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Human Lactation, Pair-bonds, and Alloparents

A Cross-Cultural Analysis

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Abstract The evolutionary origin of human pair-bonds is uncertain. One hypothesis, supported by data from forgers, suggests that pair-bonds function to provision mothers and dependent offspring during lactation. Similarly, public health data from large-scale industrial societies indicate that single mothers tend to wean their children earlier than do women living with a mate. Here we examine relations between pair-bond stability, alloparenting, and cross-cultural trends in breastfeeding using data from 58 "traditional" societies in the Standard Cross-Cultural Sample (SCCS). Analyses show that stable conjugal relationships were associated with significantly later weaning among the societies in the SCCS. The relationship between pair-bond stability and age at weaning was not mediated by women's ability to provision themselves or women's kin support. Availability of alloparental care was also inversely related to age at weaning, and the association was not significantly reduced after controlling for frequency of divorce. This study indicates that among a woman's kin relationships, a pair-bond with a child's father is especially supportive of breastfeeding. These cross-cultural findings are further evidence that human pair-bonds may have evolved to support lactation.

Keywords Behavioral ecology · Biocultural anthropology · Conjugal stability · Divorce · Human evolution · Reproductive strategies

Mothers often face a critical choice between childcare and work. Trade-offs between parenting and production create pressure for cooperative childrearing among humans. Nursing often taxes mothers' time and energy in ways that other childcare does not; hence, parental cooperation may be particularly important during lactation (Marlowe 2003). A child's father may be especially well situated to assist the nursing mother because he and the mother share identical genetic interest in their children's success. Other potential helpers do not share such "symmetrical" interests with a child's mother.

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In this study we use cross-cultural data from 58 "traditional" societies to test the hypothesis that pair-bonds are more supportive of lactation than are other kin relations.

Parental Investment and Age at Weaning

Breastfeeding is a primary mechanism among mammals for provisioning dependent offspring, and it is a key component of "parental investment" (PI hereafter). PI is defined as care benefiting one offspring at a cost to parents' ability to invest in other components of fitness—including mating effort, and investment in other offspring and genetic kin (Clutton-Brock 1991:9; Trivers 1972).

For mothers, lactation entails energetic and opportunity costs, and suppresses fertility (Valeggia and Ellison 2001; Tracer 1996; Vitzthum 1994). Human lactation requires 670 kcal/day during exclusive breastfeeding (Dewey 1997). Increased energy demand presents costs to household production and may delay future reproduction through reduced fecundity (Jasienska 2001). Breastfeeding may suppress postpartum ovulation through effects on gonadotrophin-releasing hormone (Vitzthum 1997). Costs of breastfeeding for future reproduction, or "residual reproductive value," indicate life history trade-offs. Reduction of residual reproductive value suggests that to enhance fitness most mammals should wean their offspring as soon as possible. However, 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, and 100% of lactating women returned to cycling within 20 months (Valeggia and Ellison 2004:588; see Holman et al. 2006 for similar findings), which is 10 months earlier than the cross-cultural average age at weaning of 30 months (Dettwyler 1995). Resumption of cycling while lactating might account for shorter inter-birth intervals among humans compared with other great apes (Kennedy 2005). The comparatively low reproductive cost of lactation among humans may suggest that energetic costs can be reduced by provisioning. Opportunity costs also can be substantial (Quinlan et al. 2003b): Nursing often interferes with women's work that may benefit other children or kin. We suggest that opportunity costs rather than costs to residual reproductive value are the major force driving human weaning decisions.

Weaning should occur when the maternal fitness costs of continued breastfeeding exceed the benefits. In general, a woman's access to resources for PI determines the costs of continued breastfeeding. Easy access to resources may allow mothers to spend more time in direct childcare, including nursing, because their time is not limited by labor demands. Coresident adults can make economic contributions to households that allow women to spend less time working outside the home or camp and more time in direct childcare including breastfeeding.

Human weaning has some unusual features. Other great ape species wean at about 5 to 7 years of age (Dettwyler 1995; Kennedy 2005). Based on allometric relationships between adult size (Charnov and Berrigan 1993), molar eruption (Smith 1992), and weaning age among primates, humans are predicted to wean at about 6 years, although other methods yield estimates between 2.5 and 7 years of age (Dettwyler 1995). Despite predictions for late weaning among humans, cross-culturally the average and median age at weaning is around 2.5 years (Dettwyler 1995; Kennedy 2005; Sellen

2001). These data indicate that the average age for human weaning may be at an adaptive minimum; hence, in many environments the challenge is not to find ways to reduce lactation, but rather to extend it. We suggest that maternal social support provides a solution for the unusual challenge of human lactation.

Provisioning infants with energy is not the only or perhaps even the most important function of human breastfeeding. Availability of weaning foods is not associated with age at weaning cross-culturally (Sellen and Smay 2001), suggesting that considerations other than feeding are in play. In fact, because of expensive brain growth, breastfeeding alone may not support infant nutritional needs much beyond 6 months (Kennedy 2005; McDade and Worthman 1998; Wilson et al. 2006). Many other health benefits of breastfeeding, such as resistance to infections and allergies, are well-known (Oddy 2001; Leon-Cava et al. 2002). Prolonged nursing may also have positive influence on long-term psychomotor and neural development in well-nourished populations (Horwood et al. 2001; Pollock 1994; Vestergaard et al. 1999). Breastfeeding duration has also been associated with long-term reduction in children's stress hormone levels (Quinlan et al. 2003), and increased "developmental stability" (Leone et al. 2004). Furthermore, breastfeeding may have protective effects against diseases appearing later in development and adulthood (Cunningham 1995). Nursing can be important to the mother-child bond (Hrdy 1999), associated with positive emotions and attachment linked to maternal hormones including prolactin and oxytocin (Ellison 2001:83–126). Maternal responsiveness, related to nursing, appears to influence the development of children's attachment styles and, later, conjugal relations as an adult (Belsky 1997; Chisholm 1996). Hence, breastfeeding—and its underlying hormonal correlates—may play a role in attachment organization (Else-Quest et al. 2003; Insel 2000). These findings suggest fitness benefits beyond mere energy provisioning, which means that alloparental care cannot easily substitute for nursing.

Age at weaning is influenced by the distribution of household labor (Quinlan et al. 2003b, 2005). A study of 133 preindustrial societies suggests that maternal work patterns, subsistence strategies, and the reproductive costs of prolonged lactation affect breastfeeding duration (Sellen and Smay 2001). Relatively long daily separations between mothers and infants may lead to earlier weaning by single mothers, similar to the reported earlier weaning for working women in developed countries (Arlotti et al. 1998; Bick et al. 1998; Bouvier and Rougemont 1998; Hill et al. 1997; Fein and Roe 1998; Lindenberg et al. 1990; Visness and Kennedy 1997). 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 (see Leonetti et al. 2004). Breastfeeding, however, is usually beyond the scope of alloparenting. Leaving a baby with a kinswoman prolongs periods of mother-child separation, which may hasten weaning in households with coresident alloparents (Quinlan et al. 2003b). Given these considerations, we suggest that a woman's mate (the father of her child) is particularly well situated to support lactation.

Why do Humans Form Pair-Bonds?

Human pair-bonds have multiple functions, yet recent debate focuses on their role in provisioning mothers with dependant offspring (Hawkes 2004). In many foraging societies women contribute significantly more calories to the diet than do men. Additionally, meat from men's hunting is often shared broadly within a hunter-gatherer camp; hence, woman do not appear to require a mate for provisioning. Human pair-bonds may not have evolved for caloric provisioning, but women may have entered conjugal relationships to protect offspring from infanticide (Hawkes 2004), following 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). Furthermore, the "infanticide hypothesis" suggests the dubious prediction that human pair-bonds are unnecessary and, hence, infrequent in environments with low rates of infanticide or where males tend to be less physically aggressive. In short, the debate over the role of paternal care in human pair-bonds is far from settled.

Foraging men "provide a considerable portion of the energy consumed by juveniles and reproductive-aged women. . . . It is the partnership between men and women that allows long-term juvenile dependence and learning and high rates of survival" (Kaplan et al. 2000:173). Biparental care may be particularly important during the period of lactation. Among the Hadza foragers of Tanzania, Marlowe (2003) found that husbands appear to compensate for their wives' diminished foraging return when they have young children. 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 childcare were inversely related; nursing women spent less time foraging than did non-nursing women, and women's foraging time was inversely related to their husbands' foraging (Hurtado et al. 1992). Based on these findings, Marlowe (2003) suggests that pair-bonds in human evolution may function to provision a mate and offspring during a "critical period" coinciding with lactation. His conclusion is consistent with a cross-species analysis indicating that pair-bonding "may be selectively favored in humans and other animals when mothers' feeding requirements interfere with their baby-tending" (Ember and Ember 1979:48). More recent comparative analysis, however, suggests that pair-bonds in mammals may not have evolved in response to pressures for paternal care (Komers and Brotherton 1997), although biparental care may be important for avian pair-bonds (Burley and Johnson 2002). In sum, evidence for the origin of human pairing is incomplete, but male provisioning during lactation offers a promising lead.

If pair-bonds are crucial for supporting lactation, then divorce may impair women's ability to continue nursing. 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" (Kaplan et al. 2000:173). Similar to findings for foragers, 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 (Bar-Yam and Darby 1997; Kiehl et al. 1996; Pande et al. 1997; Vega Lopez and Gonzalez Perez 1993). This association is probably related to the trade-off between breastfeeding and women's work (Arlotti et al. 1998; Fein and Roe 1998; Visness and Kennedy 1997) that may be particularly pressing among single mothers. Here we intend to fill the large gap between foraging and industrial populations by examining relations between breastfeeding and conjugal stability among traditional societies in the Standard Cross-Cultural Sample (Murdock and White 1969). If pair-bonds evolved to support lactation, then pair-bond stability should be associated with breastfeeding duration. We predict that conjugal instability measured by the frequency of divorce is associated with earlier weaning cross-culturally.

Methods

Data are from Murdock and White's (1969) Standard Cross-Cultural Sample (SCCS), which includes information on conjugal stability, alloparenting, and average age at weaning for 58 societies (see Tables A1 and A2 in the Appendix). We examined four effects on age at weaning: (1) frequency of divorce, (2) availability of alloparenting, (3) women's ability to provision themselves, and (4) kin support. We used previously published codes (Divale 2004). Weaning age in months at termination (Barry and Paxson 1971; variable 45) was recoded into the midpoint of nine intervals (from 0 to 12 months through 61–72 months). Frequency of divorce (Broude and Greene 1983; SCCS variable 744 in Divale 2004) was recoded as 1= common and 0=uncommon. SCCS categories 1 and 2 for this variable were combined to form the "divorce common" trait, and categories 3–5 were grouped into the "uncommon" trait. Frequency of divorce was dichotomized to simplify the models and because in our subsample of 58 societies three of the original SCCS categories had fewer than 10 observations: The largest category was more than four times the size of the smallest category (Table 1).

The measure of alloparental involvement is based on the SCCS variable for non-maternal relationships in early childhood (Barry and Paxson 1971; variable 52), coded as 2=principally mother, 3=<1/2 mother, and 4=primarily others. This subsample of the SCCS did not include any cases coded as 1=exclusively mother for this variable. Women's contribution to subsistence (variable 890, White cited in Divale 2004, coded from 0=0–4% to 9=85–99%) is a measure of women's ability to provision themselves. Marital residence with kin (Murdock and Wilson 1972, variable 215) indicates availability of maternal kin support and was recoded as "matrilocal residence" where uxorilocal and matrilocal=1 and all other categories=0. Matrilocal residence and women's contribution to subsistence were included as controls to examine whether the availability to a woman of kin support or her ability to provision herself mediated relations between frequency of divorce and age at weaning.

Table 1 Age at weaning and divorce as originally coded in the SCCS (variable 744)

SCCS coding for divorce	Mean age at weaning (months)	SD	*n*
1. Universal	24.79	4.27	7
2. Common, frequent	28.83	8.69	21
3. Minority of couples divorce	33.33	10.36	9
4. Rare after children born	37.70	9.39	5
5. Rare, never	31.38	7.25	16
Total	30.51	8.63	58

For this analysis, SCCS categories 1 and 2 were recorded as divorce common=1 and categories 3–5 were recoded as divorce uncommon=0

Table 2 Descriptive statistics for SCCS subsample

	N	%
Weaning age in months at termination (subsample)†		
12	1	1.7
17	2	3.4
22.5	18	31.0
27.5	4	6.9
33.5	23	39.7
38.5	5	8.6
45.5	3	5.2
54.5	2	3.4
Total	58	100
Frequency of divorce		
Divorce uncommon[a]	30	51.7
Divorce common	28	48.3
Total	58	100
Matrilocality		
Not matrilocal[a]	45	77.6
Matrilocal	13	22.4
Total	58	100
Female contribution to subsistence: average of three scores		
5–14%	2	3.4
15–24%	8	13.8
25–34%	14	24.1
35–44%	14	24.1
45–54%	14	24.1
55–64%	3	5.2
65–74%	3	5.2
Total	58	100
Non-maternal relationships in early childhood		
Principally mother[a]	14	24.1
Mother <1/2 care	30	51.7
Primarily others	14	24.1
Total	58	100
Foragers (control variable)		
Foragers[a]	14	24.1
Non-foragers	44	75.9
Total	58	100

†Subsample (n=58); mean=30.5 months; median=33.5; SD=8.6. Full sample (n=156); mean=31.2 months; median=33.5; SD=9.1

[a] Indicates reference categories in GLMs below

We included subsistence strategy (White cited in Divale 2004; variable 858) as a control variable. Variable 858 was recoded into a dichotomous variable indicating foraging and non-foraging societies (Table 2). We discuss the rationale for recoding the variable in the "Results" section.

We used a general linear modeling (GLM) strategy with linear regression in STATA 9 to examine associations between age at weaning, conjugal stability, and alloparenting. Diagnostic analyses indicated that the models did not deviate significantly from the assumptions of GLM. We computed robust standard errors for clustered data to adjust for potential intraclass correlation among the regionally clustered societies (see Appendix). To assess regional clustering, we used SCCS variable 1,858 (region; Burton 1999).

Results

Mean age at weaning was 31 months, with a median of 33.5 months, which is comparable to findings of other cross-cultural studies (Dettwyler 1995; Kennedy 2005; Sellen 2001). Descriptive statistics are in Table 2.

First we explored potential confounding effects of subsistence on relations between conjugal stability and age at weaning. In the 58 societies in our analyses, fishing and hunter-gatherer societies tended to wean children later than did pastoralist, horticultural, or agricultural societies (p=0.004, analysis not shown), and the effect was still significant after adjusting for frequency of divorce. There were no significant differences in age at weaning among food producers. Next we tested for interaction effects between frequency of divorce and subsistence strategy; no interactions were significant (p=0.50, analysis not shown). We recoded subsistence strategy (variable 858) as a dichotomous variable: hunter-gatherers and fishers (“foragers”) equal 1 and all others types equal 0 (Table 2). Again we tested for an interaction effect between frequency of divorce and “foragers” on age at weaning; the result was not significant (p=0.50). We included “forager” as a control variable in the rest of the analyses (Table 3).

Table 3 General linear models showing effect of divorce and alloparenting on age at weaning

	Variable	B	SE	*t*	*p*	Lower CL	Upper CL	Model statistics
Model 1	Divorce common	−3.96	1.26	−3.13	0.014	−6.87	−1.05	N=58
	Foragers	6.49	2.20	2.95	0.018	1.42	11.56	$F(2, 8)$=7.38,
	Intercept	30.85	0.79	39.17	0.000	29.04	32.67	p=0.015
								R^2=0.19
Model 2	Divorce common	−3.45	1.21	−2.86	0.021	−6.23	−0.67	N=58
	Foragers	5.52	2.60	2.13	0.066	−0.46	11.51	$F(6, 8)$=16.71
	Allomothers:[a] childcare							p=0.0004
	<1/2 from mother	−2.10	2.50	−0.84	0.426	−7.87	3.67	R^2=0.27
	Primarily from allomoms	−5.46	2.27	−2.41	0.043	−10.70	−0.23	
	Matrilocal residence	−0.84	2.71	−0.31	0.765	−7.09	5.41	
	Female contribution to subsistence	−0.83	1.12	−0.74	0.481	−3.42	1.76	
	Intercept	36.66	6.04	6.07	0.000	22.74	50.57	
Model 3	Divorce common	−3.35	1.35	−2.49	0.038	−6.46	−0.24	N=58
	Foragers	5.73	2.28	2.51	0.036	0.46	10.99	$F(4, 8)$=15.08
	Allomothers:[a] childcare							Prob>F=0.0009
	<1/2 from mother	−2.34	2.38	−0.98	0.354	−7.82	3.14	R^2=0.25
	Primarily from allomoms	−5.91	2.64	−2.24	0.055	−11.99	0.18	
	Intercept	33.38	1.94	17.21	0.000	28.91	37.85	

Foragers consists of hunter-gatherers and fishers (= 1) and food producers (= 0); *divorce common* (= 1, uncommon = 0) and *matrilocal* (= 1, not matrilocal = 0) are also dichotomous variables

B: unstandardized coefficient in months of breastfeeding, SE: robust clustered standard error clustered by region (SCCS variable 1858; t, p, and CL are also based on robust SE), p: two-tail significance, CL: 95% confidence limit, N of clusters=9, see Table A2

[a] Allomothers is a categorical variable where “mother is primary caregiver” is the reference category

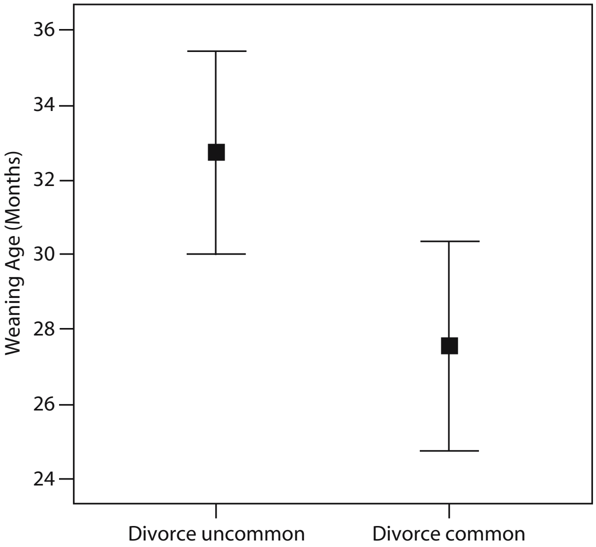

Fig. 1 Association between divorce and weaning in the SCCS (n=74). *Squares* indicate means, and *error bars* are 90% confidence intervals

Frequency of divorce and age at weaning are inversely associated in the SCCS: In a bivariate analysis (n=74), children tended to be weaned about 5 months earlier in societies where divorce was common (Fig. 1). (Table 1 shows that the association between conjugal stability and age at weaning existed in the original variable.) Controlling for subsistence strategy had little effect on the relation between divorce and weaning age (divorce B=−4.8, p=0.005; foraging B=2.9, p=0.184; n=74). Restricting the analysis to the 58 societies for which we had complete data reduced the mean difference in weaning to about 4 months between societies where divorce was common and those where it was uncommon, but the effect was still significant (Table 3, Model 1). A GLM including all predictors and control variables indicated that age at weaning was still significantly inversely associated with frequency of divorce (Table 3, Models 2 and 3).

Women's contribution to subsistence and matrilocality were included to test whether the effects of divorce were mediated by a woman's ability to provision herself or by the availability of kin support. Neither women's contribution to subsistence nor matrilocality was significantly associated with age at weaning, nor did they mediate the effect of divorce on age at weaning (Table 3). Additional analyses (not shown) included interaction terms for frequency of divorce × women's contribution to subsistence and frequency of divorce × matrilocal residence to test for moderating effects; however, neither interaction term was significantly associated with age at weaning. Similarly, an interaction term for women's contribution to subsistence × matrilocal residence was not significantly associated with age at weaning.

We also examined the relation between alloparenting and age at weaning. Availability of alloparenting was significantly and inversely associated with age at weaning (Table 3, Models 1 and 2; Fig. 2). Age at weaning tends to be lower by an average of about 5.5 to 6 months in societies where allomothers provide most childcare compared with societies where mothers are primarily responsible for childcare (Table 3, Models 2 and 3). Divorce × alloparenting interaction terms were not significantly associated with age at weaning (not shown).

In a third model we excluded the non-significant variables matrilocal residence and female contribution to subsistence. Excluding these variables did not appreciably change the results: The *p* value for the foragers control variable decreased slightly, making the effect significant at the 0.05 level. The *p* value also increased slightly to 0.055 for the primarily allomothers category of the childcare variable (Table 3, Model 2).

Robust estimates of the standard errors for clustered data were somewhat smaller than ordinary least squares estimates, indicating negative intraclass correlations which can occur when potentially important control variables are missing from the model. We saved the standardized residuals from Model 3 (Table 3) as a new variable. Then we examined bivariate correlations between the residuals and every other variable in the SCCS. Two potentially important controls emerged from the search: Importance of children's peer groups in early childhood (variable 56), which we recoded as a dichotomous variable, and pacification (variable 1654), indicating the extent to which warfare was controlled by state-level societies, which we also recoded as a dichotomous variable. (This latter variable might indicate acculturation or market integration.) When included in the analysis, the two variables did not

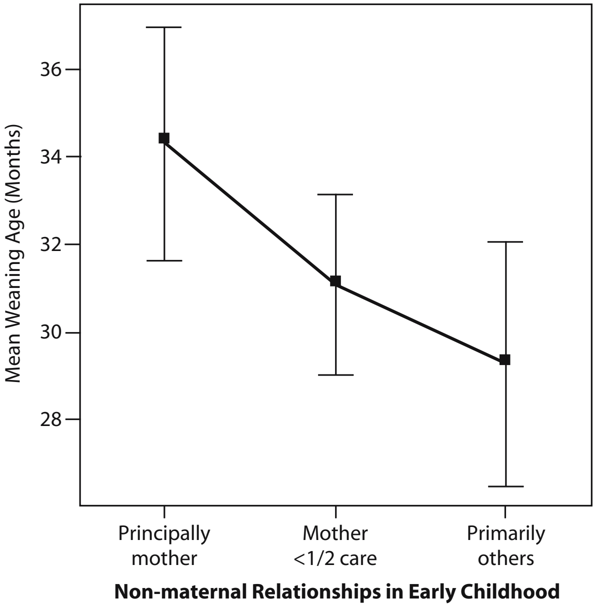

Fig. 2 Association between alloparenting and weaning in the SCCS (n=118). *Squares* indicate means, and *error bars* are 90% confidence intervals. These results for the full sample (n=118) were very similar to results for the reduced samples (n=58, Table 3; n=51, Table 4)

Table 4 General linear models showing effect of divorce and alloparenting on age at weaning including additional controls

Variable	B	SE	*t*	*p*	Lower CL	Upper CL	Model statistics
Foragers	7.37	1.45	5.07	0.001	4.02	10.72	N=51
Peer care in early childhood	−8.88	1.12	−7.93	0.000	−11.45	−6.30	$F(6, 8)=161.36$
Pacified	6.21	1.72	3.62	0.007	2.25	10.17	p=0.000
Divorce common	−4.80	1.91	−2.52	0.036	−9.20	−0.41	R^2=0.57
Allomothers:[a] childcare							N of clusters=9
<1/2 from mother	−2.19	1.35	−1.62	0.143	−5.31	0.92	
Primarily from allomoms	−5.44	2.26	−2.41	0.042	−10.64	−0.24	
Intercept	39.04	0.91	42.86	0.000	36.94	41.14	

Foragers consists of hunter-gatherers and fishers (= 1) and food producers (= 0); *divorce common* (= 1, uncommon = 0) and *Peer care* (= 1, adult care = 0) are also dichotomous variables; *Pacified* indicates whether a state-level government inhibits warfare in the society (1 = pacified, 0 = not pacified)

B: unstandardized coefficient in months of breastfeeding, SE: robust clustered standard error clustered by region (SCCS variable 1858; *t*, *p*, and CL are also based on robust SE), *p*: two-tail significance, CL: 95% confidence limit

[a] Allomothers is a categorical variable where "mother is primary caregiver" is the reference category

substantially alter the results, although their inclusion apparently eliminated the negative intraclass correlation. There was a somewhat larger difference in age at weaning between societies where divorce was common and those where it was uncommon (B=−4.8, Table 4), although the effect of alloparenting was approximately the same as in Table 3. Note that the B of −4.8 is identical to the difference for the full sample (n=74) indicated in Fig. 1. Similar to the effect of allomothers, peer care showed a negative association with age at weaning. These results support the adequacy of the general linear models.

Discussion and Conclusion

Our findings indicate that conjugal stability and weaning are associated cross-culturally. In societies where divorce was common, children were weaned 3.5 to 4.8 months earlier than in societies where divorce was less common. This finding was not mediated by women's contribution to subsistence or by matrilocal residence. Matrilocal residence itself was not a significant predictor; however, the organization of women's cooperation did predict weaning age. Availability of alloparental care was associated with significantly earlier weaning, independent of the frequency of divorce. Women's contribution to subsistence, a proxy for women's ability to provision themselves, was not significantly associated with weaning. These results indicate that among a woman's kin relationships, a pair-bond with the child's father is especially supportive of lactation.

Our previous work in a horticultural community in rural Dominica indicated that women with a coresident mate weaned their children about 4.5 months later than did women without a coresident mate (Quinlan et al. 2003b). Similar to findings here, in Dominica the availability of childcare, as measured by the number of coresident adult female relatives, was negatively associated with age at weaning (Quinlan et al. 2003b), which is consistent with other studies' findings (Lindenberg et al. 1990; Bick et al. 1998). The inverse relationship may reflect the modes of household production and childcare in small-scale societies. We suggest that future research could benefit from more attention to relations between mothers, fathers, and alloparents in structuring cooperative childrearing.

Women's roles vary in different family environments. In a conjugal family, a woman and her mate have complementary roles that reflect their common and symmetrical reproductive interest in their children. Both husband and wife share 50% of their genes with their children. In conjugal families, the father may take on a greater portion of subsistence and other external economic duties when he and his mate have an infant (see also Hurtado et al. 1992; Marlowe 2003). In a "consanguineous" or "matrifocal" household a mother shares 50% of her genes with her offspring, while other coresident adults only share, at most, 25% of their genes with the offspring of any particular kinswomen (e.g., their sister, daughter, or granddaughter). Although a single woman in an extended family environment may receive substantial assistance in domestic and economic activities, she may feel pressure to reciprocate in kind by returning to work, thereby benefiting the whole family, rather than staying home to focus on her infant. In short, kin may be willing to act as alloparents, but in many cases they may not be willing to take on other duties for a woman with small children (Leonetti et al. 2004; Quinlan et al. 2003b). Hence, the symmetry of relatedness within a conjugal family appears uniquely suited for prolonged lactation. This interpretation was supported by women's time allocation data in rural Dominica, which showed no difference in single and pair-bonded mothers' time spent working (including childcare); however, single mothers were significantly more likely to work away from home, and away from their children, than were pair-bonded women (Quinlan et al. 2003b). In other societies, however, infants may accompany their mother when she leaves the house to work (Panter-Brick 1991), suggesting that relations between mothers' work and childcare may be a fruitful area for future cross-cultural research.

Paternal investment may be important in later childhood and through multigenerational inheritance of wealth. Benefits of later paternal care depend on local conditions, including gender roles, division of labor, gender differences in contribution to diet, durable resources, etc. Although there are multiple potential payoffs to paternal care, those benefits are not as consistently experienced cross-culturally as lactation. We suggest that lactation may represent a universal "critical period" for paternal investment (Marlowe 2003) that may have created particularly strong selective pressure for human pair-bonds.

In sum, evidence from industrial populations, socioecological case studies of small-scale groups, and this cross-cultural analysis converge on the same conclusion: Stable conjugal relationships support breastfeeding in ways that other kin relations do not. These findings support the hypothesis that human pair-bonds evolved to aid provisioning during the critical period of lactation (Fisher 1987; Marlowe 2003). We concur with Kaplan et al., who suggest that "human pair bonding and male parental investment is the result of complementarity between males and females" (Kaplan et al. 2000:173). Such complementarity is at no time better expressed than during lactation.

Appendix

Table A1 Dataset for the analysis

Society	Weaning	Divorce	Matrilocal	♀ Subsistence	Non-maternal care	Peer care	Pacified	Region[a]	Forager
Alorese	27.5	1	0	7	4	1	1	3	0
Amahuaca	33.5	1	0	3	2	–	0	8	0
Amhara	22.5	1	0	2	4	1	0	2	0
Andamanese	38.5	0	0	4	2	–	0	3	1
Ashanti	22.5	1	0	5	4	–	0	1	0
Aymara	27.5	1	0	5	3	1	1	9	0
Bemba	33.5	1	0	5	4	0	0	1	0
Burmese	33.5	0	0	2	3	0	0	3	0
Cayapa	33.5	0	0	3	3	1	0	9	0
Chiricahua	33.5	0	1	6	3	1	0	7	0
Chukchee	54.5	0	0	2	2	0	1	5	0
Copper Eskimo	45.5	1	0	2	3	1	1	5	1
Cubeo (Tucano)	17.0	1	0	4	4	1	0	8	0
Fon	33.5	0	0	4	2	1	0	1	0
Gros Ventre	22.5	1	0	2	3	1	0	7	0
Hausa	22.5	1	0	1	2	0	0	1	0
Havasupai	17.0	0	0	4	3	–	1	7	0
Huichol	33.5	1	0	3	3	1	1	9	0
Ingalik	38.5	0	1	3	2	1	0	6	1
Irish	27.5	0	0	3	4	0	0	5	0
Japanese	38.5	1	0	2	3	1	0	5	0
Javanese	22.5	1	0	4	3	1	0	3	0
Kapauku	22.5	1	0	6	2	1	0	4	0
Kaska	33.5	1	1	4	4	1	1	6	1
Khmer	38.5	0	0	4	–	1	0	3	0
Kikuyu	22.5	0	0	5	4	1	0	1	0
Klamath	33.5	1	0	4	3	0	0	7	1
Konso	33.5	0	0	4	–	0	1	1	0
Koreans	33.5	0	0	3	3	1	0	5	0
Kung Bushmen	54.5	0	0	4	2	1	0	1	1
Lapps	22.5	0	0	5	3	1	0	5	0
Lepcha	38.5	0	0	5	3	1	1	2	0
Marquesans	12.0	1	0	3	4	1	0	3	0
Marshallese	33.5	1	1	3	4	1	1	3	0
Masai	22.5	0	0	5	4	–	0	1	0
Mbuti	33.5	0	0	5	4	1	0	1	1
Nambicuara	33.5	1	0	3	3	1	1	8	0
Negri Sembilan	22.5	1	1	6	3	1	0	3	0
New Ireland	33.5	0	1	5	3	1	0	4	0
Nicobarese	22.5	0	1	4	3	0	0	3	0
Nkundo Mongo	27.5	1	0	7	2	1	0	1	0
Omaha	33.5	1	0	4	3	1	1	8	0
Paiute (North)	22.5	1	1	5	3	1	1	7	1

Table A1 (continued)

Society	Weaning	Divorce	Matrilocal	♀ Subsistence	Non-maternal care	Peer care	Pacified	Region[a]	Forager
Papago	33.5	0	0	4	3	1	1	9	0
Pastoral Fulani	22.5	1	0	5	3	1	0	1	0
Saulteaux	45.5	0	0	2	2	1	0	7	1
Semang	33.5	0	0	3	2	1	0	3	1
Shavante	33.5	0	1	4	4	1	0	8	1
Siamese	33.5	0	0	3	4	1	0	3	0
Siriono	38.5	0	1	3	3	–	0	8	1
Siuai	33.5	0	0	7	2	1	1	4	0
Somali	22.5	1	0	5	3	1	1	1	0
Songhai	22.5	1	0	2	3	1	1	1	0
Tallensi	33.5	0	0	3	3	1	1	1	0
Trobrianders	22.5	0	0	5	3	–	1	4	0
Trukese	22.5	1	1	4	3	1	1	3	0
Vedda	22.5	0	1	1	2	1	0	2	1
Yapese	33.5	0	0	5	3	0	1	3	0
Yurok	33.5	0	0	4	2	1	1	7	1
Zuni	45.5	1	1	3	3	–	0	9	0

[a] Codes for region are provided in Table A2

Table A2 Regional clusters of the SCCS subsample

Region (variable 1858)		*N*	%
1	Subsaharan Africa	13	22.4
2	Middle Old World	3	5.2
3	Southeast Asia/Insular Pacific	12	20.7
4	Sahul	4	6.9
5	North Eurasia/Circumpolar	6	10.3
6	Northwest Coast of North America	2	3.5
7	North and west of North America	7	12.1
8	Eastern Americas	6	10.3
9	Mesoamerica/Andes	5	8.6
	Total	58	100

References

Arlotti, J. P., Cottrell, B. H., Lee, S. H., & Curtin, J. J. (1998). Breastfeeding among low-income women with and without peer support. *Journal of Community Health Nursing, 15*, 163–178.

Barry, H., & Paxson, L. (1971). Infancy and early childhood: Cross-cultural codes 2. *Ethnology, 10*, 466–509.

Bar-Yam, N. B., & Darby, L. (1997). Fathers and breastfeeding: A review of the literature. *Journal of Human Lactation, 13*, 45–50.

Belsky, J. (1997). Attachment, mating and parenting. *Human Nature, 8*, 361–381.

Bick, D. E., MacArthur, C., & Lancashire, R. J. (1998). What influences the uptake and early cessation of breast feeding? *Midwifery, 14*, 242–247.

Bouvier, P., & Rougemont, A. (1998). Breast-feeding in Geneva: Prevalence, duration and determinants. *Sozial und Praventivmedizin, 43*, 116–123.

Broude, G. J., & Greene, S. J. (1983). Cross-cultural codes on husband-wife relationships. *Ethnology, 22*, 263–280.

Burley, N. T., & Johnson, K. (2002). The evolution of avian parental care. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 357*, 241–250.

Burton, M. L. (1999). Language and region codes for the standard cross-cultural sample. *Cross-Cultural Research, 33*, 63–83.

Charnov, E. I., & Berrigan, D. (1993) Why do female primates have such long lifespans and so few babies? or, life in the slow lane. *Evolutionary Anthropology, 1*, 191–194.

Chisholm, J. S. (1996). The evolutionary ecology of attachment organization. *Human Nature, 7*, 1–38.

Clutton-Brock, T. H. (1991). *The evolution of parental care.* Princeton, NJ: Princeton University Press.

Cunningham, A. S. (1995) Breastfeeding: Adaptive behavior for child health and longevity. In P. Stuart-Macadam & K. A. Detwyler (Eds.), *Breastfeeding: Biocultural Perspectives* (pp. 243–263). New York: Aldine.

Dettwyler, K. A. (1995). A time to wean: The hominid blueprint for the natural age of weaning in modern human populations. In P. Stuart-Macadam & K. A. Detwyler (Eds.), *Breastfeeding: Biocultural Perspectives* (pp. 39–73). New York: Aldine.

Dewey, K. G. (1997). Energy and protein requirements during lactation. *Annual Review of Nutrition,* 17, 19–36.

Divale, W. (2004). Codebook of variables for the standard cross-cultural sample. *World Cultures: The Journal of Cross-Cultural and Comparative Research, 14*(2), 1–347.

Ellison, P. T. (2001). *On fertile ground: A natural history of human reproduction.* Cambridge, MA: Harvard University Press.

Else-Quest, N. M., Hyde, J. S., & Clark, R. (2003). Breastfeeding, bonding and the mother-infant relationship. *Merrill-Palmer Quarterly, 49*, 495–517.

Ember, M., & Ember, C. R. (1979). Male-female bonding: A cross-species study of mammals and birds. *Behavior Science Research, 14*, 37–56.

Fein, S. B., & Roe, B. (1998). The effect of work status on the initiation and duration of breast-feeding. *American Journal of Public Health, 88*, 1042–1046.

Fisher, H. E. (1987). The four year itch. *Natural History, 96*(10), 22–28.

Hawkes, K. (2004). Mating, parenting and the evolution of human pair bonds. In B. Chapais & C. Berman (Eds.), *Kinship and Behavior in Primates* (pp. 443–473). Oxford: Oxford University Press.

Hill, P., Humenick, S. S., Argubright, T. M., & Aldag, J. C. (1997). Effects of parity and weaning practices on breastfeeding duration. *Public Health Nursing, 14*, 227–234.

Holman, D. J., Grimes, M. A., Achterberg, J. T., Brindle, E., & O'Conner, K. A. (2006). Distribution of postpartum amenorrhea in rural Bangledeshi women. *American Journal of Physical Anthropology, 129*, 609–619.

Horwood, L. J., Darlow, B. A., & Mogridge, N. (2001). Breast milk feeding and cognitive ability at 7–8 years. *Archives of Disease in Childhood: Fetal and Neonatal Edition, 84*, F23–F27.

Hrdy, S. B. (1999). *Mother nature: A history of mothers, infants, and natural selection.* New York: Pantheon Books.

Hurtado, A. M., Hill, K., Kaplan, H., & Hurtado, I. (1992). Trade-offs between female food acquisition and child care among Hiwi and Ache foragers. *Human Nature, 3*, 185–216.

Insel, T. R. (2000). Toward a neurobiology of attachment. *Review of General Psychology, 4*(2), 176–185.

Jasienska, G. (2001). Why energy expenditure causes reproductive suppression in women: An evolutionary and bioenergetic perspective. In P. T. Ellison (Eds.), *Reproductive Ecology and Human Evolution* (pp. 59–84). Hawthorne, NY: Aldine de Gruyter.

Kaplan, H. S., Hill, K. R., Lancaster, J. B., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology, 9*, 156–185.

Kennedy, G. E. (2005). From ape's dilemma to weanling's dilemma: Early weaning and its evolutionary context. *Journal of Human Evolution, 48*, 123–145.

Kiehl, E. M., Anderson, G. C., Wilson, M. E., & Fosson, L. (1996) Social status, mother-infant time together, and breastfeeding duration. *Journal of Human Lactation, 12*, 201–206.

Komers, P. E., & Brotherton, P. N. M. (1997). Female space use is the best predictor of monogamy in mammals. *Proceedings of the Royal Society B: Biological Sciences, 264*, 1261–1270.

Leon-Cava, N., Lutter, C., Ross, J., & Martin, L. (2002). *Quantifying the benefits of breastfeeding: A summary of the evidence.* Washington, DC: Pan American Health Organization (PAHO).

Leone, D. V., Quinlan, R. J., Hayden, R., Stewart, J., & Flinn, M. V. (2004). Long-term implications for growth of prenatal and early postnatal environment. (abstract). *American Journal of Human Biology, 16*, 212–213.

Leonetti, D. L., Nath, D. C., Hemam, N. S., & Neill, D. B. (2004). Do women really need marital partners to support their reproductive success? The case of the matrilineal Khasi of N.E. India. *Socioeconomic Aspects of Human Behavioral Ecology: Research in Economic Anthropology, 23*, 147–170.

Lindenberg, C. S., Artola, R. C., & Estrada, V. J. (1990). Determinants of early infant weaning: A multivariate approach. *International Journal of Nursing Studies, 27*, 35–41.

Marlowe, F. W. (2003). A critical period for provisioning by Hadza men: Implications for pair bonding. *Evolution and Human Behavior, 24*, 217–229.

McDade, T., & Worthman, C. (1998). The weanling's dilemma reconsidered: A biocultural analysis of breastfeeding ecology. *Developmental and Behavioral Pediatrics, 19*, 286–299.

Murdock, G. P., & White, D. R. (1969). Standard cross-cultural sample. *Ethnology, 8*, 329–369.

Murdock, G. P., & Wilson, S. F. (1972). Settlement patterns and community organization: Cross-cultural codes 3. *Ethnology, 11*, 254–295.

Oddy, W. H. (2001). Breastfeeding protects against illness and infection in infants and children: A review of the evidence. *Breastfeeding Review, 9*, 11–18.

Palombit, R. A. (1999). Infanticide and the evolution of pair bonds in nonhuman primates. *Evolutionary Anthropology: Issues, News, and Reviews, 7*(4), 117–129.

Pande, H., Unwin, C., & Haheim, L. L. (1997). Factors associated with the duration of breastfeeding. *Acta Paediatrica, 86*, 173–177.

Panter-Brick, C. (1991). Lactation, birth spacing and maternal work-loads among two castes in rural Nepal. *Journal of Biosocial Science, 23*, 137–154.

Pollock, J. I. (1994). Long-term associations with infant feeding in a clinically advantaged population of babies. *Developmental Medicine and Child Neurology, 36*, 429–440.

Quinlan, R., Leone, D., Quinlan, M., England, B., Gangestad, S., Thornhill, R., et al. (2003). Long-term effects of household production and breastfeeding duration on children's cortisol levels, fluctuating asymmetry and growth. Paper presented at the Human Behavior and Evolution Society annual meeting, University of Nebraska, Lincoln.

Quinlan, R. J., Quinlan, M. B., & Flinn, M. V. (2003). Parental investment and age at weaning in a Caribbean village. *Evolution and Human Behavior, 24*, 1–16.

Quinlan, R. J., Quinlan, M. B., & Flinn, M. V. (2005) Local resource enhancement and sex-biased breastfeeding in a Caribbean community. *Current Anthropology, 46*, 471–480.

Reichard, U. H. (2003). Monogamy: Past and present. In U. H. Reichard & C. Boesch (Eds.), *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals* (pp. 3–25). Cambridge: Cambridge University Press.

Sellen, D. W. (2001). Comparison of infant feeding patterns reported for nonindustrial populations with current recommendations. *Journal of Nutrition, 131*, 2707–2715.

Sellen, D. W., & Smay, D. B. (2001). Relationship between subsistence and age at weaning in "preindustrial" societies. *Human Nature, 12*, 47–87.

Smith, B. H. (1992). Life history and the evolution of human maturation. *Evolutionary Anthropology, 1*, 134–142.

Tracer, D. P. (1996). Lactation, nutrition, and post-partum amenorrhea in lowland Papua New Guinea. *Human Biology, 68*, 277–292.

Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Eds.) *Sexual Selection and the Descent of Man* (pp. 136–179). Chicago: Aldine.

Valeggia, C. R., & Ellison, P. T. (2001). Lactation, energetics and postpartum fecundity. In P. T. Ellison (Ed.) *Reproductive Ecology and Human Evolution* (pp. 85–105). Hawthorne, NY: Aldine de Gruyter.

Valeggia, C. R., & Ellison, P. T. (2004). Lactational amenorrhoea in well-nourished Toba women of Fromosa, Argentina. *Journal of Biosocial Science, 36*, 573–595.

Vega Lopez, M. G., & Gonzalez Perez, G. J. (1993). Maternal factors relating to breast-feeding duration in areas around Guadalajara, Mexico. *Bulletin of the Pan American Health Organization, 27*, 350–359.

Vestergaard, M., Obel, C., Henriksen, T. B., Sorensen, H. T., Skajaa, E., Ostergaard, J. (1999). Duration of breastfeeding and developmental milestones during the latter half of infancy. *Acta Paediatrica, 88*, 1327–1332.

Visness, C. M., & Kennedy, K. I. (1997). Maternal employment and breast-feeding. *American Journal of Public Health, 87*, 945–950.

Vitzthum, V. J. (1994). Causes and consequences of heterogeneity in infant feeding practices among indigenous Andean women. *Annals of the New York Academy of Sciences, 709*, 221–224.

Vitzthum, V. J. (1997). Flexibility and paradox: The nature of adaptation in human reproduction. In M. E. Morbeck, A. Gallowya, & A. L. Zihlman (Eds.), *The Evolving Female: A Life History Perspective* (pp. 242–259). Princeton, NJ: Princeton University Press.

Wilson, W., Milner, J., Bulkan, J., & Ehlers, P. (2006) Weaning practices of the Makushi of Guyana and their relationship to infant and child mortality: A preliminary assessment of international recommendations. *American Journal of Human Biology, 18*, 312–324.

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