to daughters is rarely described in the anthropological literature, even in matrilineal regions such as south central Africa where land inheritance to daughters is the norm (Davison, 1997).

As far back as 1877, Morgan recognised paternity uncertainty and heritable wealth as underlying causes of matriliney and patriliney respectively. He recognised that paternity uncertainty led to matrilineal descent, which he believed to be the original human state. He hypothesised that the development of heritable forms of wealth, such as domesticated animals and improved land, led to the loss of matriliney and the adoption of patriliney across cultures worldwide.

After domestic animals began to be reared in flocks and herds, becoming thereby a source of subsistence as well as objects of individual property, and after tillage led to the ownership of houses and lands in severalty, an antagonism would be certain to arise against the prevailing form of gentile [i.e. matrilineal] inheritance, because it excluded the owner's children, whose paternity was becoming more assured, and gave his property to his gentile [i.e. matrilineal] kindred... With property accumulating in masses and assuming permanent forms, and with an increased proportion of it held by individual ownership, descent in the female line was certain of overthrow, and the substitution of the male line equally assured (Morgan, 1877, p. 345).

Morgan's model of cultural evolution in progressive stages was quite different to a neo-Darwinian evolutionary approach. In the behavioural ecological approach used here, matriliney and patriliney are viewed as flexible, adaptive responses to the environment, rather than as stages in cultural evolution. Nonetheless, the two factors Morgan identified, heritable wealth and paternity uncertainty, remain central to our understanding of variation in matriliney and patriliney in human social organisation.

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