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Human Pair-Bonds: Evolutionary Functions, Ecological Variation, and Adaptive Development

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Stable mating relationships are widespread in our species, with important economic, social, and reproductive implications.[1] Pair-bonds are part of the unique human mosaic, including very large brains, childhood, concealed ovulation, sexual intercourse in private, cultural symbols, and complex social groups. Yet we understand relatively little about the evolution of human pairing, its functions, and consequences for human diversity. We can define pair-bonds as the long-term affiliation, including a sexual relationship, between two individuals. The important point is that the union, whether monogamous or polygamous, is relatively enduring. Recent debate about human pair-bonds highlights apparently conflicting hypotheses: Are pair-bonds the evolutionary consequence of male mating competition[2,3] or are they an adaptation for paternal provisioning?[4,5] Unfortunately, a simple answer seems unlikely. The evidence indicates selective pressures from both mating competition and provisioning needs, suggesting different benefits of pair-bonds in different contexts. Whether a bond emphasizes mating or parenting effort may depend on environmental cues. Childhood experience evidently affects pair-bond development, suggesting further adaptive design for flexible life-history strategies.

Functional and developmental accounts of pair-bonds rarely converge, but cross-fertilization could stimulate advances. Here I review theory and data for pair-bond functions before turning to the development of human pairing behavior in a life-history perspective. My approach is to examine primate comparisons, cross-cultural analyses, and ethnographic case studies. The goal is to develop refined hypotheses for human pair-bonding through the convergence of existing data.

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PAIR-BONDS AND PROVISIONING

In 1966, Washburn and Lancaster suggested that during human evolution increasing need for biparental care created selective pressure for pair-bonds.[4,5] Children have a long and expensive developmental period during which they are dependent on others for sustenance and protection. Child rearing, hence, can be difficult for one person. A father shares fifty percent of his genes with his child, giving him more genetic interest in the child than other relatives have, making him a more motivated caregiver.[6] Fathers can care for children in at least two ways. They can provide direct care or they can help the mother, who is then freed to give direct care.

Men's fitness depends in part on parental investment decisions about pair-bonding. Parental investment is defined as expenditures benefiting one offspring at a cost to parents' ability to invest in other components of fitness.[7] Theoretically, a man's willingness to care for children depends on his options for fitness enhancement. From a parental investment perspective, abandonment by a father is predicted in environments where paternal care does not benefit men's fitness as much as do alternative behaviors, such as seeking additional mating opportunities. A comparative study of birds and mammals indicated that pair-bonding "may be selectively favored in humans and other animals when mothers' feeding requirements interfere with their baby-tending," increasing benefits of paternal provisioning and costs of abandonment.[8:48] Subsequent comparative analyses suggest that mammalian pair-bonds may not have evolved in response to parenting pressures,[3] although biparental care appears to be important in avian bonds.[9] Among humans, however, there is not a simple linear relationship between men's provisioning and pair-bond stability (Fig. 1).[10] Some parental investment predictions for pair-bonding have empirical support, but the question requires attention to alloparenting, subsistence cooperation, and paternal provisioning before weaning.

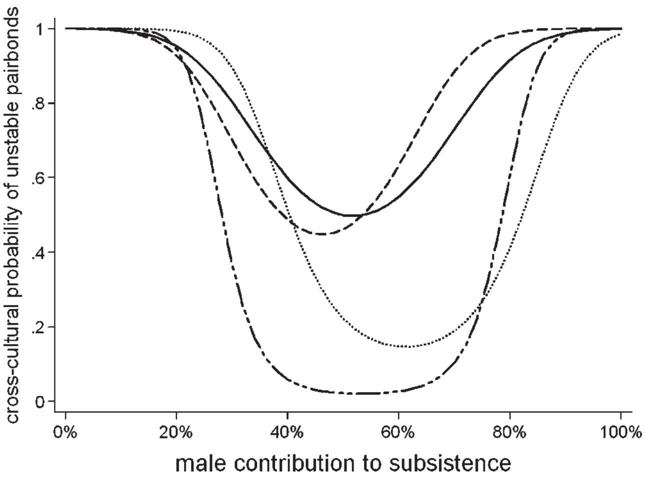

Figure 1. Pair-bond instability is a curvilinear function of men's contribution to subsistence across traditional societies. Pair-bond stability is greatest in societies where men and women contribute equally to subsistence. The graph shows predicted probabilities based on five logistic models in Quinlan and Quinlan.[10] The dash-dot line has multiple controls.

Breastfeeding May Be a Critical Period for Male Provisioning

Breastfeeding appears to be an important element of human pair-bonds because male provisioning seems to be particularly important during lactation.[6,11] Evidence from industrial populations, socioecological case studies of hunter-gather groups, and cross-cultural analysis of traditional societies converge on one conclusion: Stable conjugal relationships support breastfeeding in ways that other kin relations do not.[6] Lactation, which appears to be a universal "critical period" for paternal investment, may have created strong selective pressure for human pair-bonds.[11,12]

Breastfeeding is a primary mechanism among mammals for provisioning dependent offspring. It is also a key component of parental investment. Human female breasts and breastfeeding have unusual features compared with other apes and mammals in general. In fact the "perennial" human female breast is an evolutionary mystery probably tied to female sexual signaling.[13] These unusual features of human parental investment deserve more attention.

For mothers, lactation entails energetic and opportunity costs, and suppresses fertility.[14] Human lactation requires 670 kcal/day during exclusive breastfeeding.[15] Increased energy demand presents costs to household production and may delay future reproduction through reduced fecundity.[16] Breastfeeding may suppress postpartum ovulation through effects on gonadotrophin-releasing hormone.[17] The costs of breastfeeding for future reproduction or "residual reproductive value" indicate life-history trade-offs. Reduced future reproduction due to lactation suggests that to enhance fitness most mammals should wean their offspring as soon as possible. However, the effects of lactation on human fecundity diminish as breastfeeding continues. For example, in one study 50% of well-nourished nursing women returned to reproductive cycling within 10 months of giving birth. One-hundred percent of lactating women returned to cycling within 20 months,[18] which is 10 months earlier than the cross-cultural average age at weaning at 30 months.[19] Resumption of cycling while lactating might account for shorter interbirth intervals among humans than among great apes.[20] The comparatively low reproductive cost of lactation among humans may suggest that energetic costs can be reduced by provisioning. The opportunity costs of breastfeeding also can be substantial.[21] Nursing often interferes with women's work, which may benefit other children or kin. Opportunity costs rather than delays in reproductive cycling may be the major force driving human weaning decisions.

Human weaning shows comparatively unusual features. Other great ape species wean when offspring are about 5 to 7 years old.[19,20] Based on allometric relationships between adult size,[22] molar eruption,[23] and weaning age among primates, humans are predicted to wean at about 6 years.[19] Despite predictions for late weaning among humans, cross-culturally the average and median age at weaning is around 2.5 years.[19,20,23] These data indicate that the average age for human weaning may be at an adaptive minimum. One challenge in many human environments is not to find ways to hasten weaning, but rather to delay it. Maternal social support provides a solution for the unusual challenge of human lactation.

Provisioning infants with energy is not the only or perhaps the most important function of human breastfeeding. Availability of weaning foods is not associated with age at weaning cross-culturally,[24] suggesting that considerations other than feeding are in play. The evolution of cooking, however, may have played a role in the uniqueness of human weaning. In fact, because of expensive brain growth, breastfeeding alone does not support infant nutritional needs much beyond 6 months.[20,25] Many other health benefits of breastfeeding, such as giving infants resistance to infections and allergies, are well known.[26,27] Prolonged nursing is associated with improved long-term psychomotor and neural development in well nourished populations.[28–30] Nursing can be important to the mother-child bond, associated with positive emotions and attachment linked to maternal hormones, including prolactin and oxytocin.[31] Maternal responsiveness, which is related to nursing, appears to influence the development of children's attachment styles and adult conjugal relations.[32] Hence, breastfeeding and its underlying hormonal correlates may play a role in attachment organization.[33] These findings suggest fitness benefits beyond mere energy provisioning, in which alloparental care cannot substitute for nursing.

Support mothers receive from potential alloparents may affect their work and breastfeeding patterns. Kinswomen appear to be more willing to help each other with childcare than with other work.[34] Breastfeeding, however, is usually beyond the scope of alloparenting. Leaving a baby with a kinswoman prolongs periods of mother-child separation and reduces milk production, which may hasten weaning in households with coresident alloparents.[21] This is similar to early weaning by working women in developed countries.[35,36] Analysis of traditional cultures showed earlier weaning by 5.5 months in groups with high levels of alloparenting compared with groups in which mothers were primarily responsible for child care.[6] Given unusual features of human lactation, including nonnutritional benefits, earlier weaning is probably associated with reduced offspring fitness. Hence, the father of a woman's child seems well situated to enhance her fitness by supporting breastfeeding.

Evidence from foraging groups indicates that biparental care may be especially important during lactation. Foraging men "provide a considerable portion of the energy consumed by juveniles and reproductive-aged women...".[37:173] Among foragers, men increase their time spent in subsistence when their mate is nursing and a woman's subsistence work is inversely related to her mate's when the couple has a nursing child.[11,38] Among the Hadza foragers of Tanzania, husbands apparently compensate for their wives' diminished foraging return when they have young children.[11] Hadza women had significantly lower foraging return rates when they had nurslings; conversely, Hadza men increased foraging return and provisioning of mates with nursing children. Similarly, among the Ache and Hiwi foragers, women's time spent foraging and in child care were inversely related; nursing women spent less time foraging than did women who were not nursing. Also, women's foraging time was inversely related to their husbands' foraging.[38] Based on these findings, Marlowe suggests that pair-bonds in human evolution function to provision a mate and offspring during a "critical period" coinciding with lactation.[11] In sum, evidence of the origin of human pairing is incomplete, but male provisioning during lactation offers a promising lead.

If pair-bonds support lactation, then divorce may impair a woman's ability to nurse her child. Among foragers, "divorce or paternal death leads to high rates of child mortality among the Ache, the Hiwi, and the !Kung, but not the Hadza."[37:173] Similarly, in the world's large-scale "industrial" populations, public health studies consistently find that single mothers tend to wean their children earlier than do women living with a mate,[39] and that this has short- and long-term child health and developmental effects.[26–30] This association is probably related to the trade-off between breastfeeding and women's work, which can be particularly pressing among single mothers.[35,36] If pair-bonds evolved to support lactation, then pair-bond stability should be associated with breastfeeding duration. In a comparison of 74 traditional societies including hunter-gathers, horticulturalists, and pastoralists, the frequency of divorce and age at weaning were inversely associated: Children tended to be weaned about 5 months earlier in societies where divorce was common.[6] Although there are multiple potential payoffs to paternal care, those benefits are not as consistently experienced cross-culturally as is lactation. Moreover, strong selective pressures for provisioning during lactation suggest that perennial female breast swelling in humans mimicking lactation may function to attract male attention and provisioning.[13]

Alloparenting Is Associated With Unstable Pair-Bonds

Parental investment theory predicts stable conjugal unions in societies where parenting effort is more beneficial for men's fitness than is mating effort. When nonparental caregivers (alloparents) are important, paternal care is less important because of reduced costs of male abandonment; hence, pair-bonds may be unstable. A cross-cultural analysis shows that when alloparents are involved in childrearing, pair-bonds are less stable,[10] which is consistent with other findings. Whether alloparenting "causes" conjugal instability or is a consequence of it is not clear, but a study of intracultural variation among the matrilocal, matrilineal Khasi of Northeast India suggests that alloparenting frees fathers to expend their effort elsewhere. Among the Khasi, the presence in the household of the wife's mother was associated with smaller economic contributions from husbands[11] and increased probability of divorce.[40] Similarly, classic kinship studies show that where maternal avuncular relationships are salient, pair-bonds often are unstable and unimportant,[41] presumably because paternal care is less crucial and people are free to pursue other avenues to enhance fitness. For example, in "avunculate" societies both sexes may invest more heavily in mating effort. For some men there may be a substantial payoff in fertility; for many women there may be an advantage to increasing the genetic diversity in their offspring by having children with several men. Increased genetic diversity in offspring could be beneficial in response to high pathogens loads[42] or other environmental risks.[43]

Relations between pair-bonding and alloparenting are complicated because the availability of alloparents often improves child well-being and survival,[44] as does father-presence.[45] From a child's perspective, the ideal family environment should include two parents and alloparents. Yet alloparenting can reduce men's costs of abandoning a pair-bond. Fathers, mothers, kin, and children have conflicting interests in paternal care, suggesting a delicate balance of factors influencing the range of human family configurations. More detailed research into family composition effects, such as the Khasi case study,[34,40] will improve our understanding of human pair-bonds and the evolution of the family.

Male-Female Subsistence Complementarity Is Associated With Stable Pair-Bonds

Subsistence complementarity between men and women may lead to conjugal stability. "It is the partnership between men and women that allows long-term juvenile dependence and learning and high rates of survival".[37:173] Following parental investment predictions, conjugal unions should be least stable when women do the majority of subsistence work because paternal provisioning is unnecessary. Conversely, pair-bonds should be most stable when men do the majority of subsistence work because women and children are particularly dependent. One cross-cultural study, however, found no association between conjugal stability and the division of subsistence work.[46] However, that finding was probably due to analysis that could not detect curvilinear effects. A more recent cross-cultural analysis found that pair-bonds tend to be unstable when either men or women contribute the majority to subsistence. Conjugal unions tended to be most stable in cultures where men and women are about equally responsible for subsistence (Fig. 1).[10] This general pattern of conjugal stability holds across all subsistence types; there are no significant interactions between subsistence strategy and sexual division of subsistence labor.

Conclusions about the effects of sexual division of subsistence labor on pair-bond stability await further study. At present, the clearest evidence of associations between pair-bond stability and division of labor comes from analysis of Murdock and White's Standard Cross-Cultural Sample (SCCS).[47] The SCCS is a sample of traditional societies chosen to give a balanced representation of the range of human cultural variation. SCCS data are coded from ethnographies. Often the coded data are crude ordinal and categorical variables. Many of the approximately 2,000 existing variables have demonstrable reliability, but the reliability of most coded variables is unknown. Low reliability is a bigger problem for rejecting null results than for failing to reject positive results reported here. There are other important considerations for assessing the adequacy of cross-cultural analyses. Cross-cultural data aggregate groups of various subsistence styles, population densities, and levels of acculturation. One approach is to limit analyses to societies of one subsistence type, such as foragers. This is a crude solution likely to result in unstable statistical analyses by excluding as much as 90% of the SCCS data. A more sophisticated, sensible, and robust approach is to use appropriate statistical controls for various factors related to the agglomeration of cross-cultural data.[6] The cross-cultural analyses discussed here used careful multivariate analyses controlling for many possible confounds. Finally, for any findings, we can only draw firm conclusions with replication from a variety of data sources. Findings regarding associations between human pair-bonds and weaning, for example, are on firm ground, given convergent results from detailed case studies, multivariate cross-cultural analysis, and large-scale public health studies. Initial associations between division of subsistence labor and pair-bonding are less conclusive. We can increase our confidence in initial cross-cultural findings through close examination of the ethnographic record. The !Kung (Ju/'hoansi) foragers offer an example of conjugal complementarity in the division of subsistence labor.

> **. . . subsistence complementarity may allow a conjugal family to be self-sufficient for extended periods.[52] Living in a cooperative conjugal family allows humans the flexibility to respond to fluctuations in resource availability and social conflict.**

Among the Dobe !Kung hunter-gatherers, divorce is common early in marriage, but ethnographic and demographic accounts both indicate that marriages are quite stable after an initial "stormy" period.[48,49] Among the !Kung, 65% of first marriages precede menarche, 30% follow shortly thereafter, "and typically there is still a wait of some years before first conception".[49:177] The average age of first birth among !Kung women is about 19 years, at least 3 years after the average age of menarche.[49] These data suggest that many, if not most failed marriages occur before childbirth.

There is important food sharing between !Kung husbands and wives.[49] In the SCCS, !Kung men contribute about 40% of the diet. Meat from men contributes about 30% of calories consumed.[48] Because meat is often shared broadly beyond the nuclear family, male provisioning may not account for human pair-bonds.[50] Among the !Kung, there appear to be multiple benefits to sharing meat broadly among the camp.[51] Although established !Kung marriages are quite stable, !Kung camps may not be stable as they fission in the face of intragroup conflict. Lee describes a life-cycle of !Kung camps centered around a core group of siblings and spouses with peripheral members that may come and go.[48] In the context of this fission-fusion social organization, subsistence complementarity may allow a conjugal family to be self-sufficient for extended periods.[52] Living in a cooperative conjugal family allows humans the flexibility to respond to fluctuations in resource availability and social conflict. Such flexibility means that we are not locked into larger social groups that may spawn important conflicts of interest. Finally, the !Kung themselves suggest that subsistence complementarity may be at the heart of stable unions, because stinginess is often reported as cause for divorce.[49]

PAIR-BONDS AND MATING COMPETITION

Male-male competition can also create selective pressures for pairing and conjugal stability. Thus, pair-bonds could support mate guarding rather than parenting effort.[2,53] Sexual dimorphism in body size reflects the evolutionary history of male-male competition in a species.[53] As compared with other great apes, humans show moderate to low levels of sexual dimorphism, suggesting low levels of intrasexual *physical* competition.[55] However, competition can take on economic, social, and symbolic dimensions that are not reflected in body size. Such competition could have influenced pairing in the Pleistocene at least as far back as 40,000 years ago with the appearance of the first unequivocal symbolic artifacts.

There are at least two possibilities for effects of intrasexual competition on pair-bonds. In a comparative analysis of nonhuman mammals, the spatial distribution of females rather than male provisioning predicted monogamy.[3] Monogamy, however, is not synonymous with long-term pairing. Gorillas for example, are "pair-bonded" in the context of "harem-defense" polygyny.[56] But gorillas show no male provisioning. Pair-bond stability in harem-defense polygyny[57] and monogamy when females are spatially dispersed[3] may share a common evolutionary logic: Males defend long-term mating relationships when there is low probability of finding another available mate. The density of females across the landscape is associated with the likelihood of encountering a potential new mate. The spatial distribution of women probably has little relevance to human pair-bonds, though there might be some special circumstances, such as low-density foragers, in which groups fission into small dispersed clusters for several months of the year. The distribution of women across the Pleistocene landscape might have created selective pressures for pairing when populations were small and dispersed.

The intensity of male mating competition can increase costs of abandoning a current bond in favor of seeking a new bond. If relatively few females are available, then males should defend their current relationship and pair-bonds should be stable. Male-biased operational sex ratio, hence, is predicted to lead to stable pair-bonds, whereas female-bias is predicted to lead to less stable bonds.[58] Cross-national studies have found that promiscuity was more acceptable in populations with female-biased sex ratios and less acceptable in populations with male-biased sex ratios,[59] while a female-biased sex ratio was associated with a greater degree of single parenthood.[60]

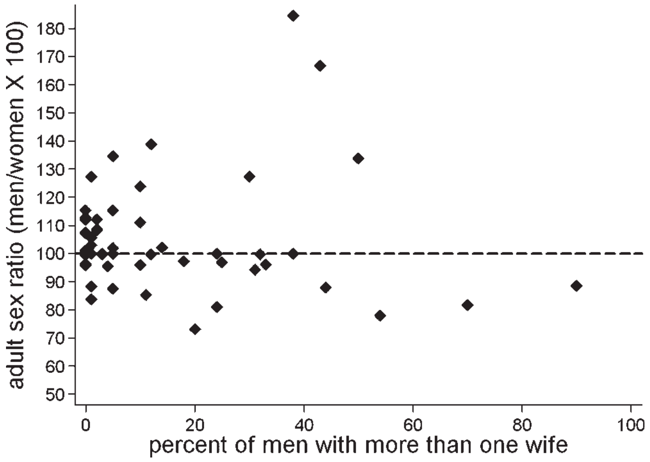

Figure 2. Sex ratio by polygyny level in the SCCS. The horizontal line at 100 on the Y-axis indicates an equal number of men and women. Values less than 100 indicate female-biased sex ratios. Few populations have a sex ratio low enough to support polygyny without creating male mating competition.

Level of polygyny may be associated with conjugal stability because polygyny creates a shortage of women, increasing male costs of abandoning a relationship. This prediction might seem problematic because in polygynous societies some men have multiple mates and some polygynous species do not have pair-bonds. Human polygyny, however, is somewhat unusual because it occurs in multi-level, multi-male groups with alliances among adult males[61] in a species with a generally balanced sex-ratio (though there is significant cross-cultural variation in human sex ratios). Figure 2 shows that most human populations have a relatively balanced sex ratio (dashed horizontal line), making high levels of polygyny difficult; few populations have a sex ratio low enough to support polygyny without creating male mating competition. Polygyny within multi-male groups with relatively balanced sex ratios creates a shortage of marriageable women, which increases pressure for mate guarding that could support pair-bond stability.

Not all polygynyous species are pair-bonded.[62] There are other factors that promote bonding in some polygynyous systems. The spatial distribution of one-male-units (OMUs) in the population may be an important factor. Where OMUs are clustered in multi-level communities, pair-bonding can occur with polygyny. Comparison of hamadryas and anubis baboons illustrates this point.[63] Anubis baboons exhibit female philopatry, no pair-bonds, and promiscuous mating. In contrast, hamadryas baboons, which are closely related to anubis, exhibit male philopatry, polygyny, and pair-bonds based on a combination of coercion and attraction. A particularly noteworthy point is that hamadryas and gelada OMUs exist in close association in locally dense multi-level populations with long-term associations between mates.[64] Similarly, human polygyny occurs in relatively densely clustered polygynous households within larger communities. Relatively close spatial association among OMUs or polygynous households may be the primary factor leading to pair-bonding in polygynous mating systems.

Polygyny levels are low among human groups[65] (Table 1), but they are high enough to create shortages of marriageable women. Figure 3 shows that polygyny limited to two wives can create a shortage of women even in populations with substantially female-biased sex ratios. (The portion of the graph below the zero line indicates a shortage of women for the remaining marriageable men.) Comparing Figures 2 and 3 shows that few societies have sex ratios low enough to avoid male mating competition generated by relatively low levels of polygyny. Hence, most men compete

TABLE 1. Prevalence of Polygyny in the Standard Cross-Cultural Sample[a]

Level of polygyny: % men with plural wives	N	% of SCCS societies	Cumulative % of SCCS societies
0–10	86	59.3	59.3
11–20	13	9.0	68.3
21–50	37	25.5	93.8
>50	9	6.2	100
Total societies	145	100	

[a] 80% of forager societies have <10% polygyny rates.[7]

to establish and maintain a single union. This reasoning suggests a somewhat counterintuitive prediction: In societies with higher levels of polygyny, pair-bonds should be relatively stable. In a recent study, human polygyny level was inversely associated with frequency of divorce, which may indicate that males maintain pair-bonds when there are fewer available women.[10] Similarly, a comparative analysis could not exclude mate guarding as a selective pressure favoring pair-bonds among nonhuman primates.[53] In short, pair-bonds could have evolved in response to male mating competition. However, an additional unpublished analysis indicates a somewhat more complex cross-cultural relationship between polygyny and conjugal stability, with divorce appearing to become less common as the proportion of polygynous unions increases to about 50%. Beyond 50%, which is a high level of polygyny among humans, conjugal unions become unstable cross-culturally. More attention to interactions among demographic factors such as spatial distribution, sex ratio, and frequency of polygyny in mating systems can improve our understanding of sexual selection in hominins,[66] which thus far is based largely on simplified models from evolutionary psychology.

A plausible alternative interpretation suggests that the association between conjugal stability and polygyny is not due to mating competition, but rather to marriage alliances between kin groups. Conjugal stability associated with polygyny may result from pressure from kinsmen who fear the economic and political consequences of divorce. There is no empirical support for this interpretation: In the SCCS, the association between the presence of corporate kin groups and frequent divorce is not significant ($p = 0.22$) and is in the opposite direction predicted (odds ratio for frequent divorce = 1.7), as is the association between patriliny and frequent divorce (odds ratio = 1.3, $p = 0.61$). However, as mentioned earlier, null results from the SCCS must be interpreted with caution.

Even low levels of polygyny during the course of human evolution could have created substantial selective pressure for increased pair-bond stability through mate guarding. But the role of polygyny in human evolution is unresolved. Some scenarios for early hominin social structure envision a chimp-like promiscuous mating system.[2] Other equally plausible arguments suggest a gorilla-like polygynous mating system.[61] Sexual dimorphism in fossils could indicate early hominin mating behavior because sexual dimorphism is associated with primate mating systems.[54] Polygynous species, like gorillas, tend to have high levels of dimorphism, while promiscuous species, like chimpanzees, tend toward moderate dimorphism. Unfortunately, paleoanthropologists, using the same data, come to different conclusions about the degree of early hominin sexual dimorphism. Many studies indicate substantial sexual dimorphism, similar to gorillas,[67] but one analysis has concluded that early hominins had a level of sexual dimorphism similar to that among chimpanzees.[68]

Human reproductive anatomy may shed additional light: Testes size, reflecting sperm competition, is correlated with mating behavior in primates.[69] Primates with large testes tend to experience intense sperm competition in promiscuous multimale groups. Primates with small testes tend to experience male-male competition through physical force in defending resources or mates in the context of harem polygyny. Human testes, which are proportional to body size, are larger than those of gorillas with harem polgyny and smaller than those of chimpanzees with promiscuous multi-male groups.[69] Human testes size suggests an evolutionary history of modest sperm competition, while cross-cultural and fossil evidence suggest the presence of at least moderate rates of polygyny. This further evidence of the unique human mosaic could complicate cross-species analysis. In sum, the cross-cultural association between polygyny and pair-bond stability suggests that polygyny and associated male mating competition may have been important

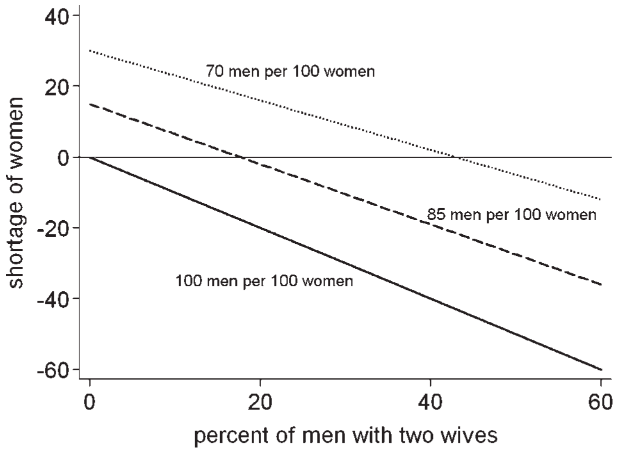

Figure 3. Shortage of women created by polygyny at three population sex ratios. Y-axis values less than 0 indicate a shortage of marriageable women for the remaining marriageable men; values greater than 0 indicate a surplus of marriageable women.

selective pressures during hominin evolution. The polygyny-pairbond hypothesis may be controversial, but the evidence is promising. These limited findings suggest that more detailed analysis of husband-wife and male-female relations across the range of human mating systems will clarify the adaptive functions of human pair-bonding.

Human pair-bonds may be a form of male mating effort through mate guarding,[2] but how do women benefit from pair-bonds? Polygyny levels might reflect male coercion; men may coerce women to stay in conjugal relationships even when there is little benefit for women in doing so.[70–73] But in many societies women often initiate divorce. One solution is for women to tolerate pair-bonds if men provision them and their offspring. Thus, male provisioning could be mating and parenting effort simultaneously (see Hewlett[74] for a similar interpretation of paternal care). The inverse relation between polygyny and men's contribution to subsistence suggests, however, that coercion occurs.[75] If men do not work to provision mates, and if fathers are not involved in direct parental care, why do women have any interest in long-term conjugal unions, monogamous and otherwise? Men may improve their mates' fitness by protecting them.

Male Aggression and Infanticide Apparently Do Not Account for Human Pair Bonds

Male-male competition can increase selective pressure for pair-bonds through infanticide and violence toward women. In some foraging societies, women contribute significantly more dietary calories than men do.[2] Often, meat from men's hunting is shared broadly; hence, women do not need a mate for provisioning.[50] Women might have entered conjugal unions to protect offspring from infanticide by aggressive males, following the suggested trend for pair-bonds among primates.[2,76–78] Men's cost of abandoning a bond could be substantial because male aggression is more dangerous for dependent offspring when they are not defended by their father. Among the Ache forager-horticulturalists, infanticide and homicide are important causes of infant and child mortality, and a co-resident father reduces the likelihood of infanticide.[79] Even among baboons that are not pair-bonded, fathers tend to protect their probable offspring.[80] Direct evidence of the role of infanticide in the evolution of monogamous pair-bonds across species, however, is lacking.[81] In a comparative analysis of nonhuman primates, 5 of 6 predictions from the infanticide hypothesis were not supported in two-adult groups.[53] Whether pair-bonds among polygynous primates function to reduce infanticide is not clear.

> **. . .findings suggest that human pair-bonds probably did not evolve to protect women and offspring from aggressive males.**

In societies where male aggression is frequent and intense, pair-bonds are predicted to be more stable, following the infanticide hypothesis.[2,76] This prediction, however, was not supported in recent cross-cultural tests.[10] Contrary to predictions, divorce was significantly more frequent where males were more aggressive. Again, ethnographic cases fill important gaps in comparative data: The Ache of Paraguay, for example, have remarkably high rates of infanticide, while the average Ache adult has about 10 marriages during his or her life.[79] In addition, a comparative study of nonhuman primates shows "no support for significant levels of male-male aggression related to male protection of females."[53:965] These findings suggest that human pair-bonds probably did not evolve to protect women and offspring from aggressive males. Cross-cultural findings are consistent with female strategies among other primates that avoid infanticide through promiscuous mating, which confuses paternity.[82,83] That, in turn, undoubtedly destabilizes pair-bonds.

Alternatively, it is possible that pair-bonds offer women protection from aggressive men, but that male combat results in realignment of mates when a winner claims the loser's mate for himself. This alternative interpretation makes the male aggression/infanticide hypothesis difficult, if not impossible, to test.

It is possible that protection from infanticide provided the initial evolutionary "kick" for human pair-bonds in our ancestors. The significant positive association between human male aggression and conjugal *instability* among contemporary populations may not reflect the adaptive function of human pair-bonds. Mismatch between current conditions and "environments of evolutionary adaptation" is possible,[84] but evolved mechanisms for human pair-bonding are unlikely to behave in ways diametrically opposed to their evolved function. The mechanics of that mismatch are not evident. If adaptations motivating human pairing evolved in response to male aggression, then the bizarre association among contemporary societies demands empirically testable explanations. Otherwise, the mismatch claim is more dogma than science.

Men's Show-off Work May Be Associated With Unstable Pair-Bonds

As mentioned earlier, male contribution to subsistence shows a nonlinear association with pair-bonds among traditional societies. At low levels of male "provisioning," pair-bonds were least stable. Conjugal stability increased up to a maximum at about 50% male-female contribution, but conjugal stability decreased beyond the 50% point. At 100% male contribution to subsistence, pair-bonds tended to be unstable cross-culturally (Fig. 1).[10] This finding suggests that men's work is not always geared to paternal provisioning. The signal value of men's work could be particularly strong in societies where men are primarily responsible for subsistence. At high levels of male contribution to subsistence, males might use subsistence resources to seek mating opportunities that conflict with stable pair-bonds.

Men’s subsistence work can be geared toward “showing off” their genetic quality through the strength and skills necessary for economic success.[85] If so, male work may not support paternal provisioning.[50] Men’s time allocation to work in different modes of production over the life course is consistent with showing off. Among Machagenka and Piro forager-horticulturalists in lowland South America, for example, young men (20 to 35 years old) spend the majority of their subsistence time in hunting. Time spent hunting dramatically tapers off in middle age (35 to 55 years) even though hunting return rates are highest during middle age after the peak in hunting time allocation.[86] This pattern is consistent with men’s interest in showing off during a mating effort life phase. (Among lowland South American hunter-horticulturalists, men could focus on the signaling benefits of hunting in early adulthood, then shift to the political benefits of gardening later in life when horticultural produce is used for food sharing or making large quantities of beer for hosting fetes for allies.[87]) If conjugal relations are fluid, then payoffs to men’s subsistence work may be greater for mating effort than for paternal investment.

Conjugal instability under male-dominated subsistence suggests some predictions for when men’s work is showing off versus paternal provisioning: Whether men’s work is showing off rather than provisioning depends on patterns of cooperation within the household or camp. When alloparents are present, then male provisioning is less important and women could choose genetically high-quality mates instead of good providers. This should, in turn, enhance the benefit of costly signaling and destabilize conjugal relations.

The nature of risk in the environment[43,83] can also influence women’s mate choice criteria and the benefits of showing off. Extrinsic mortality is the risk of dying, which is equally shared by all members of a population. More specifically, extrinsic mortality is “not sensitive to changes in reproductive decisions.”[89:182] When offspring survival and fitness is less dependent on parental care,[43] pair-bonds may be unstable and women are predicted to concentrate on men’s genetic quality.[75] Conversely, when extrinsic mortality is low and fitness depends on parental care, then fathers’ provisioning could be important. In this situation, women are predicted to concentrate on men’s parenting quality and showing off is predicted to be less salient. Furthermore, the positive association between aggression and conjugal instability cross culturally indicates other channels for costly signaling; that is, men may signal genetic quality through aggressive behavior.[10] Possible associations between extrinsic mortality and the value of “showing off” puts mate choice and pairing behavior squarely in the realm of life-history theory.

Because children can easily observe their parents’ relationship and associated parenting behavior, pair-bonding is well situated to serve important regulatory functions in child development.

The ethnography of unacculturated Marshall Islanders[90] helps make sense of men’s work and pair-bond instability. Among the Marshallese, fishing and horticulture are almost exclusively men’s work; women contribute little to subsistence. Conjugal bonds are fluid, unstable, and informal. A Marshallese proverb characterizes conjugal relations thus: “The woman does as she likes, the man does as he likes.”[91] The Marshallese, therefore offer one model for men’s subsistence contribution and conjugal instability.

Men’s returns from fishing are distributed in ways that enhance their status and are consistent with showing off. Gifts of food are the main means of establishing and maintaining personal relationships.[90] Costly signaling theory suggests that to maximize signal strength, large, difficult-to-obtain game should be shared widely and in public, whereas smaller, easier-to-obtain packages should be consumed in private and not widely shared.[92–94] A small sample of Marshallese fish-distribution events are consistent with these predictions: Large game fish (marlin, shark, and tuna) were widely shared on Majuro in the Marshall Islands, whereas smaller fish were retained for household consumption.[90] In some cases, a fisherman did not keep any of the catch because he “did not need any fish, and wished none.”[90:329] Distribution of fish occurred in public on the beach in ways that might be characterized as “demand sharing.”[91] Men’s marine foraging may be an honest signal of individual qualities that are important in mating competition, alliance building, and status attainment.[91–94] Marshallese culture also includes imposed norms that could increase costly signal strength: Women are prohibited from fishing and “fishing techniques belong essentially to the men.”[90:139]

PAIR-BONDS, SOCIOECOLOGICAL VARIATION, AND CHILD DEVELOPMENT

There appears to be predictable variation in pair-bond stability among societies and individuals. In some social environments, like that on the Marshall Islands, pair-bonds have little influence on fitness, whereas in others, like that among the !Kung, pair-bonds may be essential for survival. Recent theory and research suggest that predictable variation influences the development of life-history strategies. Because children can easily observe their parents’ relationship and associated parenting behavior, pair-bonding is well situated to serve important regulatory functions in child development.[88,95–97]

Life history reflects two basic “decisions”: whether to reproduce now or later and the amount of care to invest in each offspring.[89] These two decisions are associated with a broad suite of behaviors involving pair-bonds, interpersonal relations, and risk-taking. “Choosing” a strategy, whether consciously or not, depends on the costs and benefits of alternatives. When local success depends on high levels of skill and social competence, people are predicted to delay reproduction and invest a lot in a few offspring. When local success depends on stochastic factors more than personal competence, then people are predicted to reproduce early and invest relatively little in many offspring in hopes of beating the odds. If knowledge, skill, and social competence lead to success,[37,98] then low fertility and higher levels of parental investment are predicted to enhance parents’ long-term fitness.[57,99]

In an early influential work, Draper and Harpending[96] proposed that humans have psychological mechanisms that use cues in the childhood family environment to shape the development of reproductive behavior. Fathers’ involvement during children’s development was predicted to affect behavioral “strategies” later in life. Draper and Harpending argued that pair-bond stability and father involvement are reliable indicators of local resource stability and the long-term benefits of parental care. Their model is based in parental investment theory predicting father abandonment in environments where paternal care does not benefit men’s fitness as much as do alternative behaviors related to mating effort.[7]

Draper and Harpending also drew inspiration from the Whitings’ classic cross-cultural study of the aloofness and intimacy of husbands and wives.[100] “Aloofness” between women and their mates may influence socialization practices that shape adult behavior. Hence, an aloof relationship between parents acts as a cue for a child to develop a mating-effort strategy. Conversely, an intimate relationship between parents cues the development of a parental-effort strategy. If childhood environment reliably predicts the demands of the adult environment, then developmental “canalization” is adaptive.

Belsky, Steinberg, and Draper[95] and Chisholm[101] refined the Draper-Harpending model and human life-history theory by suggesting that parent-child attachment mediates between early father involvement and adult behavior. Generally, attachment style refers to relatively stable “internal working models of social relationships.”[102] An insecure internal model views social relationships as unstable, exploitative, and based in mistrust. Conversely, secure attachment includes stable relationships that are supportive and based in trust. Parenting behavior is associated with cultural variation likely reflecting developmental effects.[88] Cross-culturally,[88] father involvement in early childhood is one of the most consistent predictors of the adult reproductive phenotype.

Recent debate about the function of human pair-bonds focuses on mutually exclusive views of men’s work. Thus, men’s work is either for provisioning or for mating effort. This polemic neglects phenotypic plasticity as the key feature of human adaptation to a range of environments.

Father absence may create a family environment in which mothers are less responsive to their offspring because child care is more taxing and maternal attention is more focused on mating effort.[95,101] Maternal unresponsiveness during a sensitive period (birth to 7 years of age) results in insecure internal models, a mating-effort strategy, and unstable conjugal (and other) relationships. Conversely, secure attachment leads to secure internal representations, conjugal unions that are likely to be stable, and a parental-effort strategy.[95]

It has also been suggested that parental unresponsiveness related to single parenthood promotes the development of “externalizing behaviors” that often involve delinquency, violence, and other antisocial acts, as well as risky behaviors geared toward exploiting social and material resources in unstable and unpredictable environments.[95,101,103] Externalizing and lack of inhibition in early childhood may establish a developmental path toward risk-taking later in life. Such differences in development apparently shape cross-cultural trends in adult behavior reflecting evolutionary design for developmental plasticity.[88] In sum, there is substantial socioecological variation in pair-bond stability that may influence cultural models of social cognition and risk taking.

A sizeable body of research supports many predicted relations between pair-bond stability and life-history development.[97] Stressful family environments and low levels of parental care are associated with development emphasizing mating-effort behaviors; stable families and higher levels of parental care are associated with the development of greater emphasis on parental-effort behaviors.[97,104,105] Quality of parental care during childhood may indicate appropriate adult strategies and affect developmental pathways tuned to socio-environmental risk.

CONCLUSION

There may be several adaptive functions for human pair-bonds in different environments. Recent debate about the function of human pair-bonds focuses on mutually exclusive views of men’s work. Thus, men’s work is either for provisioning or for mating effort. This polemic neglects phenotypic plasticity as the key feature of human adaptation to a range of environments. There is solid evidence of paternal provisioning during lactation, indicating selective pressure for pair-bonds. Parental investment factors are further apparent in associations between alloparenting and pair-bond stability: When alloparents are more available, biparental care is less crucial and men might increase their fitness through other behaviors. Cross-cultural analyses and comparisons with other mammals suggest, however, that male mating competition also plays a part in pair-bonds. Where there is a shortage of women, conjugal unions tend to be more stable. Moreover, the inverse relation between polygyny and male provisioning[75] and the positive association between polygyny and conjugal stability[10] hints that there may be two different types of human pair-bond: a "biparental bond" geared toward child rearing and a "mate-defense" pair-bond geared toward male reproductive success. If men in pair-bonds do not protect women against aggression nor provision offspring, then men must coerce women into accepting a conjugal union.[71] This is similar to the kind of coercion suggested for some polygynyous unions.[72] Hence, women's motivation for entering pair-bonds may range from provisioning to coercion, which has important implications for behavior and well-being.

There is little evidence indicating that infanticide risk and male-male aggression promote pair-bonds in humans or nonhuman primates. It is possible that protection from infanticide provided the initial evolutionary "kick" for human pair-bonds. Among traditional human societies, however, male aggression is positively associated with conjugal instability. Mismatch between current and evolutionary environments is possible, but it seems unlikely that adaptive mechanisms would behave in ways completely inconsistent with evolved function.

Fathers' presence may serve as a cue for developing reproductive strategies. Yet many studies demonstrate that fathers' presence alone is not the only predictor of developmental outcomes.[101] It is possible that families based on "biparental" versus "mate-defense" pair-bonds provide substantially different developmental environments for children. The quality of pair-bonds may guide offspring reproductive and sexual development toward locally "expected" conditions. Better understanding of the nature and variety of human pair-bonds could open new avenues for life-history research. For example, we might expect mate defense bonds to exist even when high extrinsic mortality, which is independent of parental care, creates rapidly diminishing returns for parental effort, including paternal provisioning.[43] If we view pair-bonds as exclusively adapted for paternal provisioning, then some otherwise promising models for human reproductive behavior may be neglected.

The analysis is further complicated because the relationship between men's production and conjugal stability is not linear. Relationships among showing off, high levels of male subsistence contribution, and pair-bond instability are not clear. There may be some configuration of domestic cooperation that occurs in male-dominated subsistence economies that permits conjugal instability and "show-off" effort. It seems likely that male maternal kinsmen fill the provisioning role in such economies, but the socioecological underpinnings of that complex are not readily apparent. Relations among pair-bond stability, division of labor, domestic cooperation, mate competition, and showing off require further study.

In sum, human pair-bond behavior appears to be considerably more complex than Washburn and Lancaster envisioned in 1966. This complexity suggests important ecological variation in human mating and parenting decisions. The human adaptive complex, including culture, may well have evolved to exploit predictable environmental variation. Flexible conjugal behavior and associated developmental effects could provide important insights into this evolutionary process.

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