Comparative Study of Reproductive Skew and Pair-Bond Stability Using Genealogies from 80 Small-Scale Human Societies

RYAN M. ELLSWORTH, MARY K. SHENK, DREW H. BAILEY, and ROBERT S. WALKER

ABSTRACT: Objectives: Genealogies contain information on the prevalence of different sibling types that result from past reproductive behavior. Full sibling sets stem from stable monogamy, paternal half siblings primarily indicate male reproductive skew, and maternal half siblings reflect unstable pair bonds.

Methods: Full and half sibling types are calculated for a total of 61,181 siblings from published genealogies for 80 small-scale societies, including foragers, horticulturalists, agriculturalists, and pastoralists from around the world.

Results: Most siblings are full (61%) followed by paternal half siblings (27%) and maternal half siblings (13%). Paternal half siblings are positively correlated with more polygynous marriages, higher at low latitudes, and slightly higher in non-foragers. Maternal half sibling fractions are slightly higher at low latitudes but do not vary with subsistence. Partible paternity societies in Amazonia have more paternal half siblings indicating higher male reproductive skew.

Conclusions: Sibling counts from genealogies provide a convenient method to simultaneously investigate the reproductive skew and pair-bond stability dimensions of human mating systems cross-culturally. Am. J. Hum. Biol. 00:000–000, 2015. © 2015 Wiley Periodicals, Inc.

INTRODUCTION

There is considerable complexity and variation in marriage practices and family structure across human cultures (Flinn and Low, 1986; Fox, 1967; Murdock and White, 1969). Human mating systems integrate strategies common in other organisms, such as control of resources to attract mates, direct mating systems integrate strategies common in other organisms, such as control of resources to attract mates, direct competition for control of mates, and advertisement of phenotypic indicators of heritable qualities (Dixson, 1998; Emlen and Oring, 1977; Shuster and Wade, 2003; Thornhill and Alcock, 1983; Thornhill and Gangestad, 2008). Unlike other species, pair-bonding and reproductive decisions in humans are often culturally regulated and controlled by parents and other kin (Apostolou, 2007, 2010; Chagnon, 1982; Chapais, 2008; Fox, 1967; Levi-Strauss, 1949; Walker et al., 2011).

Morphological, physiological, and behavioral evidence suggests that our recent evolutionary history has been characterized by predominantly (serial) monogamous pair-bonding with facultative polygynous and, to a lesser but not insignificant degree, polyandrous mate systems on both short and long terms (Dixson, 2009; Geary, 2010; Low, 2000; Starkweather and Hames, 2012; Symons, 1979). Cross-culturally, a majority of societies permit polygamous marriages, although most conjugal unions in all human populations are monogamous (Murdock, 1967; Marlowe, 2000), and most sexual behavior and reproduction occurs, with important exceptions, within the context of long-term pair-bonds with biparental care of offspring (Gray and Garcia, 2013; Symons, 1979).

There are two primary dimensions of variation in human mating systems that deviate from stable monogamy and beg for socioecological explanations. The first is male reproductive skew ranging from mostly monogamous (low skew) to strongly polygynous (high skew) mating patterns (Betzig, 2012; Low, 1988). The second dimension is pair-bond stability ranging from low to high rates of conjugal dissolution and serial mate systems (Barber, 2003; Betzig, 1989). Although these two dimensions have received considerable attention, progress has been hampered by studying each in isolation and by measurement difficulty. While rates of polygyny are reported in many ethnographies (e.g., Berreman, 1972), other ethnographies describe levels of polygyny in vague terms, making it hard to quantify or even rank how common it is, thus rendering cross-cultural comparison difficult.

Pair-bond stability has proven particularly recalcitrant. Ethnographers generally describe divorce and divorce rates with incomparable descriptors such as “rare,” “not difficult,” “easy,” and “common.” Rarely do ethnographies report actual frequencies or rates of divorce (see, e.g., Pearson and Hendrix, 1979: 378). It is important to note that these problems described above pertaining to measurements of polygyny and pair-bond stability are not unique to these two phenomena. Indeed, cross-cultural comparison of any kind, on any topic, has to contend with the difficulties introduced by heterogeneity in construct formulation, measurement, and researcher bias (see Ember and Ember, 1998, 2000; Ember et al., 1991; Veneziano, 2000 for reviews).

Here, a methodology is advanced that allows for both reproductive skew and pair-bond stability to be analyzed simultaneously using information on the prevalence of different sibling types gleaned from genealogies. Full sibling sets originate from stable monogamous pair bonds. Paternal half siblings primarily stem from male reproductive skew through polygynous mating or serial monogamous mating when men remarry younger wives or are simply more likely to remarry or obtain new mates than widowed or divorced women. Maternal half siblings indicate the dissolution of pair bonds due to divorce or male death. While unstable pair bonds can also generate paternal half siblings, the overall effect is likely to be small in comparison to that generated by male reproductive skew because male reproduction is not as time limited as female reproduction.

Additional Supporting Information may be found in the online version of this article.

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given the interbirth interval necessary for pregnancy and lactation, and termination of reproduction due to menopause [Marlowe and Berbesque (2012) estimate the physiological reproductive span of females foragers to be 34 years, and that of males to be 71 years]. Pair-bond instability is also likely to potentiate reproductive skew as some men will be more able to find new partners than other men. Hence, the simple calculation of the fraction of siblings of different types allows for the decomposition of human reproductive variation into dimensions of stable monogamy (represented by full siblings), male reproductive skew (paternal half siblings), and pair-bond instability (maternal half siblings). By obviating the need to rely on inconsistent or (more or less) incommensurate concepts, variables, and measurements, our method circumvents one major limitation to conducting cross-cultural research. Use of genealogical data, given its availability, renders all populations comparable—in the present case, in a single quantifiable measure: proportions of sibling types.

**Polygyny and reproductive skew**

Humans have traditionally been described as a mildly polygynous species. According to Marlowe and Berbesque (2012), the human operational sex ratio (OSR, the ratio of sexually competing males to sexually competing females) (Emlen, 1976) is similar to that of the highly polygynous gelada baboons, yet our sexual dimorphism in body weight is similar to that of chimpanzees who have an OSR half that of humans. Thus, estimations of the degree of male reproductive skew in recent human evolutionary history may not be accurately informed by measures of sexual dimorphism as is true for nonhuman primates (Plavcan, 2012). Reproductive skew is an index of the intensity of sexual selection, and thus it is a parameter of theoretical interest in assessing the likely influence of sexual selection on the evolution of human behavior.

An alternative to investigating modern human sexual dimorphism for clues to our recent past is to examine the degree of reproductive skew in contemporary traditional societies. Degree of male reproductive skew in humans, although hampered by paternity uncertainty, has typically been quantified through various measures of polygynous marriages (Betzig, 2012; Low, 1988). In this section, we review previous research addressing the factors associated with variation in polygynous marriage across cultures. This allows predictions to be derived and tested against genealogical data as well as assesses the congruency between more traditional measures of polygyny described below and the current method of measuring reproductive skew via patterns of siblinghood.

One early attempt at investigation of the correlates of variation in polygyny cross-culturally was that of White and Burton (1988), who found that two significant predictors, as measured by percentage of women married polygynously, were climate zone and female contribution to subsistence. Polygyny is more prevalent in tropical and temperate zones where women contribute more to the diet. Low (1990) examined the relationship between pathogen stress and marriage patterns and reported a higher incidence of polygyny, as measured by several different metrics, in those societies inhabiting regions of high pathogen stress. The logic of the pathogen stress hypothesis is that in populations that experience higher pathogen and parasite loads, variation in male immunocompetence will place a premium on female mate choice for phenotypic indicators in males of disease resistance and immune function, and thus will lead to polygyny for the healthiest men (Low, 1990).

More recently, Marlowe (2000) also found polygyny, as measured by the percentage of polygynously married women, to be highest among horticulturalists, where men contribute the least to subsistence. The negative relationship between degree of polygynous marriage and male contribution to subsistence also holds within each mode of subsistence (Marlowe, 2000, 2003). According to Marlowe, where male contribution to subsistence is low, women’s mate choice is based on traits other than ability for nutritional provisioning, and polygyny in these societies may represent mate defense polygyny by men (Marlowe, 2000). A study by Marlowe (2003) of 36 hunter-gatherer societies confirmed previous findings that degree of polygyny, as measured by the percentage of polygynously married women, is negatively correlated with male contribution to subsistence, and positively correlated with pathogen stress (which is higher at lower latitudes).

The pathogen stress hypothesis accords with the hypothesis on male contribution to subsistence if lower male contribution to subsistence decreases women’s reliance on male labor and foraging returns. In these circumstances, female mate choice may be tuned more to indirect genetic benefits that men can provide, if they outweigh the benefits of male-provided material resources. These factors are interrelated in that pathogen stress is higher at lower latitudes and male contribution to subsistence is greater at higher latitudes.

A crucial issue from the standpoint of understanding human reproductive patterns is the extent to which marriage systems reflect the actual mating system, as revealed by reproductive outcomes. If measures of polygyny using data on marriage are accurate depictions of reproductive reality, then given previous findings from the studies discussed above, we predict that (1) reproductive skew will be highest in horticultural societies, compared to other subsistence modes; horticulturalists will have the highest fraction of paternal half siblings. Additionally, based on the observed relationships between pathogen stress and degree of polygynous marriage, and male contribution to subsistence and polygynous marriage, and the correlation between pathogen stress, male contribution to subsistence, and latitude, we further predict that (2) reproductive skew will be higher in societies at lower latitudes, thus paternal half sibling fractions will be higher at lower latitudes.

**Pair-bond instability**

While marriage patterns have been analyzed in depth by numerous anthropological researchers, systematic investigations of quantitative measures of pair-bond instability and divorce have been given much less attention (but see, e.g., Burton Jones et al., 2000; Quinlan and Quinlan, 2007; and discussion below). Here, predictions must necessarily be more speculative. Given the association between mode of subsistence and male contribution to diet, as well as between subsistence mode and amassable, defendable, and heritable resources, the following three predictions are derived: (1) pair-bond instability will be greater where male contribution to subsistence is lower. Thus, according to Marlowe’s findings on male contribution to subsistence by subsistence mode, horticulturalists should exhibit the highest fraction of maternal half siblings, and agropastoralists the lowest; (2) given the greater dependence on male contribution to subsistence at higher latitudes (Kelly, 1995), pair-bond instability will be lower at higher latitudes, irrespective of subsistence mode;
(3) Pair-bond instability will be greater in the absence of amassable, heritable resources. Where women are not dependent on male controlled resources for offspring success, they may be less constrained to dissolve a pair-bond (see also Goody, 1976). Foragers and horticulturalists should thus exhibit the highest, and agropastoralists the lowest, fraction of maternal half siblings.

**Partible paternity**

As our sample of societies includes several from lowland Amazonia, this affords an opportunity to investigate patterns of mating and pair-bonding as they relate to different conceptions of reproduction. Indigenous societies in this region of the world have been documented to engage in paternity societies of lowland South America (Beckerman and Valentine, 2002; Beckerman et al., 1998; Walker et al., 2010). Partible paternity societies exist side-by-side with other indigenous societies inhabiting very similar ecological niches that do not entertain the concept of multiple fatherhood. This situation allows investigation of the influence of cultural constructs in affecting the parameters of human mating systems, with some degree of control for environmental factors given that comparisons are within a single ecological region.

The partible paternity concept is attended by institutionalized patterns of polygynandrous extramarital mating that may have consequences for pair-bond stability and male reproductive skew. Hypothesized benefits of partible paternity include gene shopping by females, the procurement of investment from multiple men, and mate competition by males (Walker et al., 2010). In this context, high quality men may obtain greater numbers of sexual partners and sire more offspring with multiple women. To the extent that genealogical data reflect actual paternity, it is predicted (1) that partible paternity societies will have higher fractions of paternal half siblings than singular paternity societies. The extra-pair sexual relationships entailed in the practice of partible paternity may destabilize marital unions given a combination of sexual jealousy and reduction or splitting of paternal investment. Thus, it is also predicted (2) that pair-bond instability will be greater among partible paternity societies compared to singular paternity societies; partible paternity societies will have higher fractions of maternal half siblings than singular paternity societies.

**Paternity certainty**

Our method of using genealogical data to investigate the aforementioned dimensions of human mating systems raises the issue of paternity certainty, given that we take the attributions of paternity in the data at face value. Paternity certainty is an important concept in theoretical discussions of male mating strategies and allocations of reproductive effort to mating versus parental care (Alexander, 1974; Clutton-Brock, 1991; Geary, 2000; Kokko, 1999; Queller, 1997; Sheldon, 2002), and there are many treatments in the anthropological literature of the social structural and economic correlates of behavior consistent with variable levels of paternity certainty (see Alexander, 1979; Flinn, 1981; Gaulin and Schlegel, 1980; Hartung, 1982; Irons, 1979, 1983; Kurland, 1979). The empirical literature on actual rates of nonpaternity in humans is scarce, however, especially for small-scale traditional populations.

A review of the available evidence by Anderson (2006) showed nonpaternity rates to be quite low cross-culturally (1.7–3.3%), without significant differences between samples from different regions of the world. Consistent with these previous findings summarized by Anderson (2006), recent research by Strassmann et al. (2012) reported a low (<3%) rate of nonpaternity for small-scale Dogon agriculturalists of Mali in a highly patrilineal and patriarchal context with mate guarding and strong sanctions for extra-pair mating for women. In contrast, a study of Himba pastoralists of Namibia by Scelza (2011) found that 17% of all recorded marital births were attributed to extra-pair paternity in a context where extra-pair relationships appear to have few negative consequences and the identity of extra-pair fathers are openly discussed. These two studies illustrate two ends of a likely spectrum of paternity certainty in traditional societies.

Despite these few suggestive data points, due to the scarcity of empirical data on nonpaternity in traditional, non-Western populations, it is not possible to formally or accurately assess how actual nonpaternity may vary across contemporary or recent historical small-scale societies. Likewise, we are unable to examine whether there are particular systematic correlates of high or low rates of nonpaternity, such as mode of subsistence or marriage patterns. Finally, even if small, the impact of paternity uncertainty on our estimates is uncertain. If biological (but not social) fathers are more likely to have multiple female partners (as in the case of secondary fathers in the Ache) (Eellsworth et al., 2014), paternity uncertainty would increase the fraction of paternal siblings. Paternity uncertainty’s effect on the proportion of maternal siblings depends on the rate of nonpaternity within families: in cases in which biological (but not social) fathers father all of the children in a particular family, paternity uncertainty would not increase the proportion of maternal siblings. Given these complexities, we have no reasonable option but to take the genealogical information at face value while acknowledging that our estimates are likely inexact.

**METHODS**

Genealogies and marriage records for this study were obtained from the KinSources website (http://kinsources.net), an online peer-reviewed repository of genealogical datasets. Additional genealogies were added for 5 hunter-gatherer (foraging) societies from Hill et al. (2011), and 18 Amazonian horticultural societies from Walker et al. (2013). The small-scale societies used here are categorized as hunter-gatherers \((n = 38)\), horticulturalists \((n = 33)\), agriculturalists \((n = 6)\), and pastoralists \((n = 3)\). Because the latter two categories are small, often practiced together cross-culturally and both rely heavily on material resources (e.g., cows and land) for subsistence (Borgerhoff Mulder et al., 2009), they are lumped together for statistical purposes as agropastoralists \((n = 9)\). The total sample includes 80 societies (Fig. 1) with genealogies that allow us to calculate a total of 61,181 siblings. An Amazonian subset of 26 societies with known paternity concept (Walker et al., 2010) is used to compare singular versus partible paternity societies (see Supporting Information for sample data).

Genealogies range in depth from 3 to 16 generations but variation in genealogical depth does not affect our results.
because only information for both of ego’s parents is needed to count sib types. Individuals missing data for either mother or father are excluded. Relationships between fathers and offspring were taken at face value as reported by informants. For partible paternity societies, the primary father (generally mother’s husband) is assumed to be the biological father.

For each society’s genealogy, we count the average number of siblings for each individual that are paternal, maternal, or full. A pair of siblings counts as 1 (each has 1 sibling), a group of three siblings counts as 2 (each has 2 siblings), and so on. The sum of all sibling types goes into the denominator of our measure, and in the numerator is the number of paternal half, maternal half, or full siblings, which yields a fraction of the average individual’s siblings that are of each type.

RESULTS

Sibling types

The percent of siblings in the overall sample shows that most siblings are full (61%, range 33–100% across societies), while fewer are paternal (27%, range 0–57%) or maternal (13%, range 0–33%) half siblings. A ternary plot (Fig. 2) shows that many societies have sibling fractions that cluster toward stable monogamy (more full siblings). Most variation away from full siblings occurs along the paternal half sibling axis and is roughly twice that of variation in the maternal half sibling axis. This is due primarily to differences in polygyny and maximum reproductive rates between males and females.

Despite the fact that pair-bond instability generates both paternal and maternal half siblings, there is no correlation between the two (Table 1), probably because male reproductive skew swamps the variation in maternal half siblings. Variation in levels of maternal half siblings exists across the entire spectrum of paternal half siblings. This suggests that male reproductive skew and pair-bond stability are independent sources of cross-cultural variation in human mating patterns. Horticulturists and agropastoralists have slightly higher counts of paternal half siblings than foragers in the sample (0.25 vs. 0.19 on average) and the relationship is statistically significant \( t = 2.1, P = 0.039, n = 80 \). In other words, these results show a weak relationship between subsistence mode and male reproductive skew, but there is not a significant relationship between subsistence mode and pair-bond stability, as measured by fraction of maternal half-siblings \( t = 1.08, P = 0.282, n = 80 \).

A greater fraction of paternal half siblings correlates \( r = 0.64 \) with more polygynous marriages measured as number of wives per married man from marriage records (Fig. 3). The relationship between polygynous marriages and variation in paternal half siblings is similar for societies within each category of subsistence mode. The correlation between paternal half siblings and polygynous marriage is expected, yet important in that it indicates congruency between marriage and mating patterns, and provides validity to using our measure of paternal half sibling as an indicator of male reproductive skew in our sample. As argued below, paternal half sibling fractions may actually be a better

Fig. 1. Map of societies used in this study with designations for subsistence type.

Fig. 2. Ternary plot of the proportion of different sibling types. Maternal half sibling fraction is on the x-axis, full sibling fraction is on the y-axis, and paternal half sibling fraction is on the z-axis. Societies are designated by subsistence category. Many societies cluster toward stable monogamy (more full siblings) with variation extending mostly in the z-axis (more paternal half siblings and male reproductive skew) and less variation in the y-axis (more maternal half siblings and pair-bond instability).
Higher latitude societies have significantly fewer paternal half siblings, as predicted given previous studies of latitudinal gradients of polygynous marriage (Low, 1990; Marlowe, 2000). Full siblings are also more common, and maternal half siblings less common, at high latitudes, indicative of a greater degree of stable, monogamous mating. Multiple regressions of sibling fractions as a function of latitude and subsistence consistently show that latitudinal gradients are strongest for full and paternal half siblings with little evidence for interaction effects between latitude and subsistence. This means that the effect of latitude on sibling fractions is only partly due to variation in subsistence modes associated with latitude, and may be better explained by latitudinal variation in male contributions to subsistence.

**Partible paternity**

Sibling fractions in lowland South American societies vary systematically with paternity concept. Societies with partible paternity have lower full sibling fractions overall (0.51, 95% bootstrapped confidence interval 0.47–0.56) than do singular paternity counterparts (0.68, 95% bootstrapped confidence interval 0.60–0.76, Fig. 4). Paternal half sibling fractions are higher in partible paternity societies, while maternal half sibling fractions do not differ significantly by paternity concept. As predicted, partible paternity appears to correlate with more male reproductive skew. However, inconsistent with our other prediction, partible paternity does not appear to be associated with greater pair-bond instability. The primary difference between partible and singular paternity societies in our sample is a greater degree of polygynous mating by males in partible paternity cultures.

**DISCUSSION**

The findings of the present study show that the majority of human reproduction occurs within pair-bonds that are stable and monogamous, given that 61% of all siblings in the sample are full. Variation away from pair-bond stability and monogamous mating trends primarily toward more male reproductive skew arising from polygynous mating and resulting in higher fractions of paternal half siblings.

Results demonstrate a latitudinal gradient on sibling fractions, such that full sibling fractions increased, and paternal and maternal half sibling fractions decreased, at higher latitudes. Societies at lower latitudes are characterized by more polygynous mating consistent with a combination of both greater female contribution to subsistence and female gene shopping in environments of high pathogen load (e.g., Low, 1990; Marlowe, 2003). As reported above, this latitude gradient is not mediated by subsistence mode; that is, degree of reproductive skew is only partly explained by mode of subsistence per se in our sample of societies. This finding is consistent with previous research demonstrating a higher incidence of polygynous marriage among horticulturalists compared to other subsistence types (e.g., Marlowe, 2000), and a more general relationship between subsistence and marriage patterns (e.g., White and Burton, 1988). In addition to broad comparisons between subsistence modes, it may prove more fruitful to focus on particular socioecological arrangements that differ by subsistence mode, as leading to differences in male reproductive skew. To the extent that subsistence plays a role in variation in male reproductive skew, it may be related to the relative contribution to subsistence of men and women. For example, the societies in the current sample for which data exists show that among foragers in North America, male contribution to subsistence increases with latitude (Kelly, 1995: 263).

Marriage record data and sibling analysis demonstrate a positive relationship between polygynous marriage and reproductive skew for societies in the present sample, suggesting that marriage patterns closely correspond to patterns of mating. However, counting paternal half siblings has several advantages over counting polygynous marriages. First, variation in male reproductive skew measured by paternal half siblings includes polygynous mating outside of marriage either in the form of children born out of wedlock or children born from extra-pair matings, assuming ethnographers at least occasionally ascertained the identities of actual biological fathers. Second, available marriage records are often snapshots in time, while genealogies extend over multiple generations. Third, genealogies

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**TABLE 1. Correlation matrix for the relevant variables in this study**

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Maternal sibling fraction</th>
<th>Paternal sibling fraction</th>
<th>Full sibling fraction</th>
<th>Absolute latitude</th>
<th>Polygyny</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paternal sib fraction</td>
<td>80</td>
<td>0.038</td>
<td>-0.608**</td>
<td>-0.817**</td>
<td>-0.221**</td>
<td>0.381**</td>
</tr>
<tr>
<td>Full sibling fraction</td>
<td>80</td>
<td>-0.608**</td>
<td>-0.817**</td>
<td>-0.431**</td>
<td>0.431**</td>
<td>-0.378**</td>
</tr>
<tr>
<td>Absolute latitude</td>
<td>80</td>
<td>-0.221**</td>
<td>-0.431**</td>
<td>0.431**</td>
<td>0.592**</td>
<td>0.142</td>
</tr>
<tr>
<td>Polygyny</td>
<td>65</td>
<td>0.229</td>
<td>0.592**</td>
<td>-0.568**</td>
<td>-0.378**</td>
<td>0.282</td>
</tr>
<tr>
<td>Partible paternity</td>
<td>26</td>
<td>0.222</td>
<td>0.550**</td>
<td>-0.568**</td>
<td>0.142</td>
<td>0.282</td>
</tr>
</tbody>
</table>

Statistical significance is marked as follows: *p < 0.05 and **p < 0.01.
represent actual reproductive outcomes and not just marriages that may or may not result in offspring. Therefore, information on paternal half siblings likely constitutes a more comprehensive index of male reproductive skew than that available from the prevalence of polygynous marriages alone. Additionally, measures of actual reproductive outcomes via patterns of siblinghood across multiple generations gives an additional index of the strength and direction of sexual selection within populations over time that complements other methods of assaying differential reproductive success (see Brown et al., 2009). Alternatively, one could attempt to measure skew by estimating the dispersion of paternal skew across men. However, this was found to be difficult because later generations in genealogies include many men that have not yet finished their reproduction, a problem that is circumvented using paternal half sibling fractions. Moreover, basic genealogies, such as the majority used here, are not full demographies in the sense of including children that died young and instead often only include children that lived to a certain age.

Pair-bond instability has been given much less attention than marriage systems, and, as mentioned above, has not been consistently quantified in the ethnographic record, hampering the types of comparative analyses done for polygyny. The method of counting maternal half siblings shows little systematic variation across subsistence types or paternity concept. A study by Apostolou (2010) showed that divorce is reported as common across societies of all subsistence types, and regression analyses indicated that divorce commonness is independent of mode of subsistence. However, partible paternity societies do have a higher frequency of polygynous marriages on average than their singular paternity counterparts (1.37 vs. 1.23 wives per married man), as well as more polygynous mating as indexed by fractions of paternal half siblings. Institutionalized extramarital sexual relationships attending the partible paternity concept could be another source of the higher male reproductive skew in these populations, albeit it is surprising that ethnographers have been able to document the identity of actual fathers as opposed to social fathers married to the mother. More likely, some males who do not marry polygynously are able to remarry quicker and with younger wives in serial monogamy that contributes to more male reproductive skew. Such a pattern must hold for only some men because average rates of pair-bond dissolution, as indicated by paternal half sibling fractions, do not vary between partible and singular paternity societies.

High rates of male death in tribal warfare (Beckerman and Valentine, 2008; Walker and Bailey, 2013) in the more traditional and unacculturated partible paternity societies may make male investment relatively unreliable and risky from the perspective of women. Unreliable paternal investment, along with higher degrees of polygynous mating and marriage, result in an interrelated suite of traits emerging in partible paternity systems that includes more male mating effort, low levels of paternal investment, and high male in such contexts. However, adult sex ratio in the present sample of societies shows no systematic relationship with pair-bond stability.

Other factors that have been identified include socioeconomic development and female labor participation (Trent and South, 1989). The issue of socioeconomic development in the present study cannot be addressed, as this factor is rather ill-defined for traditional societies. Female labor force participation, however, has been shown to be positively associated with divorce in both developed and developing countries (see references in Trent and South, 1989). Additionally, moral attitudes discouraging promiscuity have recently been found to correlate with women’s economic dependence (Price et al., 2014). This, presumably, has something to do with a lessening of female dependence on male provisioning in ecologies where females contribute more to their household economies. As Irons (1983) has argued, in such contexts, females may expend more effort in establishing and maintaining social relationships with other females (co-wives, sisters, cousins) than with husbands, and this trade-off may thus attenuate the conjugal dyad.

In the present sample of traditional small-scale societies, labor force participation would seem to be comparable to female contribution to subsistence, and assuming a latitudinal gradient in male contribution to subsistence (with males contributing relatively more at higher latitudes), pair-bonds appear to be more monogamous and stable where males contribute more to subsistence. However, Quinlan and Quinlan (2007) found a curvilinear relationship between contribution to subsistence and pair-bond stability for societies in the Standard Cross-Cultural Sample, with increases in divorce rates associated with increasing disproportion in contribution to subsistence by one sex or the other.

In partible paternity societies, the strong pattern of higher fractions of paternal half siblings, indicating high male reproductive skew, could arise from mating systems where some males are able to sire disproportionately more children, irrespective of marriage patterns or pair-bond stability. However, partible paternity societies do have a higher frequency of polygynous marriages on average than their singular paternity counterparts (1.37 vs. 1.23 wives per married man), as well as more polygynous mating as indexed by fractions of paternal half siblings. Institutionalized extramarital sexual relationships attending the partible paternity concept could be another source of the higher male reproductive skew in these populations, albeit it is surprising that ethnographers have been able to document the identity of actual fathers as opposed to social fathers married to the mother. More likely, some males who do not marry polygynously are able to remarry quicker and with younger wives in serial monogamy that contributes to more male reproductive skew. Such a pattern must hold for only some men because average rates of pair-bond dissolution, as indicated by paternal half sibling fractions, do not vary between partible and singular paternity societies.

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reproductive skew. Within such a milieu, women may benefit from gaining investment potential from multiple men, in effect securing insurance on male investment in self and offspring upon cessation of investment from a primary mate as a result of divorce, death, or desertion. Female mating strategies in these contexts are expected to be tuned to choosing males both within and outside of marriage in ways that optimize access to limited and unreliable paternal investment.

CONCLUSION

Anthropologists have long struggled with the question of how best to document the comparatively rich diversity of human reproductive strategies around the world. The ethnographic record is often qualitative in nature, but statistics and hypothesis testing benefit from the ability to quantitatively estimate cultural variation. A common solution to this problem is for anthropologists to lump societies into discrete categories (e.g., rare vs. common polygyny or divorce) which have limited statistical utility. Sibling counts from genealogies provide an alternative solution to divorce which have limited statistical utility. This method introduces and has further confirmed previous findings (e.g., latitudinal scale. This method appears valuable in that its initial application to this problem is for anthropologists to lump societies into discrete categories (e.g., rare vs. common polygyny or divorce) which have limited statistical utility. Sibling counts from genealogies provide an alternative solution to divorce which have limited statistical utility. This method introduces and has further confirmed previous findings (e.g., latitudinal gradients in polygyny). The method introduced and employed in this article has broad applicability for investigations of reproductive behavior and opens new horizons for comparative ethnological analyses.

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AUTHOR CONTRIBUTIONS

R.W. and D.B. analyzed the data. R.E., R.W., D.B., and M.S. drafted and edited the manuscript. R.W. designed the study, and directed data collection.

LITERATURE CITED