

Ecological and Sociocultural Impacts on Mating and Marriage Systems

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1. Introduction

Among vertebrates, humans have some of the most diverse arrays of behaviors known. Consider mating systems: in most vertebrates, a species is characterized by a single mating system (although, if it is something other than polygyny, “extra pair copulations,” or EPCs, are likely to exist alongside the dominant pattern). Our mating arrangements, in contrast, are extremely diverse. Non-marital mating arrangements may be relatively open, and children acknowledged, or may be entirely clandestine. In most societies, arrangements are not simply the outcome of one man’s and one woman’s desires, but rather the culmination of negotiations by members of the older generation; an individual might be betrothed before birth to another not yet born, for example. Marriage itself typically involves the giving or exchange of goods (in some societies from the bride’s family to the groom’s; in others vice versa), and sometimes of women or of services. Perhaps only the Dunnock (*Prunella modularis*), a British little brown bird, exhibits within a single species (sometimes within a single population) mating diversity comparable to that of humans: there are monogamous pairs, polyandrous females with their mates, polygynous males with their mates, and polygynandrous groups of males and females, each of whom has multiple mates (Davies 1992).

Nonetheless, mating systems in other species tend to have not only ecological influences, but also more phylogenetic constraints than typical of human reproduction. For example: among mammals, because females are specialized for post-natal infant nutrition,

some form of polygyny is the default mating system; in many birds, because males may be able to assist in feeding, social monogamy (usually with EPCs; e.g., Reichard & Boesch 2003) is relatively common.

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1.2. Marriage *and* Mating

Not only do humans exhibit many mating arrangements, but we are also more complex than all other species in another aspect of our reproduction. We complicate matters: we have not only mating systems, but marriage systems, in which more than the simple reproductive interests of male and female may be important. Human marriage is a social institution involving societal rules about allowed number of spouses at any one time, allowable consanguinity in pair-bonds, allowable ages of mates, and so on.

This distinction between marriage versus mating highlights an extraordinary feature of our cultural life. Compared to other mammals, we are probably not unique in the ways we might expect. Social transmission—learning from others—is not even a peculiarly human phenomenon, although its importance to us is extreme. We have more complex social rules than other species (see Dunbar 2003, Hill and Dunbar 2003), and we have elaborated culture to such an extraordinary degree that cultural and genetic evolution are almost certainly linked in most human cultures (e.g., see Richerson & Boyd 2005). But there are predecessors in other species: other organisms exhibit complex and multilayered behaviors such as alliance formation in intragroup and intergroup conflict; moreover, other species can have reciprocal and rather complex “political”—coalitional—behavior. Humans have developed many such phenomena to new extremes, but it is rare to find unique human phenomena, without parallels or predecessors in other species (Alexander 1979). Yet though we may have few truly new or unique behaviors, we often exhibit behaviors that are unusual in their extremity.

In a few cases, we do appear to be unique in ways that are important to marriage patterns: namely, the complexity of “third party” interests. Other species, for example, exhibit territoriality; but an absent “owner” loses the territory. We go further and define property rights, in which the holdings of absent owners are supported and protected by (disinterested) third parties; our legal systems, in fact, are specifically concerned with third-party decisions that are accepted by a group as fair. With regard to mating and marriage patterns third party roles are well-defined in most societies (see below, and the chapter by Plotkin, this volume).

Here I wish to explore how human mating and marriage systems are affected by ecological conditions (e.g., the distribution, abundance, and defensibility of resources), by cultural practices, and by the interactions of these two forces. Given the great diversity in marriage rules and rules about association and sexual conduct across societies, it would be easy to throw up one's hands and regard these patterns as somehow "purely cultural." There are, however, often (sometimes non-obvious) influences of the distribution, abundance, and predictability of resources that shift the likelihood of success and persistence for different cultural systems.

Thus, cultural and genetic changes over time seem to be inevitably linked, and marriage rules lie at the heart of this phenomenon. But defining "culture" in a way useful to hypothesis-testing is difficult, and culture and genetics change in different ways. Under natural selection, genes are passed from parents to children, and may be passed intact, lost (failure to pass), or passed in a mutated form. Cultural beliefs and behaviors may be passed, lost, or changed as well—but they may be passed not only "down" but "up" (as parents acquire beliefs from their children, for example), transversely (as siblings learn from each other), and obliquely (as children learn from non-related teachers, or adults learn from younger non-relatives; Cavalli-Sforza & Feldman 1981, Boyd and Richerson 1985, Richerson and Boyd 2005). Our cultural practices are so deeply intertwined with all aspects of our lives and sociality that Richerson and Boyd (2005) argue that rather than culture being an emergent property of our evolution as a smart social ape (as was once thought), it is an intrinsic force helping shape human evolution.

Certainly it is true that cultural inventions feed back into social actions. Here, without attempting to define where things start and stop, I explore the mutual influences of

essential resources and cultural practice in testing hypotheses: What influences marital residence? Are dowry and bride price randomly distributed? What about infanticide, and discriminatory parental solicitude? In the face of such complexity, how resource conditions correlate with particular cultural aspects of mating and marriage systems is of interest. The underlying hypothesis is that the cultural institutions we see are those that, given the particulars of resource abundance, distribution, and economic defensibility, allow individuals in at least some lineages to profit both reproductively and (at least sometimes) in terms of physical resources.

1.3. Why Polygyny is Common

It is important to understand why polygyny is the default—likeliest, *ceteris paribus*—mating system among species that have gametic sexual reproduction, including humans. The “male-female phenomenon”—a consistent pattern of differences between males and females in behavior—is pervasive. There are two non-alternative reasons for this pattern, both resulting in profitability to making *either* large, or small, gametes (Epelman et al 2005, Hurst 1992, 1995, Hurst & Hamilton 1992, Parker et al 1972)—but not both. The evolution of anisogamy changes the costs and benefits for possessors of large, versus small gametes, and means that small-gamete-makers (“males”), barring unusual ecological circumstances, profit most by specializing in high-risk, high-gain mating effort. If they spend parental effort (Low 1978) it is likely to be of the generalizeable sort (e.g., watching for predators). In contrast, large-gamete-makers (“females”) have more to lose if an offspring is lost, and will specialize, *ceteris paribus*, in

parental behavior, which tends to have more linear returns for effort, and is often offspring-specific true parental investment (Trivers 1972).

Whenever females can raise offspring successfully without male assistance, the mating system is likely to be polygynous; males will concentrate their effort on seeking matings. A female and her dependent offspring will comprise the ecologically independent unit. Females will be able to raise offspring alone when the offspring are precocial (as in chickens and many other bird species), or when she can provide for an altricial (helpless) child by herself. The first is common in many birds, and the second is true of many primates (the mother nurses, carries and protects the infant, and while the father is often nearby and may occasionally play with the infant, he is primarily concerned with his own status and rank among males). When these conditions are met, by far the most common result is *female specialization in parental effort and male specialization in mating effort*.

For mammals, these biases are exacerbated, because females are physically and physiologically specialized for carrying the fetus internally, and for nourishing the offspring after birth. For both sexes in many mammals, five traits seem to contribute to reproductive success: age, body size, dominance rank, early development patterns (high early growth rate), and quality of mates chosen. For females, these typically contribute to getting good nutrition and converting it into healthy and successful offspring. For males, the payoff is typically greater mating success.

When males take risks in direct mating competition, they are likely to die sooner than females. Thus, for males, lifetime breeding success is most variable in species with direct conflict over mating access, whether by prolonged defense of territories (as in elephant seals) or in competition over single females (e.g., some butterflies). Male lifetime

breeding success tends to be least variable in species in which males compete indirectly, as in many human societies (more below).

2. The Resource Ecology of Primate Mating Systems

2.1. Polygyny

Underneath all the complex “add-ons” of our culture, we are primates; as Strier (2003) noted, primate studies can enrich our understanding of human systems. It is important to understand that ecological conditions (distribution of resources, safe cover, presence of predators, etc) set the stage for the particulars of solitary-versus-group living, and that they interact with phylogenetic constraints to yield different mating systems (e.g., Strier 2003). The result is rich patterned variation in the kind (e.g., all-female, all-male, mixed; kin, non-kin, mixed) and stability of groups. Within mammals, including primates, the fact that females are specialized to give post-natal nutritional care (nursing) means that there is a bias toward polygynous systems, but even within polygynous systems, resource distribution affects the type of polygyny. If reproductively useful resources are predictably abundant and economically defensible, there will be resource-defense polygyny (e.g., territoriality), as in the defense of birthing beaches by male elephant seals (e.g., Le Boeuf & Reiter 1988). Among primates, however, moving groups of either a single male with multiple females, or multi-male, multi-female groups are more common than resource-defense polygyny.

In most primates, because females and their young comprise an independent ecological/economic unit (see Strier 2003, Low 2000: Chapter 4 for an overview),

polygyny is the likeliest mating system. But the *kind* of polygyny is ecologically influenced. When the terrain is open, with little safe cover, predation risk is likely to be high—and groups will be larger than others that live in heavy cover.

About half of primate species live in multi-female groups. Females tend to distribute themselves in response to predation and food pressures and males, in turn, tend to distribute themselves around females (Altmann 1990, Ridley 1986; see also Strier 2003: chapter 5, Shuster & Wade 2003). Two major hypotheses for the formation of primate groups are: [1] avoiding predation through “selfish herd” groups (e.g., Cheney & Wrangham 1987, Hamilton 1971), and [2] defense of food by multifemale groups (e.g., Barton et al 1996, van Schaik 1996, 1989, van Schaik & Hrdy 1991, Wrangham 1980). It is not clear that these are true alternative hypotheses; both may operate.

Whether one or several males join a group of females depends, again, on ecological conditions. When predation pressure is high and food is rich, the likeliest result is multi-male, multi-female groups, as in savannah baboons. When predation is a risk, females are likely to forage in groups (e.g., Alexander, 1974) and the number of males in a group shifts with the number of females (e.g., Altmann, 1990, Mitani, 1996). Female group size (the number of females available) appears to be the primary determinant of the number of males in a multi-male group (Mitani et al 1996, van Schaik and Hörstermann 1994). In mountain populations of savannah baboons, males distribute themselves in an ideal free distribution in response to female availability (Henzi et al. 1998); further, they “herd” females when this will increase the distance between troops (and the likelihood of outsiders trying to join). Within multi-male groups, there is a strong correlation between male rank and reproductive success (e.g., review by Strier 2003:168-170), but there are some clear costs

to male reproductive striving: males who are mate-guarding feed less, and may suffer reduced energy intake (Alberts et al. 1996) When female groups are small, a single male may succeed in monopolizing the group (e.g., Mitai et al 1996), although again, if predation risk is high, even small groups of females may have multiple male consorts (van Schaik and Hörstermann 1994).

2.2. Monogamy and Polyandry

Monogamous, single-pair primates are rare. There are three hypotheses about the evolution of monogamy in primates. One simply argues that when two-parent care is markedly more effective than maternal care alone, monogamy will evolve (e.g., Kurland & Gaulin 1984, Wright 1984). The second suggests that monogamy evolves when mated males are able to protect their infants from infanticide by other males in the group (e.g., van Schaik 1996, van Schaik & Dunbar 1990, van Schaik & Paul 1996). The third suggests that for primates, as for many other species, ecological factors influence a male's ability to monopolize more than one female (e.g., Mitani 1984). There are clear ecological implications for each hypothesis; sadly, there have been few tests.

Polyandry is even rarer than monogamy. Some tamarins are polyandrous: females give birth to large twins (about 25% of the mother's weight), who also grow rapidly. Soon after birth they are so large that the mother cannot carry both. The reproductive unit most commonly comprises a female and two males; both males help care for the offspring, carrying it, playing with it, and protecting it. The "extra" male may be an unrelated male (in which case the female mates with both males) or a non-reproductive son who remains

with his parents (Terborgh and Goldizen 1985, Sussman and Garber 1987, Goldizen and Terborgh 1989).

2.3. Ecological and Social Interactions Affect Individual Traits

These mating arrangements, created by the ecology of resources, have a further impact on individual traits (Harvey and Harcourt 1984): individuals in pair-living monogamous, single-male polygynous, and multi-male polygynous species differ in extraordinary ways. Testis size, canine size, and male body size relative to female body size are all smallest in males living in monogamous arrangements. Males in single-male group species face high-risk, high-gain challenges from other males to fight for control of the females; they are physically much larger than females and have very large canines, as in gorillas.

Males in multi-male group-living species have a more subtle problem as well: other males are always about, sometimes in shifting coalitions. Sneak matings by other males in the group are, like overt fights, a serious problem. Males in such species are bigger than females (though not so strikingly as in single-male group species), have large canines, but also have extremely large testes. Here competition exists not only between individuals, but devolves to the level of sperm competition (e.g., see Dixson 1983, Dixson & Anderson 2004, Maestriperi & Roney 2005, Simmons et al 2004). Males in socially monogamous pair-living species are not much larger than females and have, relative to body size, the smallest canines and the smallest testes. The ecology of group living thus influences male-male competition—and secondarily body size, canine size, and testis size (Harvey and Harcourt 1984). Humans fit in the “multi-male polygynous group” portion of the

continuum (male body size moderately larger than female, testes relatively large), consistent with reports of 2-22% EPCs in socially monogamous as well as polygynous societies (Simmons et al 2004).

3. Human Ecology, Mating, and Marriage

As noted above, humans have elaborated on these basic ecological patterns: we have not only the complexity of genetic versus social mating systems, but we have *marriage* systems as well as *mating* systems, and these are not identical (e.g., Reichard & Boesch 2003, Betzig 1997). Human marriage is a social institution involving not just mating patterns but societal rules about number of spouses at any one time, consanguinity, ages of mates, and so on. Far more than the self-interest of potential mates is involved; in fact, in most societies, the prospective bride and groom may not make the choice of mate—others, usually male relatives, do. Some basic patterns in human mating and marriage systems reflect social solutions to ecological problems. Other patterns reflect [1] intensification of human sociality and intergroup conflict; [2] elaboration of non-parental (mostly nepotistic) care and associated shifts in human life history; and [3] extraordinary elaboration of non-kin “third-party” influences in human social patterns (Low 2003a). Each of these has important impacts on human mating and marriage systems.

3.1. Polygyny

For the reasons outlined above, under most ecological conditions, polygyny will be sought by males of most species. Humans are no exception: broad data about the prevalence of different marriage arrangements are found in Murdock’s *Ethnographic Atlas*

(1967), *Atlas of World Cultures* (1981), and Murdock and White's *Standard Cross-Cultural Sample* (1969). They suggest that about 83% of societies are polygynous, almost none (0.05%) are polyandrous, and those societies coded as "monogamous" are mostly "monogamous or mildly polygynous," and thus genetically polygynous. In part this may be because human males, for a variety of reasons, appear to have solved many problems that lead to monogamy in other primates without relinquishing polygyny. A man need not guard his wife if he has family (or eunuchs) to do so; mate guarding is clearly present and effective in many polygynous societies. Human residence patterns mean that men are able to monopolize multiple females under most conditions. Most societies are patrilocal, so that a man lives among his kin and a woman comes to live among her husband's kin. Groups of related males can effectively defend resources, including wives.

Environmental conditions correlate in interesting ways with marriage systems. In theory, one would expect fluctuations in major environmental variables (those that, like rainfall, may strongly influence certain resource availabilities) to be associated with increased variance in men's abilities to compete for resources, and thus polygyny. Further, when resources can be effectively garnered by women, the possibility of polygyny should be enhanced; that is, when women can provide the resources necessary for healthy children, men can concentrate their efforts into acquiring more wives (and the subsequent reproductive success that generates). In contrast, when a father must contribute true parental investment into his offspring, he has less available for mating effort. And indeed there appear to be some relationships. As rainfall becomes more constant, the degree of polygyny decreases, and the more women contribute to the subsistence base, the more polygynous the society is likely to be (Low 1990a).

3.1.1. Pathogens, Disease, and the Distribution of Polygyny.

In a curious interaction, the ecology of pathogen and disease transmission interacts with mating (and subsequently, marriage) systems. Hamilton and colleagues (Hamilton 1980, 1982, Hamilton et al 1990, Hamilton & Zuk 1982) argued that pathogens might provide the kind of environmental unpredictability that would foster the evolution of sex; subsequent work (Low 1988, 1990b) suggested that pathogens might also influence sexual selection. Indeed, if one examines the distribution of pathogens with the characteristics specified by Hamilton (life threatening, leaving a mark), there is an association with marriage rules. The pattern is not linear, because men are likely to seek polygyny whenever possible: it is simply that monogamy disappears in high-pathogen stress areas (Low 1990b).

Polygyny, no matter how it is measured, increases with the level of exposure to pathogens meeting Hamilton's criteria. Level of pathogen stress alone accounts for 28% of the variation in the degree of polygyny around the world, independent of geographic region or any other factor (Low 1988, 1990b, 2003a). Under high pathogen stress, a woman's best strategy may be to become the second or subsequent wife of a healthy man (a form of Orians' polygyny threshold; Orians 1969), because a successfully polygynous man has more children than a monogamous one. For men the situation is more complex. Across societies, most polygyny, for a variety of reasons, is sororal: men marry sisters. In areas of high pathogen stress, however, polygyny tends to both more common than in low-stress areas, and also non-sororal. In addition, the capture of women for mating is more common than in low-stress areas. Men may profit genetically from this shift: their children will not be more numerous, but genetically more variable—an advantage in the face of pathogen

stress (Low 1990). Here it is worth noting that, in several mammalian species, including humans, some male-female “matches” in the major histocompatibility complex (MHC), result in improved offspring immunocompetence. That is, rather than a uniform preference for “good genes” in this highly polymorphic region, there may be mate preferences (by both males and females) for mates who will produce more heterozygous offspring (e.g., Roberts et al. 2005, Jordan and Bruford 1998, Tregenza and Wedell 2000, Penn and Potts 1999, Potts et al 1991).

However, there are potential costs to polygyny in terms of other kinds of diseases and pathogens, principally from sexually-transmitted diseases. Charles Nunn and colleagues (Nunn et al 2000, 2003) found, in both primates and carnivores, that the prevalence of multiple matings correlated with heightened white blood cell counts (a reflection of increased disease exposure). They concluded that the risk of sexually-transmitted diseases may well be a major factor leading to systematic differences in immune system. Comparative population analyses within humans are in their infancy (Goncalves et al 2003, 2004), and this is a fruitful avenue to explore.

3.2. Monogamy and Polyandry

The ecological conditions that favor greater male expenditure on offspring-specific true parental investment include: [1] relatively safe adult life (low mortality), combined with conditions that [2] allow adults to extend that safety to their offspring (e.g., species like geese), resulting in [3] greatly enhanced offspring success with care by more than one parent. As noted above, men have often circumvented these culturally under many conditions, allowing them to invest without the constraints of true genetic monogamy.

Fewer than 16% of traditional human societies are socially monogamous. What this means is unclear, because social monogamy seldom reflects genetic monogamy (Reichard & Boesch 2003). Many socially monogamous societies—societies with one-spouse-at-a-time rules—would be polygynous in a biological definition: more men than women fail to marry, and more men than women remarry after death or divorce, producing families in these later unions. The most reproductive men have many more children than the most fertile women. These things mean that the variance of men's reproductive success is high compared to women's. However, we seldom have the data to calculate the biologically important relationships from anthropological data.

Social monogamy is unevenly distributed geographically. Almost 45% of living arrangements in “circum-Mediterranean” societies are coded as some form of monogamy, and four forms are described. In contrast, only 2.7% of African societies are considered monogamous, and these three societies are all independent nuclear families (Low 2003a). Many ethnographies suggest that monogamy is more common in relatively harsh ecological conditions (e.g., very dry, very cold, low plant productivity), which perhaps might make monogamous two-parent care reproductively advantageous (also true for polyandry, see below). Although the examples are suggestive, there are no clear statistical patterns, probably for two reasons: [1] there are few “monogamous” societies with sufficient data to test; and [2] the use of the term “monogamy” is anthropological—it means monogamous-to-mildly-polygynous. There are some statistically significant associations between monogamy and certain environmental conditions (Low 1989, 2003a). Within monogamous societies, it could be rewarding to explore the strength of ecological influences on family organization, which might be more responsive to ecological constraints than monogamy

itself. Social monogamy in humans includes many forms, and some of these seem likely to have quite different biological impacts.

Polyandry, even rarer than monogamy in human marriage arrangements, is almost always fraternal (brothers marry a single woman), and appears to result from brother-brother coalitions in order to combat resource scarcity or from attempts to control the distribution of a resource like land, which is immobile and loses its value when too finely divided. Polyandry is rare for several reasons, including the fact that men who share sexual access to one woman will have fewer descendants under most circumstances than men who have either sole access to one woman or access to more than one woman. However, as Mace (1997) points out, such men may fare no worse than younger brothers in systems with primogeniture, in which the oldest son inherits but younger sons do not. Polyandry simply throws these conflicts into sharp relief.

Resource constrictions clearly affect these costs and benefits. Among the Nyimba of northwestern Nepal, brothers marry a single woman, but if there are more than two brothers in the marriage, the likelihood of “conjoint” marriage (adding another wife) or “partitioning” (in which one or more brothers leaves the household and forms a new household) is greatly increased (Levine & Silk 1997).

4. Social Correlates in Human Systems

Human social conventions, just as canine size and testis size in primates in general, might be expected to vary with mating system. Hartung (1982, 1983, 1997) found that inheritance tends to be male-biased in polygynous systems; in such systems, resources

influence male reproductive success more than female reproductive success. In bride price systems, for example, young, high-reproductive-value women may cost more than older women (Borgerhoff Mulder 1988, 1995)—which means that wealthier men can have more, and younger, wives than other men. Cowlshaw and Mace (1996), using a phylogenetic approach, confirmed this pattern, and Mace's further work (Mace 1998, 2000) has modeled the ways in which such systems are likely to succeed.

Although polygyny is the commonest marriage system across human societies, it is also true that human males are extraordinarily paternal. Nonetheless, patterns of paternal investment vary greatly across societies, apparently independent of the marriage system. In polygynous societies with low confidence of paternity (e.g., where men and women live apart), it is common for children's maternal uncles to invest in them, rather than their (putative or nominal) father, for example. In traditional societies with few heritable resources, stepfathers may invest as much time and training in step-children as in their genetic children (e.g., Hewlett 1992, Hewlett et al 2000). In modern socially monogamous (but genetically polygynous) societies with remarriage, there exist both high resource stakes and considerable step-parenting. In these conditions, step-children are, in many societies, more vulnerable than genetic children to lowered investment (Anderson et al 1999a, 1999b, Hofferth & Anderson 2003, Lancaster & Kaplan 2000), child abuse, and infanticide (Daly & Wilson 1984, 1985, 1987, 1988; see review in Low 2000: Chapter 6).

Dowry, a marriage system in which the bride's family gives resources to the groom or groom's family, is 50 times more common in monogamous, stratified societies than in polygynous or nonstratified monogamous ones (Gaulin & Boster 1990, 1997, Lang 1993); in these societies males typically vary greatly in their status and wealth. Women married to

wealthy, high-status men benefit reproductively, so it pays would-be brides (usually, the brides' fathers) to compete, bargaining for wealthier men as mates. In many of these societies, poorer women's families must pay more dowry than wealthy women's families; dowry becomes a form of mate competition among women (Gaulin and Boster 1990, 1997; Srinivasan 2005). Such mate competition may have costs, as in modern rural India. Since about 1950, demographic shifts have resulted in declining numbers of potential grooms for potential brides of marriageable ages—and dowries have risen steadily. By 1990, a dowry was likely to be over 50% of a household's assets. Wives from poor families, able to pay less in dowry, are less likely to marry; if they marry, they have a high risk of being abused by their husbands. Further, domestic violence and spousal abuse have correlated with increases in dowry worth; "insufficient dowry" is an important recorded cause of spousal abuse (Rao 1993a, 1993b, 1997).

4.2. Further Social Rules and Ecological Influences

A number of social rules surround marriage. Some of these, like rules of marital residence, appear to arise from the ecology of resource distribution. Fully two-thirds of the 862 societies in Murdock (1967) mandate living with the husband's kin. There are, of course, complexities: the rule may involve either patrilocality or virilocality (these are equivalent except for the details of how the man's kin are distributed spatially), and may also have a minor pattern, or different rules, for the first years of marriage. Matrilocality, living with the wife's kin, is relatively rare and is associated with external warfare combined with women contributing greatly to subsistence (Ember & Ember 1971).

Consider marriage arrangements as alliance formation—in terms both of getting and protecting resources from others, and in terms of resource impact on reproductive success, men typically profit more from alliances than do women. It does appear that many arrangements cross-culturally favor men's interests over women's when there is a conflict. In Whyte's (1978, 1979) examination of women's status in preindustrial societies (using the 93 odd-numbered societies of the Standard Cross-Cultural Sample), the most common patterns favored men's interests. In terms of the older generation's rule in arranging marriages, men (fathers, uncles) monopolize arrangements or have more say than women in 55% of societies. With regard to the influence of the potential bride and groom, men had more ability to initiate or refuse arrangements in 34% of societies; women in 4%. Women moved farther away from their natal localities than did men in 69% of societies. Mild to strong institutionalized deference of wife to husband exists in 66% of societies. We typically think of such norms as "simply cultural" but I suggest that although the "resource connection" to these norms may be hidden, it helps generate the patterns we see.

The relative importance of resource control for men's versus women's reproductive success plays out further in an interesting and widespread set of patterns: prohibitions and preferences in cousin marriages. In many societies, first cousins are the preferred or mandated mates. Genealogically, a man might marry any of four types of first cousin:

- [1] His father's brother's daughter (FBD)
- [2] His mother's brother's daughter (MBD)
- [3] His father's sister's daughter (FZD)
- [4] His mother's sister's daughter (MZD)

The first and fourth of these are called “parallel cousin” marriages (the parent and his/her sibling are the same sex); the second and third are called “cross cousin” marriages. For some time, anthropologists considered the choice of type of cousin to be purely a cultural phenomenon. For example, Murdock (1949:287) argued that “Since the daughters of the father’s brother, father’s sister, mother’s brother, and mother’s sister are consanguineally related to male Ego in exactly the same degree, all intercultural differences in marriage regulations applying to the several types of cousins represent divergences from biological expectations.”

However, as Flinn and Low (1986) pointed out, this is an incomplete idea of the concept of “biological expectations.” The ecology of resource concentration—who gets how much of what—leads to a far more complex set of predictions; part of the underlying hypothesis is that marriage rules and preferences will be manipulated in the reproductive interests of those who control them. For example, societies with symmetrical cross-cousin marriage rules (either FZD or MBD allowed) also tend to exchange women (rather than goods or resources): these societies are also characterized by poor resource bases and the absence of inheritance rules (Flinn & Low 1986). In richer resource areas, asymmetrical cousin marriage rules also show relationships to resource distribution and men’s coalitions around resource control. The most striking, perhaps, is that MZD, which would enhance nepotism and reciprocity among *female* kin, is virtually unknown, regardless of other factors. The other asymmetrical rules (FBD, MBD, FZD) all enhance the power of coalitions among male relatives, and are associated with residency patterns that enhance the particular kind of male coalition (e.g., FBD is associated with patrilocal residency, while MBD is associated with avunculocal residency; see the chapter by Cronk and Gerky, this volume).

5. Conflicts Between the Sexes and Third-Party Interests

Marriage is about far more than simple mating. The partitioning of polyandrous households among the Nyimba (above) resulted from conflicts of interests among brothers. Such reproductive conflicts of interests—not only between polyandrous brothers, but between co-wives and the two sexes—add, along with third-party interests, further complexity and variation to the mating and marriage arrangements of humans.

Women seldom fully share men's reproductive interests, and each partner has kin who may act to shift the balance of reproductive costs and benefits. In socially monogamous systems, the reproductive interests of parents typically converge to some degree, but this does not necessarily protect women's reproductive interests. Women's interests seldom converge completely with their husbands' even in socially monogamous situations. Consider socially-monogamous modern Thailand: surveys of men's and women's attitudes about sexual matters (Knodel et al 1997) highlight this sexual conflict of interests. There is a long tradition of men, married as well as single, visiting sex workers in the context of men's social evenings out. In addition, some men have "minor wives" whom they support at least partially. Thai wives have historically had little ability to constrain these behaviors, and have held a long-standing preference that their husbands, if sexually active outside marriage, visit sex workers, because the transaction is brief, and represents only a minor diversion of resources from the wife and children. In contrast a minor wife can represent a real drain of resources. However, with the spread of HIV, an increasing proportion of women prefer the husband to have a minor wife; while the resource conflict is heightened, the health risks are reduced.

When marriage systems concern not only male and female reproductive interests, but the interests of third parties, those third parties (particularly kin) can influence social patterns. Third-party interests are particularly elaborated in humans: there can be legal and political arrangements that enforce marriage arrangements in the interests of third parties, even when those parties are not present. Specific areas of the law (e.g., family law and part of criminal law) deal in particular with third-party interests in sexual behavior, reproduction (and the avoidance of reproduction), and conflict resolution within families (e.g., see Jones & Goldsmith 2005).

In many societies, parents may use children's marriages to form alliances with wealthy and powerful families. In some societies, children are betrothed well before puberty; in a few societies, they are promised even before birth. Among the Arunta of central Australia, for example, a couple may be betrothed even before birth, and the marriage will take place even if the parents who made those arrangements have died.

In most societies, social and cultural inventions such as marriage, divorce, inheritance, involve the interests of other individuals—sometimes individuals with no apparent interest in the particular decision (caliphs, ministers, shamans, etc.). Such human-invented conventions, like physical resource conditions, affect the costs and benefits of marriage for individuals. Thus, marriage patterns in humans follow a variety of rules, as ecological and socio-cultural complexities interact.

6. When Culture and Ecology Interact

Most of the cultural rules about mating and marriage discussed above have clear ecological influences. In theory we can invent *any* sort of cultural innovation. We can invent cultural innovations that are, in fact, deleterious to the persistence of our lineage—nothing

prohibits that. In fact, because we did not evolve to consider issues like reproductive success as conscious goals, perhaps biologically deleterious practices should arise frequently. Whether such innovations spread and persist is another issue (e.g., see Richerson and Boyd 2005: 235-236).

Consider celibacy. Individual decisions to become celibate probably have little effect on lineage persistence (unless, of course, it is your only child who becomes celibate).

Institutionalized celibacy can present another situation. In the Catholic Church, celibacy was not always required of the religious, but it has been mandated now for several hundred years (priestly marriage was forbidden in 1139, but effective enforcement appears to date from the Council of Trent in 1545-1563). When Catholic families were large, the designation of a younger son for a celibate life in the Church resulted in lowered competition among brothers (for example, land inheritance), some elevation of status from having a priest in the family, and possibly some resource improvement also. Celibacy did not spell the death of lineages; in fact, it could be profitable to a lineage. In contrast, today's Catholic Church is having difficulty in the wealthier parts of the world in recruiting people for the celibate religious life. A devout family faces a difficult decision if there is only one son and he is being urged into the priesthood (e.g. Rice 1990, Sipe 1990). The Shakers, too, required celibacy in relatively modern times; few if any individuals remain alive today. Nothing prohibits our invention of rules that might be reproductively deleterious, even ridiculous—but such rules will not become and remain the common rules.

Similarly, the strong son-preference of several modern Asian nations, within the context of large-scale cultural rules (e.g., China's One Child policy during the 1980s) and modern technology, has created an interesting ecological problem for many lineages (see review in Low 2000: Chapter 10). Even before the One-Child policy, large-scale rules—rules not even aimed at

reproduction—resulted in frequent dramatic increases in mortality and decreases in fertility. The social and political upheavals of state interventions such as the Cultural Revolution and the Great Leap Forward created high birth deficits, and high mortality, particularly in rural areas (Ting 2004 a,b). These rules were not intended to affect fertility and mortality, but were principally aimed at compressing income and educational opportunities across social classes (Ting 2004a). In response, white-collar parents appear to have made a quantity-quality tradeoff, having fewer children but educating them better, than lower-status parents; the disruption of families (e.g., sending educational elites to work in rural areas) also heightened mortality rates. In an analysis of three Chinese provinces over 50 years (Ting 2004a, b), only one natural event (an earthquake in Hebei Province) created a shift in mortality that could even be detected at the scale of the effects of the political rules. The unintended impact of these rules on overall population parameters was, in fact, far greater (through impacts on birth and death rates) than the One Child policy (Ting 2004a, b).

Although the One Child policy had little effect on population numbers, the proportion of families with just one child did increase, and family sex ratios shifted—principally in third and fourth births. The sex ratio for first births was 105.6 (the same as the world average). The sex ratio of third births was when there were already two daughters was 224.5; when there were already two sons, it was 74.1 (Peng 1991, Wen 1993). The result has been a change in what biologists call the “operational sex ratio”—the sex ratio of potential mates in the adult population. Now, men born in the 1980s are having trouble finding brides. In parts of Korea, Japan, and India, a similar situation obtains. It will be interesting to see, as brides become rare and valuable, whether the value of daughters will increase, as some theoretical studies suggest (Kumm & Feldman 1997).

Women in the Western developed nations of the world also face a conflict between social goals and reproductive success. Seeking hard-won social gains like equal pay is laudable, but it is also clear by now that women face harsh tradeoffs when it comes to having children, gaining resources, and allocating those resources to them. Below-replacement fertility is now common in several western European nations, and in the US fertility is just above replacement levels. It is clear that, whether the demographic transition made ecological sense in terms of switching from high fertility to high investment in competitive circumstances (Easterlin 1978, Low 1993, 2003b), Western women's current reproductive patterns no longer make any ecological sense (Borgerhoff Mulder 1998, Low et al 2002, 2003, Richerson & Boyd 2005).

The more we examine the connections between cultural practices and human reproduction, the clearer it becomes that most really persistent cultural practices, perhaps especially those of mating and marriage, usually make ecological sense. Examples of cultural institutions and/or practices that run counter to our evolution are instructive. In a sense, we are our own experiment.

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