

Evolutionary Ecology of Human Pair-Bonds

Cross-Cultural Tests of Alternative Hypotheses

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Human pair-bonds may have multiple evolved functions. One long-standing hypothesis suggests that pair-bonds evolved for male provisioning. Alternatively pair-bonds may occur as a response to male mating competition when benefits of staying with a current mate outweigh costs of seeking new mates. A third hypothesis suggests that pair-bonds function to protect against infanticide by aggressive males. Tests of these hypotheses used data from the Standard Cross-Cultural Sample on divorce, alloparenting, polygyny, male contribution to subsistence, and male aggression. Results were not consistent with the infanticide and/or male aggression hypothesis; however, parental investment and male mating competition accounted for significant cross-cultural variance in conjugal stability, suggesting that human pairing has multiple functions. Pair-bonds tended to be stable when men and women contributed equally to subsistence, and unstable when either sex contributed the majority to subsistence. The authors use the ethnographic record to explore relations among pair-bonds, mating competition, showing off, and conjugal complementarity.

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Pair-bonds may be elemental in human social organization. We define *pair-bonds* as the long-term affiliation of two individuals including a sexual relationship.¹ Among humans this relationship is usually associated

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with marriage, broadly defined. Stable mating relationships appear widespread among our species, and they apparently have important economic, reproductive, and social implications. Yet we understand little about the evolution of human pairing. There are several apparently conflicting hypotheses for the function of pair-bonds. Here, we derive hypotheses from two related lines of reasoning: parental investment and sexual selection theories. Sexual selection requires sex differences in parental investment. Compared with men, women have higher minimal levels of parental effort (time, energy, etc. associated with producing viable offspring) because they are physically tied to reproduction through pregnancy and lactation. Conversely men can “invest” relatively little in one child—a very small amount of time and energy in a single copulation is all that is required. If female reproduction is relatively expensive and male reproduction is relatively cheap, then women should be choosy about their mate’s genetic quality and willingness to help care for their children. Men, in turn, should compete for access to choosy women. This basic sex difference creates a set of sexual conflicts between men and women that are played out in various human “mating systems” around the world (see Low, 2000). One key element in human mating systems is the stability of conjugal unions or pair-bonds. We test alternative hypotheses for the evolution and socioecological variation of human pairing using data from the Standard Cross-Cultural Sample (SCCS; Murdock & White, 1969) that includes societies across the spectrum of human subsistence practices, social organizations, and world regions.

Cross-cultural analysis can be particularly useful in studies of human evolution. We can examine covariation in socioecological context and specific traits. The approach allows us to explore the current adaptive function of a trait and the selective pressures that may have provided the initial “evolutionary kick” that led to the existence of the trait in our species. Here we examine the adaptive function and socioecology of human pair-bonds through analysis of cross-cultural variation in conjugal stability. Variation in cross-cultural conjugal stability may help explain the evolution of human mating systems better than studies of monogamy or polygyny because the latter refer explicitly to marriage rules rather than mating behavior (Low, 2003). In contrast the frequency of divorce reflects the stability of male–female long-term mating relationships, which may have been particularly salient in the course of human evolution (Lancaster & Lancaster, 1987). The socioecological associations we explore here have important implications for the evolution of human pair-bonds and the evolutionary ecology of contemporary mating behavior.

Biparental investment is one potential benefit of human pair-bonds (Lancaster & Lancaster, 1987). *Parental investment* is defined as expenditures

(cash, time, attention, etc.) benefiting one offspring at a cost to parents' ability to invest in other offspring or reproductive opportunities (Clutton-Brock, 1991, p. 9). Father abandonment, hence, is predicted in environments where paternal care does not benefit men's fitness as much as alternative behaviors (Trivers, 1985).² A cross-species analysis of mammals and birds indicated that pair-bonding "may be selectively favored in humans and other animals when mothers' feeding requirements interfere with their baby-tending" (M. Ember & Ember, 1979, p. 48). More recent comparative analysis, however, suggests that pair-bonds in mammals may not have evolved in response to pressures for paternal care (Komers & Brotherton, 1997), although biparental care may be important for avian pair-bonds (Burley & Johnson, 2002). Children have a relatively long and expensive developmental period when they are dependent on others for their livelihood and protection. Parental care can be a difficult task for one person. Because a father shares 50% of his genes with his offspring, from an inclusive fitness standpoint, he is the most likely caretaker in addition to the child's mother who is bound to the child through pregnancy and lactation (Quinlan & Quinlan, in press). A father can care for his children in at least two ways: He can provide direct care or he can help the mother who is then freed to give direct care. Male provisioning may be particularly important during lactation (Marlowe, 2003a; Quinlan & Quinlan, in press). Among foragers men increase their time spent in subsistence when their mate is nursing, and women's subsistence work is inversely related to her mate's when the couple has a nursing child (Hurtado, Hill, Kaplan, & Hurtado, 1992; Marlowe, 2003a).

A male has other fitness interests in addition to paternal provisioning. He can choose to put his time and energy in pursuing mates rather than providing for his offspring. The trade-off to male mating and parenting effort depends on the costs and benefits of alternatives. When women and children are largely dependent on males for subsistence, then the cost of abandoning a pair-bond may be higher than the benefit of pursuing additional mates. When other individuals help the mother, then a man's cost of abandoning a relationship is reduced. This line of parental investment reasoning leads to two cross-cultural predictions: (a) In societies where male contributions to subsistence are high, women are dependent on men, and pair-bonds are predicted to be relatively stable; (b) In societies where alloparents are commonly available, a father's cost of abandoning a relationship is reduced, and pair-bonds are predicted to be relatively unstable.

Male mating competition can also increase selective pressures for pairing and conjugal stability, thus pair-bonds could reflect male mating effort (through mate guarding) rather than parenting effort (Hawkes, 2004). There

are at least two possibilities. Comparative analysis indicates that the spatial distribution of females rather than male provisioning predicted monogamy among nonhuman mammals (Komers & Brotherton, 1997). Monogamy, however, is not synonymous with long-term pairing. Gorillas for example, are “pair-bonded” in the context of “harem defense” polygyny (Watts, 1996). Yet gorillas show no male provisioning. Pair-bond stability in harem defense polygyny (Emlen & Oring, 1977) and monogamy when females are spatially dispersed (Komers & Brotherton, 1997) may share a common logic: Males defend relatively long-term mating relationships when there are high costs to abandoning that relationship to search for another mate. In either case the probability of finding another female who is not bonded may be relatively low. The density of females across the landscape is positively associated with the probability of encountering a potential new mate. The spatial distribution of women seems to have little relevance to variation in 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 intensity of male mating competition can increase the costs of abandoning a current bond in favor of seeking a new bond. If there are relatively few females available, then males should defend their current relationship, and pair-bonds should be relatively stable. In one case, male-biased operational sex ratio is predicted to lead to stable pair-bonds and female bias is predicted to lead less stable bonds (Pedersen, 1991). Cross-national studies found that promiscuity was more acceptable in populations with female-biased sex ratios, less acceptable in populations with male-biased sex ratios (Schmitt, 2005), and female-biased sex ratio was associated with a greater degree of single parenthood (Barber, 2003). Unfortunately, the SCCS does not have sufficient sex-ratio data for multivariate analysis.³ The level of polygyny similarly may be associated with conjugal stability because polygyny creates a shortage of women, increasing the male cost of abandoning a relationship.⁴ This prediction may appear problematic because in polygynous societies some men manage to have multiple mates. However, polygyny usually occurs at low levels (40% would be a very high level of polygyny), indicating that most men compete to establish and maintain a single mating relationship. This reasoning leads to a somewhat counterintuitive cross-cultural prediction: In societies with higher levels of polygyny, pair-bonds are predicted to be relatively stable. The prediction does not take female choice into account; however, rather we assume (for now) that pair-bonds also benefit women or that women are coerced into conjugal unions. We return to these possibilities later in the discussion.

Male mating competition can also increase selective pressure for pair-bonds through infanticide. Human pair-bonds may not have evolved for male provisioning; however, women may have entered conjugal relationships to protect offspring from infanticide by aggressive males (Hawkes, 2004; Mesnick, 1997). Men's cost of abandoning a bond is greater where male mating competition is intense, not only because of the reduced probability of finding another mate but also 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 coresident father reduces the likelihood of infanticide (Hill & Hurtado, 1996). Even among baboons, which are not pair-bonded, fathers tend to protect their probable offspring (Buchan, Alberts, Silk, & Altmann, 2003). The effect of male aggression on pair-bond stability follows the suggested trend for pair-bonds among primates (Palombit, 1999). Direct evidence for the role of infanticide in the evolution of pair-bonds across species, however, is lacking (Reichard, 2003). In societies where male aggression is frequent and intense, pair-bonds are predicted to be more stable (Hawkes, 2004; Mesnick, 1997).

In sum, we test alternative hypotheses with data from the SCCS (Murdock & White, 1969). Hypotheses derived from parental investment theory predict stable conjugal relationships in societies where male provisioning is particularly important and unstable conjugal relationships when alloparents are available and important. Hypotheses derived from sexual selection theory predict that pair-bonds are stable when male mating competition through polygyny is intense and when males are highly aggressive.

Method

Data are from Murdock and White's (1969) SCCS,⁵ which includes information on conjugal stability, alloparenting, polygyny, and aggression for 37 to 72 societies (depending on the analyses). We examined four effects on conjugal stability: (a) male aggression, (b) male contributions to subsistence, (c) availability of alloparenting, and (d) level of polygyny. We also included quadratic terms for each predictor to examine curvilinear effects. Quadratic terms with $p < .10$ were retained in the models.

The outcome variable *frequency of divorce* (Broude & Greene, 1983; SCCS variable 744 in Divale, 2004) was recoded into 1 = *divorce common* and 0 = *divorce uncommon: Universal or almost universal and common, frequent, not uncommon* were recoded as *divorce common*. And *moderate: a small*

minority of couples divorce, frequent in first years of marriage before children, and Rare, isolated instances, never were recoded as *divorce Uncommon*. Frequency of divorce was dichotomized to simplify the models because with this small sample several categories had few observations, making an ordinal logit analysis inappropriate.

We used four predictor variables indicating parental investment and mate competition. Alloparental involvement is predicted to be positively associated with frequency of divorce because alloparenting reduces the cost of father abandonment for offspring well-being and ultimate fitness. We used nonmaternal relationships in early childhood (Barry & Paxson, 1971; variable 52) as a measure of alloparenting, which was recoded as 1 = *principally mother* to 3 = *primarily others*. Men's contribution to subsistence is predicted to be inversely related to frequency of divorce because the extent of male contribution to subsistence indicates maternal and child dependency. The variable was recoded from variable 885 (female contribution to subsistence; White cited in Divale, 2004) by subtracting variable 885 from 100. Male aggression is predicted to be inversely related to frequency of divorce because women may attempt to maintain pair-bonds to avoid infanticide in environments where males are highly aggressive. Aggression was calculated as the sum of SCCS variables 1665 homicide, and 1666 assault; C. R. Ember & Ember, 1992) and ranges from 2 (low on both variables) to 18 (high on both variables). Level of polygyny is predicted to be inversely associated with frequency of divorce because the intensity of male mating competition increases the cost of leaving one mate to find another when polygyny makes women scarce and male competition relatively intense. Polygyny (Murdock & Wilson, 1972; variable 79) was coded as 1 = *polyandry* (with no cases in this analysis), 2 = *monogamy*, 3 = *< 20% polygynous men*, 4 = *> 20% polygynous men*.

After constructing the initial predictive models we conducted an extensive search for potential control variables. We added potential controls to logistic models to explore relations with social complexity, economy, subsistence strategy, population size, community structure, weather patterns, latitude, region, acculturation, modernization, and contact with "Western-industrial" populations. One significant control variable was retained in the models: A region dummy variable for Eurasia that was recoded from variable 200 (Divale, 2004, p. 37).

We used logistic regression in STATA 9 to examine associations between conjugal stability and the predictor and control variables. Results are presented as adjusted log odds (LOs) in Table 1. LOs are adjusted for other predictor and control variables in the model. Positive LOs indicate that divorce was more likely to be common, and negative LOs indicate that

Table 1
Multivariate Logistic Regression Models Showing
Effects on Divorce Cross-Culturally

	Log Odds	Robust SE	p value	Lower CL	Upper CL
Variables: Model 1 (<i>n</i> = 37, <i>R</i> ² = .52, <i>p</i> = .10)					
Male aggression	.31	.15	.036	.02	.60
Male % contribution to subsistence	-.64	.34	.063	-1.31	.04
Male % contribution to subsistence squared	.006	.00	.033	.00	.01
Level of polygyny	-2.50	1.18	.034	-4.80	-.19
Importance of allomothers	1.66	.94	.076	-.18	3.49
Eurasian region	-9.85	3.47	.005	-16.66	-3.04
Constant	17.82	10.81	.099	-3.37	39.01
Variables: Model 2 (<i>n</i> = 58, <i>R</i> ² = .21, <i>p</i> < .01)					
Male % contribution to subsistence	-.49	.17	.003	-.82	-.16
Male % contribution to subsistence squared	.004	.00	.004	.00	.01
Importance of allomothers	.75	.38	.047	.01	1.49
Eurasian region	-3.11	1.07	.004	-5.21	-1.01
Constant	12.20	4.88	.012	2.63	21.76
Variables: Model 3 (<i>n</i> = 50, <i>R</i> ² = .17, <i>p</i> = .08)					
Male aggression	.12	.07	.097	-.02	.26
Level of polygyny	-.34	.49	.490	-1.29	.62
Eurasian region	-2.74	1.10	.013	-4.91	-.58
Constant	.19	1.50	.900	-2.75	3.13
Variables: Model 4 (<i>n</i> = 44, <i>R</i> ² = .41, <i>p</i> = .05)					
Male aggression	.23	.12	.054	.00	.46
Male % contribution to subsistence	-.37	.19	.054	-.74	.01
Male % contribution to subsistence squared	.004	.00	.020	.00	.01
Level of polygyny	-1.58	.78	.042	-3.10	-.05
Eurasian region	-7.48	2.33	.001	-12.04	-2.92
Constant	11.22	6.38	.078	-1.27	23.72
Variables: Model 5 (<i>n</i> = 72, <i>R</i> ² = .14, <i>p</i> = .01)					
Male % contribution to subsistence	-.31	.12	.009	-.54	.08

(continued)

Table 1 (continued)

	Log Odds	Robust SE	<i>p</i> value	Lower CL	Upper CL
Male % contribution to subsistence squared	.003	.001	.007	.001	.005
Eurasian region	-2.83	.85	.001	-4.50	-1.17
Constant	8.51	3.45	.014	1.75	15.28

Note: The outcome is divorce common = 1, uncommon = 0; *p* value = two-tailed significance for log odds based on robust SE; CL = 95% confidence limit based on robust SE; R^2 = pseudo-coefficient of determination; *p* = model significance; $R^2 = .09$, $n = 85$, $p = .09$ for Eurasian region as the only variable in the model.

divorce was less likely to be common. We computed robust standard errors for clustered data to adjust for potential intraclass correlation among the regionally clustered societies. We used language family (Burton, 1999; variable 1859 in SCCS) as the clustering variable.

Results

The multivariate analysis showed some surprising results. As predicted, availability of allomothers was positively associated with divorce: Divorce was more common when nonmaternal child care is more common (LO = 1.66, $p = .005$; Table 1, Models 1 and 2). This finding suggests that pair-bond stability responds to requirements for paternal care. Other findings, however, suggest that mating competition is also important, reflecting socio-ecological contingencies for human pairing.

Level of polygyny was positively associated with pair-bond stability (LO = -2.5, $p = .034$): Divorce was less common in societies where polygyny occurs at higher levels (Table 1, Models 1 and 4). This finding suggests that pair-bonds respond to male mating competition in addition to requirements for parental care. Pair-bonds might be more stable where mating competition makes women scarce for many men. This relationship was possibly confounded because polygyny has been associated with a female-biased sex ratio (M. Ember, 1974). Level of polygyny in this analysis, which includes sororal and nonsororal polygyny, was not associated with sex ratio (Table 2). The conflicting results may be due to different operational definitions of *polygyny* used here and in M. Ember (1974), the latter more restrictive. It is not clear, in addition, that the average female bias of

Table 2
Mean Sex Ratio (male/female \times 1000) by Polygyny Level

	N	M	SD	SE	Minimum	Maximum
Monogamy	11	101.6	7.5	2.3	89.4	115.5
Polygyny < 20%						
plural wives	25	102.6	16.4	3.3	65.6	138.9
Polygyny > 20%						
plural wives	22	102.8	28.7	6.1	67.8	184.6
Total	58	102.5	20.7	2.7	65.6	184.6

Note: $F = .014$, $p = .99$; Sex ratio data are from C. R. Ember & Ember (1992) variable 1689 in Divale (2004).

Table 3
Mean Excess Male Mortality From War by Polygyny Level

	N	M	SD	SE	Minimum	Maximum
Monogamy	17	3.2	2.7	.7	0	6
Polygyny < 20%	40	1.9	2.3	.4	0	6
plural wives						
Polygyny > 20%	21	3.4	2.4	.5	0	6
plural wives						
Total	78	2.6	2.5	.3	0	6

Note: $F = 3.4$, $p = .04$. Male mortality from war are unpublished data obtained from Ember & Ember (n.d.)

111 females to 100 men reported for societies with polygyny by M. Ember (1974, p. 200) is sufficient to offset a shortage of marriageable women created by polygyny. Excess male mortality in war has also been associated with polygyny (M. Ember, 1974; M. Ember, Ember, & Low, n.d.). Male mortality in war was associated with polygyny level here; however, it was not a linear (or monotonic) relationship (Table 3); hence, including it as a control would have no influence on the logistic regression models. The predicted relationship between polygyny level and male mating competition should hold in sororal and nonsororal polygyny; we see no reason to restrict the analysis to one or other. In sum, factors that may be confounded with polygyny level did not account for the association between polygyny and conjugal stability reported here.

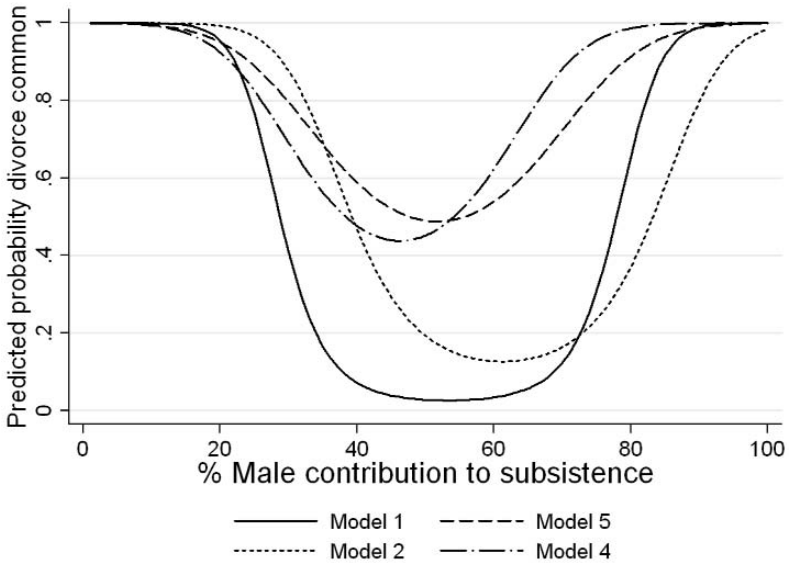
Contrary to predictions from the infanticide and/or male aggression hypothesis (Hawkes, 2004; Mesnick, 1997; Palombit, 1999), male aggression was positively associated with frequency of divorce ($LO = .31, p = .036$): Divorce tended to be common in societies where males were more aggressive (Table 1, Models 1 and 4). This suggests that human pair-bonds were not selected for in response to male aggression; however, we discuss an alternative interpretation later.

Analysis of male contribution to subsistence presented one of the most surprising results. The model showed a quadratic effect of male contribution to subsistence on the frequency of divorce (Figure 1 and Table 1, Models 1, 2 and 5). As predicted, divorce tended to be common when men contributed little to subsistence ($LO \text{ for male contribution to subsistence} = -.64, p = .063$), and the probability of divorce decreased as men contributed more. However, divorce became more common at high levels of male contribution ($LO \text{ for male contribution to subsistence squared} = .006, p = .033$). Plots of the predicted probability of divorce (Figure 1) show that divorce was relatively uncommon in societies where men and women contribute equally to subsistence. This result suggests an interesting kind of male–female complementarity that was not easily predicted.

Logistic regression is somewhat problematic with small samples. The problems are greater as the ratio of sample size to covariates decreases. We tested the adequacy of these results by selectively removing terms from the models. Models 2, 4, and 5 (Table 1) suggest that results for men's contribution to subsistence were fairly robust; however, there were some differences in the predicted probabilities (Figure 1). Similarly, Models 1 and 2 (Table 1) indicate that results for allomothers were also robust. The effect of polygyny on the frequency of divorce was mediated by male contribution to subsistence: Polygyny was not a significant predictor of divorce when it entered the model without male contribution to subsistence ($LO = -.34, p = .49$; Model 3, Table 1). This mediation was due to the inverse relationship between degree of polygyny and male contribution to subsistence (Marlowe, 2000, 2003b). However, Model 4 (Table 1) suggests that effects of polygyny were also robust.

In a previous analysis of SCCS data, we showed that weaning was relatively early in societies where divorce was common (Quinlan & Quinlan, in press). We also showed that age at weaning was inversely associated with presence of allomothers (Quinlan & Quinlan, 2007). We included age at weaning (Barry & Paxson, 1971; variable 45) in an additional logistic regression analysis (not shown) including all of the variables in Model 1 (Table 1). Age at weaning mediated the effect of allomothers on frequency

Figure 1
Relationship Between Male Contribution to Subsistence and Probability That Divorce is Common Among Standard Cross-Cultural Sample (SCCS) Societies



Note: Lines indicate predicted probability from the models in Table 1.

of divorce, and neither variable was a significant predictor when they entered the model together. If allomothers was removed from Model 2 (Table 1) and replaced with weaning age, then weaning age was a significant predictor of divorce ($LO = -.051$, $p = .04$, not shown in Table 1). This finding supports the prediction that pair-bonds at least partially respond to parental care requirements.

East Eurasian region was a significant and strong predictor of divorce. Eurasian groups tended to divorce relatively infrequently (LO ranges from -2.83 to -9.85 in Table 1). Inclusion of the Eurasian indicator variable was an important mediator of other effects. There was also one interaction effect. The interaction effect for aggression \times Eurasia on divorce was significant ($LO = -8.36$, $p = .000$, $n = 50$) when it entered a model with aggression and

Eurasia. The interaction indicated that aggression had little effect on conjugal stability among East Eurasian populations. We interpret the East Eurasian effects as the result of diffusion (Low, 2003, p. 164) or cultural phylogenetics associated with mating systems (Borgerhoff Mulder, George-Cramer, Eshleman, & Ortolani, 2001) that explain about 9% of the cross-cultural variance in conjugal stability. Further analysis (not shown) indicated that East Eurasian region was significantly associated with male contribution to subsistence and level of polygyny, suggesting that diffusion or phylogenetic effects may have ecological underpinnings.

Discussion

These results are consistent with multiple selective pressures on human pair-bonds. Pair-bonds may respond to high levels of male mating competition. And cross-cultural conjugal stability also appears consistent with male parenting effort. Level of male aggression, however, was associated with conjugal stability in the opposite direction predicted.

The infanticide and/or male aggression hypothesis for pair-bonds was not supported in these analyses. Contrary to predictions, male aggression was positively associated with frequency of divorce. Divorce was most frequent where males were most aggressive. The Ache of Paraguay (who are not in our sample), for example, have very high rates of infanticide and very high divorce rates. The average Ache has about 10 marriages during his or her life (Hill & Hurtado, 1996). This finding suggests that human pair-bonds may not have evolved to protect women and offspring from aggressive males (Hawkes, 2004; Palombit, 1999). Alternatively it is possible that pair-bonds do offer women protection from aggressive men; however, that male combat results in realignment of mates when winners claim the loser's mate for themselves and when women choose to leave an old mate in favor of new mate who is better able to protect them. This alternative interpretation makes the infanticide and/or male aggression hypothesis difficult if not impossible to test.

Mating competition indicated by polygyny level was inversely associated with frequency of divorce, which may indicate that males maintain pair-bonds when there is a shortage of women. In a similar analysis of human mating systems Marlowe (2000, pp. 52-54; 2003b) argued that the inverse relation between polygyny and male contribution to subsistence may reflect female choice for male provisioning. He also suggested that polygyny has different causes in different subsistence modes (Marlowe, pp. 52-54; 2003b).

Our analysis of conjugal stability sheds additional light on the nature of human mating systems: Subsistence strategy was not a significant predictor of conjugal stability nor did subsistence mediate the effect of polygyny on conjugal stability. In short, we cannot reject the hypothesis that pair-bonds evolved in response to male mating competition. Human pair-bonds may be a form of male mating effort through mate guarding (Hawkes, 2004). This finding raises an important question: How do women benefit from pair-bonds? Polygyny levels might reflect male coercion (Marlowe, 2003b; Strassmann, 2000); hence, men may coerce women to stay in a conjugal relationship even when there is no real benefit for women to do so. However, in many societies women typically initiate divorce (e.g., Gregor, 1985, pp. 27-28; Lee, 1993, pp. 83-84). One solution may be that women agree to pair-bonds if men agree to provision them and their offspring; hence, male provisioning could be mating and parenting effort simultaneously (see also Hewlett, 1992, for a similarly confounded interpretation of paternal care). However the inverse relation between polygyny and men's contribution to subsistence suggests that coercion may occur (Marlowe, 2000). A further complication is that there may be different influences on polygyny depending (at least in part) on the relatedness of cowives (White & Burton, 1988). In short, if men's work does not result in some kind of provisioning, and if men are not engaged in other forms of direct parental care, then why do women have any interest in long-term conjugal unions, monogamous and otherwise? This question requires additional research.

Paternal investment considerations are apparent in the effects of alloparenting: When alloparents are available, pair-bonds are less stable. These results are consistent with other findings. A remarkable study of the matrilineal Khasi in Northeast India corroborates these results: Among the Khasi the presence of wife's mother was inversely associated with the husband's economic contribution to the family (Leonetti, Nath, Hemam, & Neill, 2004) and probability of divorce (Leonetti, Nath, & Hemam, n.d.). Similarly, the effect of male contribution to subsistence on frequency of divorce may reflect the benefits of provisioning, though that interpretation is not straightforward.

Male contribution to subsistence showed a surprising quadratic effect: At low levels of male "provisioning" pair-bonds were least stable; however, conjugal stability increased up to a maximum at about 50% male-female contribution. Beyond that 50/50 point, conjugal stability decreased when at 100% male contribution pair-bonds tended to be unstable cross-culturally.⁶ Pair-bonds may be worthless to women when men contribute little to subsistence. Conversely at high levels of male contribution to subsistence, males might use subsistence resources to seek mating opportunities that

conflict with stable pair-bonds. However, where subsistence depends on male–female cooperation or reciprocity, pair-bonds are stable, suggesting male–female complementarity in some environments that is not strictly male provisioning and female child rearing. In some societies men and women may need each other to provide for offspring and each other.

Pair-Bonds and Showing Off

When men are responsible for most subsistence, then men’s subsistence work may be particularly geared toward “showing off” their genetic quality as potential mates through the strength and skills necessary for economic success (Hawkes & Bliege Bird, 2002). If so, male provisioning may not reflect paternal provisioning (Hawkes, O’Connell, & Blurton Jones, 2001). The pattern of men’s time allocation to work in various 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 (age 20 to 35 years) spend the majority of their subsistence time in hunting; and time spent hunting dramatically tapers off in middle age (age 35 to 55 years) even though return rates from hunting are highest during middle age well after the peak in time spent hunting (Gurven & Kaplan, 2006, p. 30). This pattern is equally consistent with men’s interest in showing off as it is with skill development for resource maximizing for paternal investment (though Gurven and Kaplan, 2006, did not address the show-off implications of the data). If conjugal relations are fluid, then payoffs to men’s subsistence work may be greater for additional mating opportunities than for paternal investment. This line of reasoning suggests that pair-bonds may be least stable in societies where men contribute the most to subsistence.

Ethnography of Marshallese islanders (Spoehr, 1949; included in our analysis of the SCCS) helps to interpret the curvilinear association between sexual division of subsistence and pair-bond stability. Among the Marshallese fishing and horticulture are almost exclusively men’s work; women contribute little to subsistence (pp. 134–154). 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” (Erdland, 1914, n.p.). The Marshallese, hence, are a good fit for the logistic model of men’s subsistence contribution and conjugal stability. Men’s returns from fishing are distributed in ways that enhance their status and are consistent with showing off. Fish are the principal form of tribute to chiefs, who can reciprocate for distinguished service by granting lands and distinctions to commoners

(Spoehr, 1949, p. 153). Gifts of food are the main means of establishing and maintaining personal relationships (Spoehr, 1949, p. 154). A small sample of Marshallese fish distribution events seems consistent with costly signaling: Spoehr (1949) reported that large game fish (marlin, shark, and tuna) were widely shared on Majuro in the Marshall Islands whereas smaller fish were retained for household consumption (p. 239). In some cases the fisherman did not keep any of the catch because he "did not need any fish, and wished none." Distribution of fish occurred in public on the beach in ways that might be characterized as "demand sharing" (p. 239). Men's marine foraging may then be an honest means of signaling individual qualities important in mating competition, alliance building, and status attainment (Bliege Bird, Smith, & Bird, 2001; Smith & Bliege Bird, 2000; Smith, Bliege Bird, & Bird, 2003). Marshallese culture also includes imposed norms that may increase the strength of costly signals: Women are prohibited from fishing, and "fishing techniques belong essentially to the men" (Spoehr, 1949, p. 139).

In sum, the association between male-dominated subsistence and conjugal instability suggests some predictions for when men's work is showing off and when it is geared toward paternal provisioning: When alloparents are present, male provisioning is less important, and women may choose genetically high-quality mates rather than good providers, which should in turn enhance the benefit of costly signaling and destabilize conjugal relations. Conversely, when pair-bonds are unstable, males may pursue work that demonstrates their genetic quality, and costly signaling should be a main focus of men's work. Finally, the nature of risk in the environment (Quinlan, 2007; Quinlan & Quinlan, 2007) may influence women's mate choice criteria and the benefit of showing off. When there is high extrinsic mortality (or risk), then fitness is less dependent on parental care (Quinlan, 2007), pair-bonds may be unstable, and women are predicted to concentrate on signs of men's genetic quality. Conversely when extrinsic mortality is low and fitness depends on parental care, then father's provisioning may be especially important, women are predicted to concentrate on men's parenting quality, and showing off is predicted to be relatively unimportant. Furthermore, the positive association between aggression and conjugal instability cross-culturally may reflect other channels for costly signaling. These possibilities raise issues about the direction of causality in the current analyses. Does showing off cause conjugal instability or does conjugal instability (related to other factors) cause showing off? The current study cannot resolve this issue. We suggest that further research on costly signaling should consider the division of labor, conjugal stability, and the nature (extrinsic vs. intrinsic) of environmental risk.

Pair-Bonds and Sexual Complementarity

Our cross-cultural analysis suggests that subsistence complementarity leads to conjugal stability (see also Kaplan, Hill, Lancaster, & Hurtado, 2000). We use the ethnographic record to further explore relations between conjugal stability and sexual complementarity in subsistence. Among the Dobe !Kung, divorce is common early in marriage; however, ethnographic and demographic accounts indicate that marriages are quite stable after an initial “stormy” period (Howell, 2000, pp. 236-239; Lee, 1993, pp. 83-84). 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” (Howell, 2000, p. 177). Average age of first birth among !Kung women is about 19 years (Howell, 2000, p. 128), at least 3 years after the average age of menarche. These data suggest that many if not most failed marriages occur before childbirth.

There is important food sharing between !Kung husbands and wives (Howell, 2000, p. 228), and in the SCCS !Kung men contribute about 40% of the diet. Meat from men contributes about 30% of calories consumed (Lee, 1993, p. 50). Because meat is often shared broadly beyond the nuclear family, male provisioning may not account for human pair-bonds (Hawkes et al., 2001). And among the !Kung there appear to be multiple benefits to sharing meat broadly among the camp (Wiessner, 2002). Although established !Kung marriages are quite stable, !Kung camps may not be stable as they fission in the face intragroup conflict (Lee, 1993). Lee (1993) described a life cycle of !Kung camps centered around a core group of siblings and spouses with more peripheral members that may come and go (pp. 62-66). In the context of this fission–fusion social organization, conjugal complementarity may allow a conjugal family to be self-sufficient for extended periods of time (e.g., Bell, 2001). Cooperative conjugal units allow humans residential flexibility to respond to local 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 individual 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 (Howell, 2000, pp. 52-53).

Husband–wife subsistence complementarity is also present in more complex social systems. Among the Trobriand islanders, who have very stable conjugal unions, subsistence cooperation among husbands and wives takes on a symbolic dimension with clear referent to reproductive complementarity. The Trobriand taro and yam gardening process, from preparation to harvest, takes approximately 9 months, and Trobrianders speak about

subsistence using terms also used for fertility and birth (Austen, 1939; Brindley, 1984). Although Trobrianders do not recognize a direct connection between coitus and conception (Malinowski, 1929), they believe that fathers have an essential social and developmental role in forming children. Through a sexual relationship, a man is said to prime a woman for pregnancy, just as a man cuts the path to the plot, and prepares a garden for planting (Brindley, 1984). A man also helps the fetus grow by keeping the mother's body warm (Austen, 1934). Trobrianders reckon that an infant is formed from the flesh of its mother; however, a father maintains such close contact with the mother during pregnancy and with the child when it is born, that his physical features become impressed on the child (Austen, 1934, pp. 112-113). Men's child rearing does not replicate mothering, "rather fathers direct their contributions to enhancing the child's potential [social] power" (Weiner, 1988, p. 56). Complimentarity in parenting roles may shape or reflect the Trobriand (Kivila) term *kopoi*, which translates to breastfeeding as well as paternal nurturing (Weiner, 1988).

Trobrianders refer to *gardens*, *harvesting*, and *produce* with metaphors for *human gestation*, *birth*, and *babies*. The formula of the garden magician at the preliminary harvest includes the recitation, for example, "The belly of my taro—taro round off . . . The belly of my garden becomes smooth like a trimming-board." Then, at the main harvest ceremony, the magician recites, "The belly of my garden leavens . . . The belly of my garden lies down . . . The belly of my garden swells as with a child." Then the magician extracts the first yam and ceremoniously cuts the stem in a manner that alludes to human birth (Brindley, 1984).

Nine months before the harvest, the horticultural year begins with the first gardening phase (Brindley, 1984; Malinowski, 1935). This period occurs during the dry, sunny season and entails intense male magic and labor (clearing, planting, and building fences). The second phase, which occurs during the rainy season, is the time of subterranean plant growth, and is dominated by women who, with continual weeding, maintain a clean, healthy growing environment for the tubers, as is the female role in gestation (Brindley, 1984; Malinowski, 1929; Margot-Duclot & Vernant, 1946). Finally, harvesting is a joint wife-husband activity, and the *tuber-birth* metaphor is pursued through the harvest customs. Husband and wife have specific duties to perform with regard to the newly harvested tubers. "The woman, for instance, does not dig the tuber out of the soil, which symbolizes her womb, but is mainly involved in caring for and cleaning it, as with her child" (Brindley, 1984, p. 103). In sum, many ritualized and symbolic aspects of subsistence among the Trobrianders serve as an expression of conjugal and reproductive complementarity.

Conclusion

There appear to be multiple factors supporting human pair-bonds, including male mate competition and paternal investment. More research into the nature of male–female subsistence complementarity may prove useful for understanding human pair-bonds. A cross-cultural analysis of foragers' sexual division of labor, for example, shows a pattern of ecologically contingent complementarity (Marlowe, 2007) that may have important influence on pair-bonds. Further studies should also begin to address the demands that the development of offspring's social competency place on biparental care (Quinlan & Quinlan, 2007), and the nature of environmental risk (Quinlan, 2007) in shaping exigencies for pair-bonds. Finally, relations among pair-bond stability, division of labor, mate choice, and showing off require further analysis. We hope that the current study helps stimulate more interest in evolutionary approaches in comparative ethnology and better analyses.

Notes

1. Such relationships may occur in monogamous or polygynous mating systems. The important point here is that the relationship is relatively enduring.
2. We define *fitness* as an individual's genetic representation in future generations.
3. Variables 714, 1689, and 1690 in Divale (2004) give some sex-ratio data, but not enough for multivariate analysis.
4. M. Ember (1974) found that female-biased sex ratio was associated with polygyny cross-culturally. However, that relationship did not hold in these data, which include sororal polygyny to examine the level of polygyny as a proxy of male mating competition. We discuss this potential confound further in the results sections.
5. Data are from *World Cultures: Journal of Comparative and Cross-Cultural Research*, 2004, 15(1).
6. An earlier cross-cultural study found no significant association between female contribution to subsistence and divorce (Hendrix & Pearson, 1995, p. 224); however, the gamma statistic used in that study could not have detected the curvilinear association shown in Figure 1 and Table 1.

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