

Paternal investment and the human mating system

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Abstract

Paternal investment has long been considered responsible for the evolution of predominantly monogamous marriage in humans. However, male–male competition resulting in mate-guarding and male coercion could be equally important. In this review, I use a comparative approach to examine the effect of variation in human paternal investment on our mating system. I conclude paternal investment is important but so too is mate-guarding. I propose a model of our mating system incorporating both factors. Variation in the mating system is explained by variation in male resource control and contribution, resulting in ecologically imposed monogamy or polygyny, as predicted by the polygyny threshold model, as well as variation in male–male competition for status, resulting in socially imposed monogamy or polygyny. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Human monogamy has long been attributed to our sexual division of labor and a need for paternal investment, given our long period of offspring dependence (Westermarck, 1929; Morris, 1967; Lovejoy, 1981). More recently, this ‘paternal investment theory’ has been challenged on theoretical and empirical grounds (Hiatt, 1974; Smuts and Gubernick, 1992; Hawkes et al., 1995; van Schaik and Paul, 1996). Monogamy may be the consequence of mate-guarding by one or both sexes (Gowaty, 1996; Hawkes et al., nd.), or males preventing food theft (Wrangham et al., 1999), or

infanticide (van Schaik and Dunbar 1990; Palombit 1999), and/or male sexual coercion (Mesnick, 1997; Wilson and Mesnick, 1997). Here, I am not as concerned with the origin of marriage as with how variation in paternal investment and other factors influence our mating system. To evaluate this, I use a comparative approach and look at variation across human societies by mode of subsistence to analyze important ecological variation.

By paternal investment, I mean: (1) direct care, such as holding and grooming infants, and proximity to children, which might reflect baby-sitting, as well as; (2) indirect care, which here I restrict mainly to provisioning (male contribution to subsistence). There are few data on other potential types of care such as teaching or arranging marriages. In Section 2, I briefly review relevant sex-

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ual selection theory. In Section 3, methods are outlined. In Section 4, I describe ecological variation and paternal investment across subsistence modes. In Section 5, I analyze variation in our mating system in relation to variation in paternal investment. In Section 6, I propose a model of our mating system. Finally, in Section 7, I draw conclusions.

2. Theory

Mating systems are the outcome of sexual selection due to differential investment in gametes (anisogamy) and parental care. Parental investment in one offspring usually subtracts from investment available for others, including future offspring, thus parental effort subtracts from mating effort (Trivers, 1972). The sex that invests more usually has the lower potential reproductive rate, benefits less from mating effort, and is the sex in demand (Clutton-Brock and Parker, 1992). The mating system is also influenced by the operational sex ratio (OSR) (Kvarnemo and Ahnesjö, 1996). For example, when many males compete for few females the result is less likely to be harem polygyny than (1) increased monogamy; or; (2) promiscuity and sperm competition. But the OSR is itself influenced by parental investment. Even if there are equal numbers of adult males and females, many females are not ovulating when they are pregnant and lactating (high maternal investment), and male–male competition should be intense for those few who are. When the number of copulations per conception increases, however, each copulation should be contested less (Mitani et al., 1996).

Without paternal investment, the mating system is largely determined by female spacing, which in turn constrains male access to females (Emlen and Oring, 1977). If resources come in spatially heterogeneous, rich patches and predators are a threat, females should form groups, and males can achieve polygyny if they can exclude other males, which becomes more difficult as the number of females increases (Nunn, 1999). If resources are of low quality and evenly distributed, females may do better to be solitary, and a male might

not be able to monopolize more than one female. When there is paternal investment, however, it too influences the mating system. For example, in a few bird species, paternal care is greater than maternal care, females compete for access to males, and the result is polyandry (Reynolds, 1987).

If some offspring survive with care from only one parent, it may pay the other parent to desert, and because paternity confidence (PC) is lower than maternity confidence in species with internal fertilization, males might be more likely to desert (Trivers, 1972). Maynard Smith (1977, 1978) argued, however, that it is the effect of paternal investment on offspring survivorship and the effect of desertion on re-mating, not PC, that determines whether a male should stay or desert. If desertion enhances a male's chance of re-mating, it may pay him to desert, but the mean PC for the population does not affect the relative advantage of staying or deserting since it applies equally to present and future offspring.

In reality, not all males within a population have the same PC, so the potential gain in offspring survivorship from providing care varies across individuals within a population. However, if males provide care only to gain sexual access to females, they may be indifferent to PC (Smuts and Gubernick, 1992). In birds, manipulation of paternity causes males of some species, but not others, to reduce feeding, suggesting variation in the relevant PC cues, or in the degree to which provisioning is facultative (reviewed in Wright, 1998). Nonetheless, across bird species, the more essential paternal investment is for offspring survival, the higher is PC, and the greater is paternal provisioning (Birkhead and Moller, 1996).

Among many species of birds, offspring are dependent on bi-parental provisioning and 90% of species are socially monogamous (Lack, 1968). Even though we now know that many bird species are less genetically monogamous than once thought, it appears that social monogamy often results from a female forming a bond with a male who will help her rear her offspring (Black, 1996). On the other hand, when males defend territories, the quality of the territory determines how many females can be supported. If a male's territory can

support two females as well as others can support one, the polygyny threshold has been reached (Verner and Willson, 1966; Orians, 1969), and this is called ‘resource-defense polygyny’. Rather than defending resources, in many mammals, a male may defend his females directly, which is called ‘harem-defense polygyny’.

Men can take advantage of gossip and monitoring by kin and friends to help them guard women, thus harem-defense polygyny might not be the best term to use for human mate-guarding even though it is essentially the same thing. I will therefore use the term socially imposed monogamy or polygyny. When human marriage is not explained by the polygyny threshold, it could be due to male: (1) status competition; (2) mate-guarding; (3) coercion, or to female; (4) gene-shopping; (5) preference for socially dominant males; and (6) preference for a bodyguard. It is difficult to tease these apart since they can theoretically work together to push the mating system in the same direction. For this reason, I will simply focus on male-mate status competition and mate-guarding (haremdefense), and distinguish this from resource-defense and the polygyny threshold.

3. Methods

To analyze variation in human paternal investment and the human mating system, I used the Standard Cross-Cultural Sample of 186 societies, chosen to provide an unbiased sample of the world’s ethnographically described societies (Murdock and White, 1980). There are problems inherent in the comparative method beyond sampling bias. There is the problem of assessing causation using mean values of traits for groups, overlooking potentially important within group variation. Nonetheless, the comparative approach is a powerful way to look for patterns in the data. The coding of data in the Standard Cross-Cultural Sample is mostly based on readings of ethnographies and rarely on original, quantitative data. Nevertheless, these data should not be systematically biased and significant results should be valid.

Codes used for variables of interest are described in Appendix A. Mode of subsistence (Murdock and Morrow, 1980) and political organization (Tuden and Marshall, 1980) were used to reflect important ecological variation such as resource control. Father–infant and father–child proximity (Barry and Paxson, 1980) were used as proxies for direct care. Mate contribution to subsistence, and time spent in subsistence activity (Whyte, 1980) were used as measures of provisioning. Social stratification (Murdock and Provost, 1980), ranging from egalitarian to class structure, was used to reflect variation in male status. Value placed on aggressiveness in males (Whyte, 1980) was used to gauge something about male–male competition and coercion. Degree of polygyny (Murdock and Wilson, 1980) was used to reflect the mating system, as was frequency of women’s extra-marital affairs (Whyte, 1980).

There are various ways of measuring degree of polygyny (Low, 1988a). Here, the percent of males polygynously married is used. This is not the best measure to capture the degree of sexual selection because it does not tell us whether polygynous males have two wives or ten. Percent of females polygynously married is a better measure (Hartung, 1982) but, unfortunately, has not been scored for many societies. Since most associations tested were the same using either measure, percent of polygynously married males should be sufficiently reliable to assess the relative degree of polygyny across societies. I have scored degree of polygyny in a way that reflects the relative breeding sex ratio of societies. That is, I assume the ratio of breeding males to females is highest for a society classified as having polyandry, followed by monogamy, then slight polygyny (< 20% of men polygynous), and finally general polygyny (> 20% of men polygynous).

Subsistence was categorized into the following four modes. (1) Hunter–gatherers, henceforth called foragers ($n = 42$) are those who practice no agriculture, or acquire less than 10% of their diet from cultivated foods; (2) Horticulturalists ($n = 70$) are those who acquire the majority of their diet from agriculture but not intensive agriculture; (3) Pastoralists ($n = 17$), are those who acquire the majority of their diet from their domestic animals;

(4) Agriculturalists ($n = 57$) are those who practice intensive agriculture with the plow, irrigation, and/or fertilizers. There are only a couple of societies among agriculturalists that might be considered industrial states. For comparison, therefore, I have added my own description of

them at the bottom of Table 1. All correlations reported are Spearman's rho unless otherwise specified.

4. Ecological variation and paternal investment

Mode of subsistence accounts for considerable variation in the level of paternal investment, mating system, and related traits (Table 1). The four subsistence modes represent important ecological variation in resource control. Resource control affects carrying capacity, population density, and stratification, and thus the relative status of men and their ability to gain mates. Since foragers exploit wild plant and animal foods, they do not control their resources, are nomadic, have low population densities, and are usually egalitarian. Horticulturalists have control of resources though their simple technology does not permit the accumulation of much surplus wealth. Even so, their population density rises, accompanied by greater variation in male status. Pastoralists control their resources since they own livestock, and have low population densities since they are usually nomadic to move their herds, which can vary considerably in size, resulting in wealth but usually not class distinctions. Agriculturalists are sedentary, control resources, and produce surplus wealth, which results in high population density and social stratification (Table 1, Fig. 1).

Women reside with their husband's kin (virilocality) in 63.4% of societies. Among foragers, however, virilocality is less common (48%) (Fig. 2), post-marital residence is often flexible and best described as multilocal (Ember and Ember, 1983), and descent bilateral (traced through both parents). Once wealth exists and there is stratification, post-marital residence tends toward virilocality (Table 1). Virilocality means males stay with their kin, allowing them to control resources when subsistence is based on defendable resources, to accumulate wives, and to pass wealth on to sons who can use it to acquire wives. This may account for the correlation between virilocality and stratification ($r = 0.203$, $P = 0.005$, $n = 186$) and men's time in subsistence activity ($r = 0.212$, $P = 0.048$, $n = 87$).

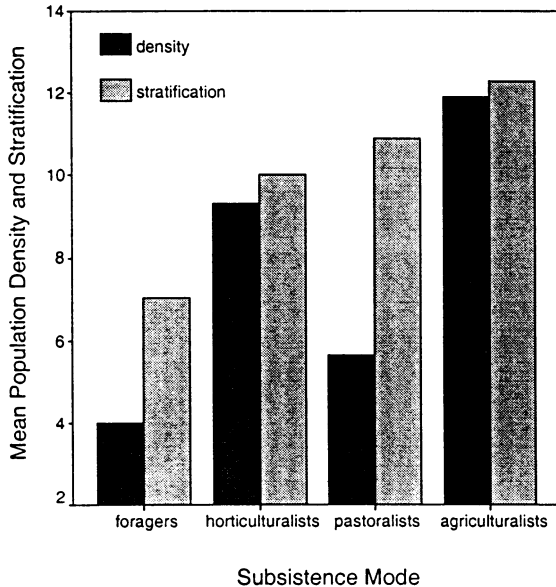


Fig. 1. Population density and social stratification by subsistence mode, converted to same scale ($n = 186$).

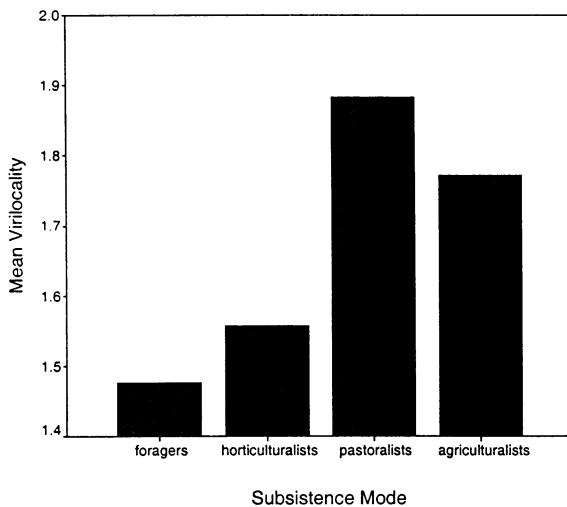


Fig. 2. Degree of virilocality by subsistence mode ($n = 186$).

Table 1
Mean level of traits related to the human mating system by subsistence mode (The Standard Cross-cultural Sample)

Subsistence	Wealth variation	Residence	♂ Direct care	♂ Provisioning	♀ Affairs	Mating system
Foragers	None	Multilocal	High	Moderate/high	Moderate	Ecol. Imp. Mon./Soc. Imp. Polyg.
	Social stratification = 1.40	Virilocality = 1.48 (48% of societies). Population density = 0.33	Father–infant proximity = 3.2.9. Father–child proximity = 3.72	Contribution to subsistence = 4.50. Time spent in subsistence = 1.74	Women's affairs = 1.94 (SD = 0.83)	Monog. = 10% . Slight polyg. = 69%. Gen. polyg. = 21%
Horticulturalists	Low/moderate	Viri./uxorilocal	Moderate	Low	High	Socially imposed polygyny
	Social stratification = 2.00	Virilocality = 1.56 (56% of societies). Population density = 2.1	Father–infant proximity = 3.16. Father–child proximity = 3.42	Contribution to subsistence = 3.81. Time spent in subsistence = 1.70	Women's affairs = 2.52 (SD = 3.82)	Polygyny = 3.23. Polyan. = 1%. Monog. = 13%. Slight polyg. = 47%. Gen. polyg. = 39%
Pastoralists	High Social stratification = 2.18	Virilocal	Low	Very high	High	Polygyny threshold
		Virilocality = 1.88 (88% of societies). Population density = 0.88	Father–infant proximity = 2.69. Father–child proximity = 3.33	Contribution to subsistence = 5.00. Time spent in subsistence = 2.00	Women's affairs = 2.22 (SD = 0.67)	Polygyny = 3.12. Polyan. = 6%. Monog. = 18%. Slight polyg. = 35%. Gen. polyg. = 41%
Agriculturalists	Very high Social stratification = 2.46	Virilocal	Low	High	Low	Polygyny threshold
		Virilocality = 1.77 (77% of societies). Population density = 2.96	Mean infant proximity = 2.81. Father–child proximity = 3.29	Contribution to subsistence = 4.61. Time spent in subsistence = 2.27	Women's affairs = 1.39 (SD = 0.67)	Polygyny = 2.98. Monog. = 26%. Slight polyg. = 49%. Gen. polyg. = 25%
Industrial states	High/moderate	Neolocal	Moderate	Moderate	High	Soc. Imp. Mon.

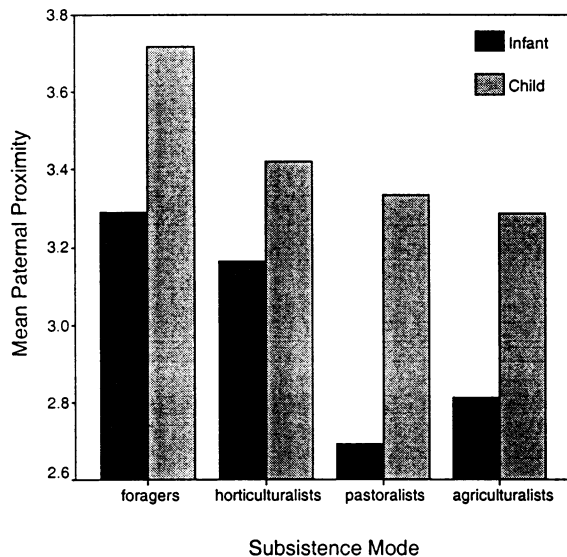


Fig. 3. Father–infant and father–child proximity by subsistence mode ($n = 139$).

4.1. Direct care

Fig. 3 shows how father–infant and father–child proximity varies by mode of subsistence. Foragers have the highest level of father–infant proximity, followed by horticulturalists, then agriculturalists, and lastly pastoralists. Father–child proximity varies similarly, except that proximity is higher for pastoralists than agriculturalists. The amount of time forager men spend holding infants varies from 1.9–22% of daylight hours (Marlowe in prep). Because couples spend so much time net hunting together, Aka Pygmy men in the Central African Republic held infants far more than men in any other society (Hewlett, 1991). Among Hadza foragers of Tanzania, with whom I work, men held infants 5.4% of the time they were in camp, compared to women’s 22% (Marlowe, 1999a). Across societies, men’s interaction with their children is about 25–35% that of the mother, but as the child gets older the discrepancy decreases (Lamb et al., 1985), partly because level of direct care declines with child’s age. Though men devote a much lower percentage of time to direct care than women do, it is high by primate standards. Furthermore, among foragers, men are

often near their children and baby-sit toddlers while mothers are out foraging. Hadza men, for example, are near their biological children (8 years old and younger) 11.6% of the day and sleep with them at night, providing protection during 12 h of darkness (Marlowe, 1999b).

Men in agrarian societies tend to provide less direct care than do men in foraging societies. For example, in four agrarian societies studied, fathers held infants (3–18 months old) 0% of the time among the Black Carib of Belize, Logoli of Kenya, and Samoans of American Samoa, and 3% among the Newar of Nepal (Munroe and Munroe, 1992). Among the horticultural Yanomamo, men provided very little direct care, especially polygynous men (Hames, 1992), and Ye’kwana men provided less direct care than did children’s siblings (Hames, 1988). Among most pastoralists, where men own livestock, a woman’s decision to marry a man probably depends more on the size of his herds than his direct care, thus it is not surprising that pastoralist men have the lowest level of proximity to infants. In industrialized societies, direct care may be higher than it is in the mostly pre-industrial agricultural societies in the Standard Cross-Cultural Sample. From self-reports, men in the U.S. interacted with their children (0–5 years old) 3.6% of daylight hours (Pleck, 1983), and interaction time has been increasing slightly over the past few decades (Lamb, 1987).

4.2. Provisioning

Fig. 4 shows the level of male contribution to subsistence (provisioning) across subsistence modes. Male provisioning is highest among pastoralists and lowest among horticulturalists. The reason male provisioning is low for horticulturalists is that women perform most of the garden labor once land has been cleared. Male provisioning is high among pastoralists where men usually own and control the livestock. Among agriculturalists, men also usually own land and livestock, but women also work in the fields as well as the house.

Among foragers, male contribution to subsistence varies from 25–100% (Kelly, 1995) Ap-

pendix A (though exactly how this is measured is not always the same). Because there is less edible plant food for women to gather in colder climates, male contribution is higher at higher latitudes, 87% in the Arctic, 67% in temperate climates, and 48% in the tropics (Hiatt, 1974) and inversely correlated with effective temperature (Pearson's $r = -0.61$, $P < 0.01$, $n = 70$) (Kelly, 1995). The importance of paternal provisioning was probably

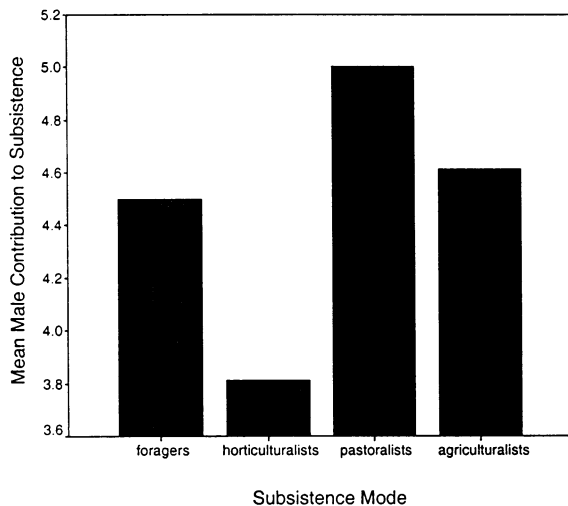


Fig. 4. Male contribution to subsistence by subsistence mode ($n = 92$).

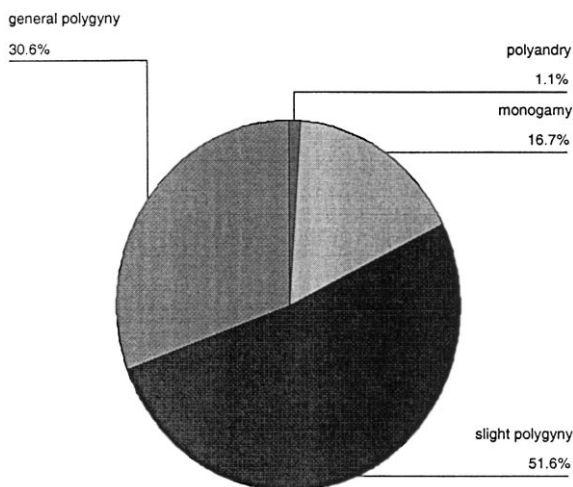


Fig. 5. The human mating system in the Standard Cross-cultural Sample ($n = 186$).

overemphasized in the past, but recently the pendulum may have swung too far in the other direction. While there are some foraging societies in which men contribute 100% and women 0% to subsistence, there are none where men contribute 0% (Kelly, 1995), and in 77% of societies men contribute more than women (Ember and Ember, 1983). In addition, there is no reason male contribution to subsistence (over and above personal consumption) must be over 50% to represent a benefit to females, and therefore to influence the mating system.

Male contribution to subsistence among foragers, unlike contribution among agrarian societies, is much less clearly paternal provisioning. This is because the foods that most forager males acquire are widely shared outside the household (Hawkes, 1990). In forager camps everyone usually lives in close proximity with little family privacy. When males acquire large food packages like big game, everyone in camp often receives roughly equal shares. If all households receive the same amount of food, variation in male contribution may not lead to variation in direct benefits to the wife of a good hunter and thus its effect on the mating system is less straightforward.

5. The mating system

Despite the considerable cross-cultural variation in our mating system, marriage is a human universal. Across societies, polyandry is rare (1%), polygyny is common (82%), but the majority of marriages (even in polygynous societies) are monogamous (Murdock, 1967). In 17% of societies, polygyny is prohibited or extremely rare (Fig. 5). Among foragers and other stateless societies it is almost always allowed, yet its frequency is lower than among mid-range and early (small) state societies (Fig. 6). In large states (which are agriculturalists), the few males at the very top taking large numbers of females, at least until monogamy is legally imposed. Because degree of polygyny drops for agriculturalists, who have the highest degree of stratification, these two variables are negatively correlated. However, if we look only at foragers and horticulturalists (with one

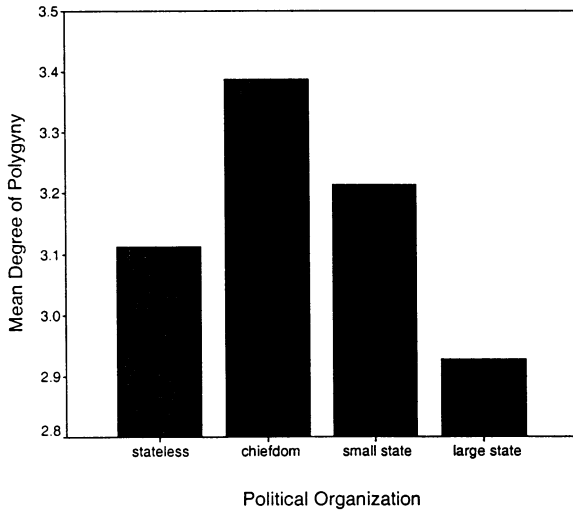


Fig. 6. Degree of polygyny by political organization ($n = 184$).

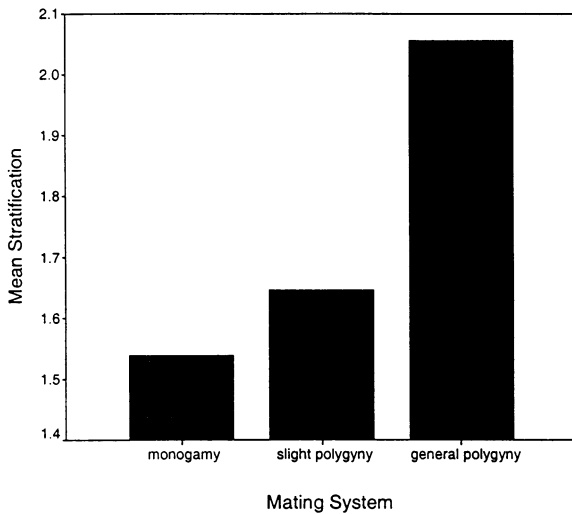


Fig. 7. Social stratification by mating system for foragers and horticulturalists ($n = 111$).

polyandrous society excluded), social stratification, which should reflect degree of variation in male status, is positively correlated with degree of polygyny ($r = 0.225$, $P = 0.017$, $n = 111$) (Fig. 7).

A few societies, such as the Nyinba of Nepal, practice polyandrous marriage among brothers, which has often been explained as a response to a shortage of land and/or male labor sufficient to make a monogamous household viable (Levine

and Silk, 1997). Polyandry may be more common than the percentage of polyandrous societies implies, since we now know of societies, such as the Ache, where many men have been polyandrously married at some time. In addition, people in several other South American societies such as the Bari, Canela, Mundurucu, and Mehinaku believe it takes the semen of several men to produce a baby (Beckerman et al., 1998; Hrdy, 1999). In two of these 'partible paternity' societies, the Bari (Beckerman et al., 1998) and Ache (Hill and Hurtado, 1996), children with more than one father had lower mortality, presumably due to greater provisioning. While this may seem exotic, it is perhaps not so different from the very common situation of U.S. children receiving support from both their biological father and current stepfather. As long as the biological father contributes child support, such children might well gain by having two fathers.

Fig. 8 shows the variation in the degree of polygyny by mode of subsistence. Note that it is highest for horticulturalists, where men contribute the least to subsistence, which raises the question of how horticultural men achieve this. The answer is suggested by Fig. 9 and Fig. 10, which show the effect of paternal investment on the mating system. Fig. 9 illustrates the negative correlation between degree of polygyny and father–infant proximity ($r = -0.199$, $P = 0.013$, $n = 154$). Controlling for mode of subsistence and male contribution in a linear regression, father–infant proximity is still negatively related to degree of polygyny ($\beta = -0.222$, $P = 0.036$, $df = 71$). This inverse relationship between direct care and degree of polygyny is present for all modes of subsistence, and is to be expected, since we can assume men must trade off parenting for mating effort.

Much more interesting, and probably more important, is the negative relationship between degree of polygyny and male contribution to subsistence ($\beta = -0.323$, $P = 0.002$, $df = 90$) (Fig. 10), which exists within each mode of subsistence. There is also a negative relationship between degree of polygyny and men's time spent in subsistence activity ($\beta = -0.244$, $P = 0.023$, $df = 85$). Controlling for mode of subsistence and fa-

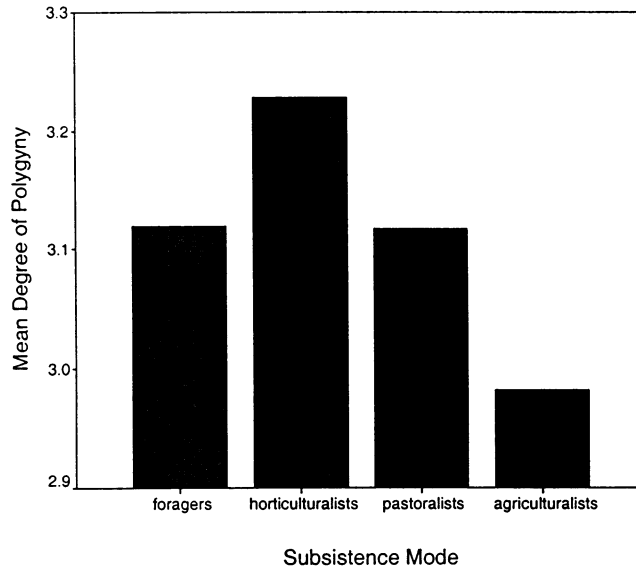


Fig. 8. Degree of polygyny by subsistence mode ($n = 186$).

ther–infant proximity, male contribution to subsistence is even more negatively related to degree of polygyny ($\beta = -0.412$, $P = 0.000$, $df = 71$).

At first glance, the negative correlation between degree of polygyny and male contribution to subsistence is perhaps counter-intuitive. I think this is because we tend to assume that where male contribution is greater, there would be greater variation in male contribution, which according to the polygyny threshold model should lead to greater polygyny. Mean level of male contribution to subsistence fails to capture the variation within a society. Nonetheless, mean level of paternal investment across societies tells us something important. The higher mean male contribution to subsistence, the more females will value male provisioning, and the more they do, the more female choice should push the mating system toward the polygyny threshold model. Therefore, if we assume variation in male contribution to subsistence within societies of the same subsistence mode to be equal (the null assumption), we ought to expect greater monogamy with greater average male contribution to subsistence.

While paternal investment has a clear effect on the human mating system, there is not one simple relationship between the two. For example, the

degree of polygyny is highest for horticulturalists where paternal investment (father–infant proximity + contribution to subsistence) is lowest, but also for pastoralists where paternal investment is highest (Fig. 11). In fact, when one polyandrous pastoralist society is excluded, the degree of polygyny is equally high among pastoralists and

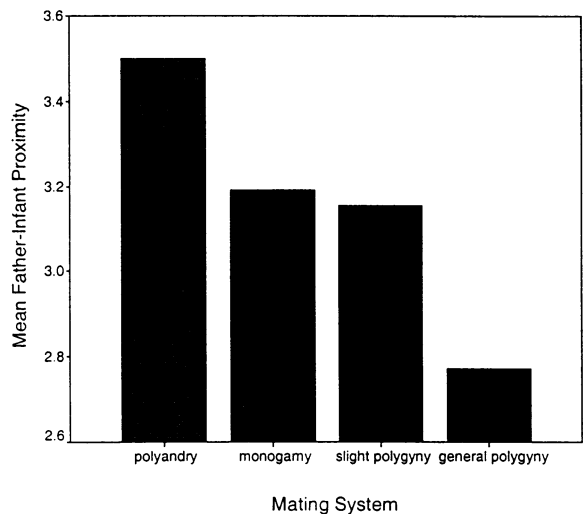


Fig. 9. Father–infant proximity by mating system ($n = 154$).

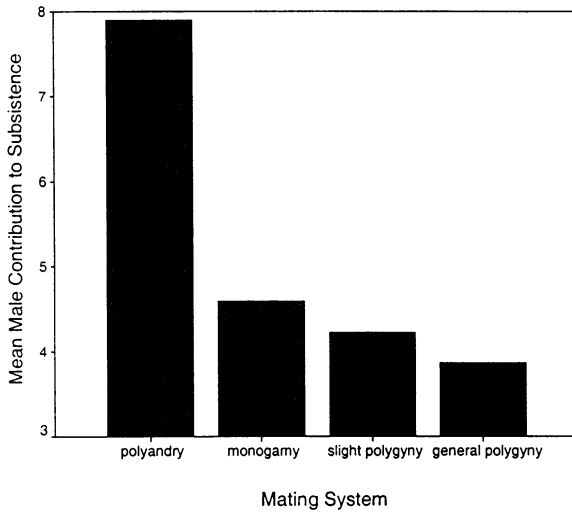


Fig. 10. Male contribution to subsistence by mating system ($n = 92$).

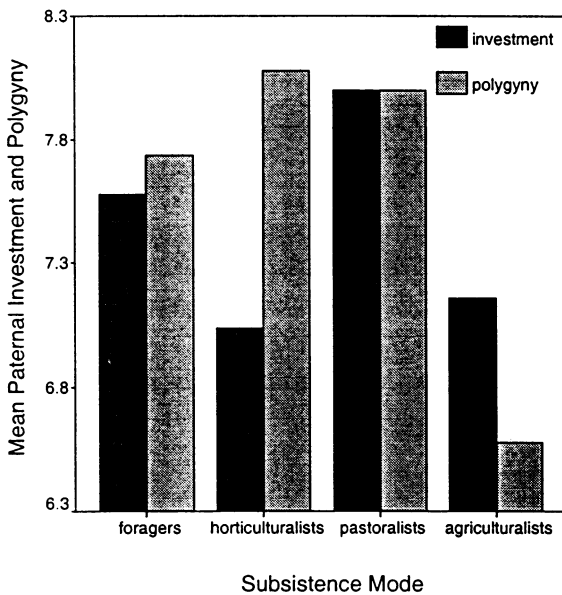


Fig. 11. Paternal investment (father–infant proximity + male resource contribution) and polygyny by subsistence mode, adjusted to same scale ($n = 77$).

horticulturalists. I argue this illustrates human polygyny results from two difference causes, the polygyny threshold, and harem-defense (social imposition). Polygyny among pastoralists, where men control herds and male status is tightly

linked to wealth, is due to the polygyny threshold. Among horticulturalists, where there is less variation in wealth and females do most of the subsistence labor, polygyny is due to male–male competition for status, rather than wealth, leading to harem-defense or socially imposed (even coercive) polygyny.

The polygyny threshold applies well to many societies where males can monopolize resources. Among Kipsigis agro-pastoralists, for example, men's wealth predicts their number of wives (Borgerhoff-Mulder, 1990). Given that marriages are arranged, we must ask whether this is because of female choice (parents' and daughters' interests overlap), or coercion from the bride's or groom's family. If polygyny results from female choice, the reproductive success of women in monogamous and polygynous marriages should be about equal (unless it is an inherent trait of wives). Consistent with female choice, among the Kipsigis, women married men who offered the best breeding opportunity (acres of land/wives + 1), regardless of the number of their wives (Borgerhoff-Mulder, 1990).

In contrast to the Kipsigis, women in polygynous marriages among the Temne of Sierra Leone had lower fertility than did women in monogamous marriages (Dorjahn, 1958). Among the Dogon of Mali, even though wealth and nutritional status were not significantly lower for children of polygynous parents, such children had higher mortality rates (Strassman, 1997). Hames (1996) found that polygynous households among the horticultural Yanomamo received more food from others than did monogamous households, presumably as payment to men who attain their higher status through political skills and leadership in warfare. Even so, this economic benefit was not enough to offset the division of resources among wives and reach the polygyny threshold.

Sororal polygyny may represent a compromise between male coercion and female choice, since co-wives who were sisters had fertility intermediate between monogamous and non-sororal, polygynous women in Arnhem land, Australia (Chisholm and Burbank, 1991). Josephson (1993) found that polygynously married Mormon women had fewer children but the same number

of grandchildren as monogamously married women because the children of high-status men had an advantage in obtaining mates, making up for the lower fertility of their polygynously married mothers. It might pay women to mate with polygynists, even if they receive fewer resources, as long as their sons are more likely to be successful polygynists and leave them many grandchildren (the sexy son hypothesis).

There is some evidence that direct male–male competition may have a stronger effect on the mating system than even paternal investment (Fig. 12). In a linear regression using father–infant proximity, male contribution to subsistence, and value placed on male aggressiveness (hereafter, male aggressiveness), the strongest predictor of degree of polygyny was male aggressiveness ($\beta = 0.459$, $P = 0.000$, $df = 65$), followed by male contribution to subsistence ($\beta = -0.368$, $P = 0.001$, $df = 65$). Since male contribution to subsistence and male aggressiveness are positively related to each other, yet male contribution is negatively, and aggressiveness positively related to degree of polygyny, the effect is not simply a result of

covariance. Male aggressiveness is also negatively correlated with father–infant proximity ($r = -0.330$, $P = 0.006$, $n = 69$), suggesting it might reflect mating effort. This effect of male–male competition on the mating system is also not an artifact of agriculture, since there are even stronger effects in the same direction for foragers alone (Beta for father–infant proximity = -0.395 , Beta for male contribution = -0.380 , Beta for aggressiveness = 0.562 , $df = 13$). Aggressiveness could be more the consequence than the cause of polygyny but since it is the strongest predictor of degree of polygyny it might be that it reflects the level of male–male contest or status competition and perhaps coercion driving the mating system.

The negative correlation between paternal investment and degree of polygyny implies that where men invest little, women are indifferent to, or prefer the winners of male–male competition or ‘good-genes males’. If women receive nothing from men but sperm we should expect them to choose men on the basis of genetic quality and mate polygynously. Even with some male investment, it may pay women to gene shop, perhaps more so where pathogens are prevalent, since there is a positive correlation between degree of polygyny and pathogen prevalence across cultures (Low, 1988b). Because women can gain from both resource-shopping and gene-shopping, they should desire both providers and good-genes males, but when they prefer physically attractive males, such males may invest less because they gain more from mating effort, as occurs in zebra finches (Burley, 1988, for humans, see also Waynforth, 1999). Consequently, the average female may have to compromise and settle for an average male. On the other hand, females may try to have it both ways by bonding with a ‘provider’ but mating with a ‘good genes male’ at ovulation. Such a strategy should be facilitated by concealed ovulation, continual attractiveness, and continual sexual activity, which might explain the evolution of these traits in the human female (Benshoof and Thornhill, 1979; Baker and Bellis, 1995; Gangestad and Simpson 1995 in press).

Concealed ovulation allows women to exchange sex for gifts, but also to potentially bias concep-

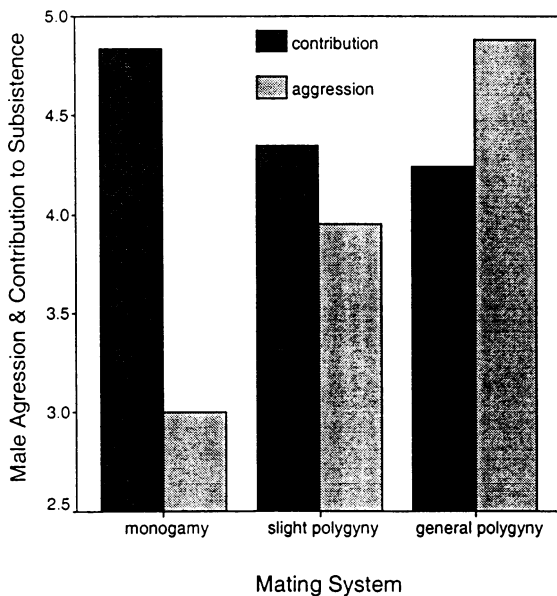


Fig. 12. Male contribution to subsistence and aggressiveness by mating system (two polyandrous societies excluded) ($n = 80$).

tion by strategically timing extra-pair copulation. Cuckoldry may be more costly in agricultural societies where females are more dependent on males, and men have law on their side. Cuckoldry may also be more difficult for women in most foraging societies than for women in industrial societies like the U.S. where there is greater privacy and anonymity, and greater legal protection (Marlowe in press). Estimates of genetic cuckoldry among humans range from 10% in a rural Midwestern U.S. community (cited in Smith, 1984), to 9% among the Yanomamo (Neel and Weiss, 1975), to less than 5% among Aka foragers (Hewlett, 1988), and 0–2% among the Ju/'hoansi foragers (Harpending pers comm).

Women's extra-marital affairs are highest (with a large SD) among horticulturalists (Table 1), where paternal investment is lowest and polygyny highest. Affairs are lowest for agriculturalists, which is probably due to the high level of resource shopping by agricultural females as suggested by the negative correlation between affairs and stratification. In a multiple linear regression, women's affairs were more frequent in less stratified societies ($\beta = -0.303$, $P = 0.007$, $df = 72$), and more frequent where male aggressiveness was lower ($\beta = -0.249$, $P = 0.026$, $df = 72$). Higher male aggressiveness could limit women's affairs by threatening wives and other men.

5.1. Divorce

If paternal investment is important, we might expect its impact on offspring survivorship to affect divorce rates (Hurtado and Hill, 1992; Emlen, 1995; Ens et al., 1996; Davis and Daly, 1997). The chance of an Ache child dying by age 2 when the parents divorced was 27.5%, compared to 15.9% when the parents stayed together (Hill and Kaplan, 1988). When Ju/'hoansi women had been married twice, their children were twice as likely to die as when they had been married only once (Pennington and Harpending, 1988). Of course it could be that offspring mortality is causing divorce, rather than the other way around. A test of four foraging populations revealed that mating opportunities, as reflected in fertility units ($OSR \times \text{Total Fertility Rate}$), ac-

counted for divorce rates better than did the effect of father's presence on offspring survivorship (Blurton Jones et al., 2000).

The OSR determines the bargaining power of the two sexes. If there are few available females, males might invest more in their wives. If there are many potentially good husbands, females might be more demanding and quicker to divorce. When marriage is lengthy, men should place a premium on the residual reproductive value of women. With increasing age a woman's value in the mating market will decline, restricting her marriage options. In addition, women have more difficulty getting remarried when they have a greater number of children, at least in Western cultures (Buckle et al., 1996). Women should, therefore, have little interest in divorce except to escape abusive, infertile, or polygynous marriages.

The more dependent females are on male resources the less willing they should be to divorce. Males, on the other hand, should never have an interest in divorce as long as their wives are fertile and they can keep adding wives. Of course, when a man's wife refuses to let him take on another wife, he may be interested in divorce if he can thereby gain a younger wife with greater residual reproductive value. Serial monogamy allows higher-quality/higher-status men to achieve polygyny as they age by having greater access to younger wives (Marlowe, 2000). The evolution of menopause means that the human OSR has become more male-biased, since a certain percentage of adult females is removed from the breeding population and it should pay some men to divorce older women. Menopause may have therefore increased human monogamy.

5.2. Culture

There is a strong effect of geographic region on many variables such as paternal proximity and degree of polygyny, even after controlling for other variables like mode of subsistence, stratification, and political organization, which suggests culture may be as important as ecology. The effect of cultural inertia, even long after humans migrate to different habitats may be a uniquely human trait, limiting our ability to explain as much of the

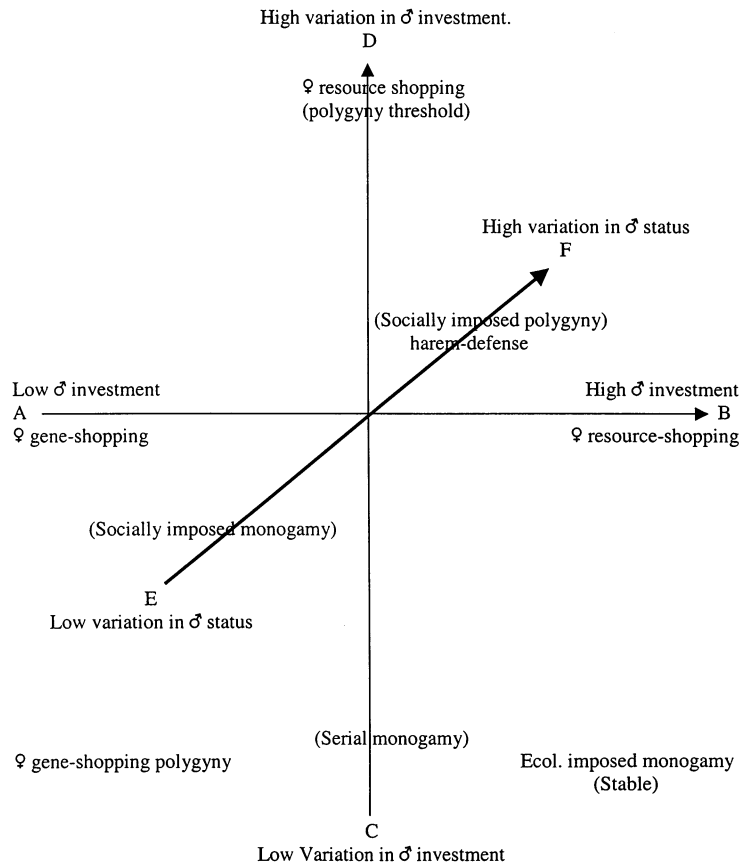


Fig. 13. A 3D model of the human mating system. Along one axis (C–D) is variation in male investment (direct care + provisioning). Along another axis (E–F) slanted and in bold to signify a 3rd dimension, is variation in male status. High variation in wealth but not status = socially imposed monogamy; high variation in status but not wealth = socially imposed polygyny. The higher male contribution is (A–B), the more dependent females are on males, and the lower is the divorce rate.

variation in the mating system with ecology as we can for other species. On one extreme is socially imposed polygyny, such as among Australian foragers, where over 40% of men could be married polygynously. Females were betrothed at birth in some Australian societies and marriages were arranged between high status old men, some of whom might obtain up to 10 wives, while younger men had none (Hart and Pilling, 1960; Goodale, 1971). The effective mating system may have been less polygynous, since there were affairs (Hiatt, 1996), but surely it was far more polygynous than that of most foragers. On the other extreme is socially imposed monogamy. In most state societies, wealthy men had many wives until egalitar-

ian movements forced them to share power, which resulted in socially (legally) imposed monogamy in many large states (Betzig 1986; MacDonald, 1995).

6. A model of the human mating system

Fig. 13 is a simple model of the human mating system. For the sake of simplicity, this model assumes an OSR of 1.0. Along one axis (A–B) is the extent of male investment (direct care + provisioning), which will influence the degree of female resource-shopping and dependence on males, and thus marital stability. However, even when male

contribution to subsistence is high, marital stability may be low if the effect of OSR (Hurtado and Hill, 1992), or an even distribution of male-acquired foods among females overwhelms the effect of high male investment. Along another axis (C–D) is the degree of variation in male investment or wealth. When males provide all income but some have much more than others, the richer males will achieve polygyny. When males provide all income but there is little variation, ecologically imposed monogamy prevails because the polygyny threshold is not reached. Where there is almost no male investment, females should gene shop and mate polygynously. When males provide an intermediate level of investment with little variation, females are only moderately dependent on males and the result is serial monogamy and slight polygyny.

Along a third axis (E–F), perpendicular to the other two, is variation in male status resulting from male–male competition. Often this axis correlates highly with variation in wealth (C–D), but it can vary independently. For example, when males provide no investment at all, and there is therefore no variation in investment, polygyny may result not only from female gene-shopping, but from male–male competition. Variation in male status could reflect variation in fighting and guarding ability, or political skills and kin networks, and can theoretically be independent of female choice. If there is little variation in wealth (e.g. no wealth) and low male contribution to subsistence, but great variation in status, there is harem-defense, or socially imposed polygyny. On the other hand, even when wealth varies, variation in male status can be minimized with laws against polygyny, which tend to accompany democratic movements, resulting in socially imposed monogamy, as in industrialized societies (Table 1).

7. Conclusion

Paternal investment is clearly one important factor explaining the prevalence of human monogamy. All else equal, the greater the level of paternal investment, the more monogamous the

mating system. This is because when paternal investment is high, it pays females to resource shop. Only if there is great variation in male investment, will the polygyny threshold lead to a more polygynous mating system. However, male–male status competition can override the effect of resource variation and lead to legally imposed monogamy, especially in industrial states. When paternal investment is low, other factors such as male–male status competition, mate-guarding, coercion, or female gene-shopping can lead to socially imposed polygyny. Our mating system can therefore only be understood in terms of both resource-defense and harem-defense polygyny.

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Appendix A

Hadza are listed as males contributing 20% to diet (Kelly, 1995) but my own data reveals it to be 45%, thus, the lowest male contribution to diet for any society is 25%. Codes from the Standard Cross-Cultural Sample:

Subsistence mode: 1 = foragers, those with < 10% of subsistence from agriculture; 2 = horticulturalists, those with > 10% of subsistence from agriculture but no intensive agriculture; 3 = pastoralists, those with more of subsistence derived from domestic animals than all other types combined; 4 = agriculturalists, those with more of subsistence from intensive agriculture (e.g. plow and irrigation), than all other types combined.

Population density: 0 = < 1/sq. mi.; 1 = 1–5/sq. mi.; 2 = 6–25/sq. mi.; 3 = 26–100/sq. mi.; 4 = > 100/sq. mi. *Social stratification*: 1 = egalitarian; 2 = wealth or slave distinctions only; 3 = 2 or more classes.

Political organization: 1 = stateless; 2 = chiefdom; 3 = small state; 4 = large state.

Virilocality: 1 = non-virilocal; 2 = virilocal.

Father–infant and father–child proximity: 1 = no close proximity; 2 = rare instances of close proximity; 3 = occasional or irregular close proximity; 4 = frequent close proximity; 5 = regular, close relationship or companionship.

Male contribution to overall subsistence: 1–8 (low to high, relative to female contribution).

Male time spent in subsistence activity: 1 = less than females; 2 = same as females; 3 more than females.

Degree of polygyny: 1 = polyandry; 2 = monogamy; 3 = slight polygyny (< 20% of men); 4 = general polygyny (> 20% of men).

Women's affairs: 1 = rare; 2 = not uncommon; 3 = common.

Value placed on male aggressiveness: 1 = little or no emphasis; 2 = moderate emphasis; 3 = marked emphasis.

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