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Reports

Relatedness, Co-residence, and Shared Fatherhood among Ache Foragers of Paraguay

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Hypotheses on the benefits of the practice of partible paternity are tested using demographic data for Ache foragers of Paraguay. Partible paternity refers to the institution of multiple males considered to contribute to the conception of a single offspring. Analyses focus on patterns of primary and secondary co-fatherhood among men, genealogical relationships between co-fathers, and relation between band co-residence and co-fatherhood. Results indicate that men who had more secondary fatherhood also had more primary fatherhood; co-fathers are more closely related, on average, than men who are not co-fathers; and co-fathers were also more likely to reside together than men who were not co-fathers, even after controlling for relatedness. Results are most consistent with women choosing co-fathers of offspring in ways that maximize likelihood and amount of investment (*multiple investors* hypothesis) and men competing for more mates with at least partially affiliative outcomes (*mate competition* and *male alliance* hypotheses).

Anthropologists have long taken an interest in cross-cultural variability of human sexual and reproductive behavior (Betzig, Borgerhoff Mulder, and Turke 1988; Ford and Beach 1952; Low 2000; Marshall and Suggs 1971; Symons 1979). One of the most challenging issues of late concerns the concept and practice of partible paternity. Partible paternity refers to the institutionalized claim that a child can have more than one genitor (Beckerman and Valentine 2002; Walker, Flinn, and Hill 2010). The concept is found in most indigenous cultures of lowland South America, being nearly ubiquitous across several large language families (Arawá, Carib, Pano, Tupi, and Macro-Je) and possibly as much as three times as common as the concept of singular paternity (Walker, Flinn, and Hill 2010). At last count in our sample 61 lowland societies are known to have partible paternity and only 24 with singular paternity.

Partible paternity presents a challenge because it is seemingly at odds with paradigmatic views on human sexuality derived from evolutionary biological theory (Daly and Wilson 1983; Symons 1979). In comparative perspective, paternal investment in humans is more intensive and arguably more important to offspring success than in any other primate (Bribiescas, Ellison, and Gray 2012; Geary 2000). However, within our species, levels of investment vary according to a number of factors. In particular, there is evidence from numerous cultures that paternal investment is contingent upon paternity certainty (Geary 2010). To this end, men place a premium on sexual fidelity of long-term mates and employ a variety of mechanisms to ensure their investment is directed at genetic descendants (Wilson and Daly 1992). Shared paternity implies polyandrous mating and thus is puzzling in light of the aforementioned traits of human males. Recent research has demonstrated that polyandrous arrangements are more common cross-culturally than previously thought (Starkweather and Hames 2012). Thus, we must give serious consideration to the once suspect notion that women can benefit from multiple mating and polyandrous relationships (Hrdy 2000) and that human reproductive strategies are more complex than traditionally conceived by sociobiologists.

Partible paternity must be viewed within the larger context of the dynamic interplay of men's and women's reproductive pursuits. From an evolutionary perspective, a crucial question concerns potential fitness benefits to men and women from the concept and practice of divisible fatherhood. Although the concept is widespread among indigenous South American populations, there is variation in its practice. Some societies have traditional prescriptions as to which males may share paternity. For example, the virilocal, patrilineal Curripaco exclude the role of secondary fatherhood except when paternity is shared between brothers (Valentine 2002:191). Similar restrictions on co-fatherhood are reported for the virilocally-biased Yanomami (Ales 2002:71, 80). On the other hand, loose regulation of co-fatherhood and extramarital sex is found in societies without strong unilineal descent and virilocality/patrilocality, such as the Canela (Crocker 2002) and Barí (Beckerman et al. 2002). It appears that the Ache did not have explicitly formulated rules or preferences concerning shared paternity. This diversity suggests that no one hypothesis may be universally satisfying. Rather, the behavior surrounding this concept in any given culture will reflect unique histories of inter- and intrasexual reproductive competition, and thus who benefits from its practice, and how, might differ across populations.

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In the present paper we present demographic data from censuses of forest-dwelling (pre-contact) Ache hunter-gatherers of Paraguay that contribute toward an understanding of the reproductive consequences of partible paternity and how male and female strategies play out within the sociocultural milieu of sharable fatherhood for this particular population. Analysis is focused particularly on (1) patterns of primary and secondary co-fatherhood among men, (2) genealogical relationships between co-fathers, and (3) the relation between band co-residence and co-fatherhood.

Hypothesized Benefits of Partible Paternity

Investigation of these variables permits preliminary testing of some hypothesized benefits of partible paternity to Ache men and women (see table 1). Specifically, with regard to women, it is hypothesized that benefits may derive from garnering investment from multiple males (*multiple investors hypothesis*; Beckerman et al. 2002; Hrdy 2000; Walker, Flinn, and Hill 2010). If so, it is predicted that women should choose co-fathers in ways that maximize the likelihood and amount of investment in themselves and their offspring. Another hypothesized benefit to females is genetic diversification of offspring (*gene shopping hypothesis*; Walker, Flinn, and Hill 2010). In populations with a high level of genetic homogeneity (Ache have one of the lowest levels of genetic heterozygosity in the world; Lewis 2010; Wang et al. 2007), partible paternity may grant women greater leverage in choosing different fathers for successive children. If women indeed benefit from genetic diversity of offspring, co-fathers should be less likely to be close relatives of one another. A third hypothesis states that women benefit through the short-term exchange of sex for resources (*sex for resources hypothesis*; Shapiro 2009), resulting in all men who had sex with a woman prior to pregnancy considered as possible fathers. This hypothesis predicts that long-term social ties between women, their children, and co-fathers will not figure as important features of partible paternity systems and that men should give mating presents to women and not the other way around.

For men, it is hypothesized that benefits may derive from increased mating access to more women and, by extension, greater chances at siring offspring with multiple females (*mate competition hypothesis*; Walker, Flinn, and Hill 2010). The Ache recognize two types of fatherhood: primary fathers are often the husband of a child's mother. Secondary fathers are other men who had a sexual relationship with a child's mother prior to pregnancy and birth (Hill and Hurtado 1996). If particularly desirable men benefited from partible paternity through higher potential fertility, it is predicted that men with

Table 1. Hypothesized benefits of partible paternity tested in the present study

Hypothesis	Benefits of partible paternity	Predictions	Evidence	Supported?
Female strategy:				
Multiple investors	Investment in offspring from multiple men	Females choose co-fathers of offspring in ways that maximize likelihood and amount of investment; most children will have secondary fathers	Higher survival of offspring with secondary father; co-fathers more likely to be co-resident and/or kin; most children have secondary fathers	Yes
Gene shopping	Genetic diversity of offspring through polyandrous mating	Co-fathers will be unrelated or distantly related	Co-fathers are more closely related, on average, than men who are not co-fathers	No
Sex for resources	Gifts from males in exchange for short-term sexual access	Absence of long-term social bonds between co-fathers, women, and offspring	Participation in couvade rituals signals public recognition of co-fatherhood. Secondary fathers maintain social ties to co-fathered children and mothers	No
Male strategy:				
Mate competition	Greater potential fertility through increased sexual access	Men who have more secondary fatherhood will also have more primary fatherhood	Secondary fathers have co-children with more women than do men who are not secondary fathers; men with more secondary fatherhood also have more primary fatherhood	Yes
Male alliance	Alliances between men who are co-fathers of the same children	Co-fathers will be close kin; co-fathers will be residents of same band	Co-fathers are more closely related, on average, than men who are not co-fathers. Co-fathers are more likely to be co-resident	Yes

more primary fatherhood would also have more secondary fatherhood. Another hypothesized benefit to men is the establishment and strengthening of alliances between individuals who were co-fathers of the same children (kin bonding or *male alliance hypothesis*; Walker, Flinn, and Hill 2010). This hypothesis predicts that co-fathers would have affiliative types of relationships, such as being close relatives and/or residents of the same band.

Study Population

The Ache are Tupi-Guaraní-speaking foragers who traditionally inhabited the tropical forests of Eastern Paraguay (Hill and Hurtado 1996), making first peaceful contact with outsiders in the early 1970s, before which they were nomadic hunter-gatherers moving camp every few days. Band size among forest dwellers was flexible and ranged from three to more than 100 individuals at any given time (Hill and Hurtado 1999), with a mean experienced band size of about 20 adults, with—from adult ego's point of view—consanguineal kin (both close and distant) constituting 20%, and unrelated individuals 25%, with spouse and affines comprising the remainder (Hill et al. 2011). Pre-contact Ache marriages were extremely flexible and based on courtship with minimal influence from parents or other adults. There were no prescribed marriage partners, and incest restrictions extended only to parents, siblings, cross- and parallel first cousins, and godparents (Hill and Hurtado 1996:227). Polygynous and polyandrous marriages were permitted but infrequent. Informants report that forest-living Ache women exercised considerable autonomy in their choice of mates and in the persistence or dissolution of marital bonds. The Ache showed the highest rate of divorce of any foraging group for which data exist, with women having an average of 10 spouses by age 30 (Hill and Hurtado 1996:231), although in later years of life marriages tended to have a higher probability of enduring.

According to the Ache, any man who has engaged in sexual intercourse with a woman several months prior to discovering her pregnancy, and up to the day of birth, may contribute to the paternity of that woman's offspring. Paternity was not necessarily limited to one individual, and most Ache claimed more than one man as a father (Hill and Hurtado 1996:273). The Ache recognized two types of paternity. *Primary fathers* (the "one who put the child in") were usually husbands or men who were involved in long-term mating relationships with a women and had the most frequent sexual intercourse with her prior to discovery of her pregnancy. *Secondary fathers* included other men who had sex with a woman prior to and during her pregnancy (the "ones who mixed it"). Interestingly, the Ache seemed to recognize that the timing of copulation with a woman in relation to discovery of pregnancy bears on the probability of being the primary father of her offspring (Hill and Hurtado 1996:274). Secondary fatherhood was most often achieved when men are younger, while older men tended more often to be primary fathers (Hill and Hurtado 1996:288). As part of the institution of partible paternity, secondary fathers were sometimes expected to undergo dietary and activity restrictions associated with *couvade*, a public statement of their status as new "fathers."

Assignment of paternity to men was the province of females, and claims of primary paternity were liable to change with a woman's situation (e.g., when potential fathers died or were no longer in residence; Hill and Hurtado 1996:442). Analyses of childhood mortality have shown that children with a primary father and one secondary father had the highest survivorship, suggesting that having two fathers was optimal for child survival (see Hill and Hurtado 1996:444 and 465, fig. 13.4). The finding that one secondary father is associated with higher survivorship has also been reported by the only other study to examine this effect by Beckerman and colleagues (2002) for the Barí of Venezuela. While for the Barí, Beckerman et al. argued that improved survivorship was due primarily to improved fetal nutrition resulting from provisioning by secondary fathers, the mechanism for the Ache remains uncertain (although protection from infanticide upon the death or desertion of the primary father may be important, see Hill and Hurtado 1996).

Methods

Calculating Primary and Secondary Fatherhood

In calculating primary and secondary fatherhood, we used previously collected census data for precontact Ache (Hill and Hurtado 1996), which yielded a sample of 237 men. Only men aged 18 or older who were primary fathers or secondary fathers of at least one child were included in the analysis. Of these men, 110 were reported as primary father of at least one child, 20 were reported as secondary father of at least one child, and 107 were reported as primary and secondary father of at least two children. For deceased individuals, "age" was defined as age at death. For living individuals, "age" was defined as their current age. Of the 284 children in our sample, 106 had one father, 120 had two fathers, and 58 had more than two fathers.

To determine the relationship between primary and secondary fatherhood in terms of number of children, the number of children each man was a secondary father of was entered into a Poisson regression model controlling for age and age squared. The dependent variable was the number of children of whom a man was the primary father.

Calculating Co-residence

To calculate co-residence we have censuses for 58 pre-contact Ache bands from interviews (Hill et al. 2011). Census data spanned the time frame 1958–1970, yielding a total of 157 adult men sampled over this period. Each co-residing dyadic pair of adults was considered a single data point; if the same pair co-resided in more than one band, they were counted multiple times, with the matrix entry for each dyad repre-

senting the proportion of censuses in which both individuals were found to be co-residing together.

Calculating Genetic Relatedness of Co-fathers

To calculate relatedness, we have complete genealogical and marital histories for adults in the Ache population covering the twentieth century (Hill and Hurtado 1996). The relatedness matrix for the entire northern Ache population was used to calculate relatedness for the 157 men who appeared in the pre-contact camp censuses. The relatedness values among all Ache men was estimated using Descent software (Hagen n.d.). In this calculation, only consanguineal relationships were considered. The estimate takes reported primary fatherhood at face value and assumes that individuals with no known genealogical links have a genetic coefficient of relatedness of zero.

Co-fatherhood, Genetic Relatedness, and Co-residence

To calculate relationships between co-fatherhood, genetic relatedness, and co-residence, three square similarity matrices were calculated for the 157 men who occurred in the residence censuses. A co-fatherhood matrix, in which all co-father pairs were coded as 1 and all other pairs were coded as 0, was calculated. A genetic relatedness matrix was calculated based on the full genealogy. The values of co-residence were bound between 0 (two men never occurred together in the censuses) and 1 (two men always co-resided in each census).

For our analyses, we used multiple regression on distance matrices (MRM using the ecodist package in R; Goslee and Urban 2007). For regression coefficients, MRM uses permutation tests of significance, and for the following analyses, we used 10,000 permutations per model. First, single predictor models were used to assess the relationships between all three matrices. Next, we regressed co-residence on co-fatherhood and relatedness. Finally, we regressed co-fatherhood on co-residence and relatedness.

Results

Primary and Secondary Co-fatherhood

The results of the Poisson regression model showed that the effect of number of children secondarily fathered on number of children primarily fathered was significant and positive (regression weight = .094; $z = 5.24$, $P < .0001$). Men who had more secondary fatherhood also had more primary fatherhood. A man with 0, 1, 2, 3, 4, or 5 secondary children is predicted to have 2.92, 3.21, 3.53, 3.88, 4.27, or 4.69 primary children, respectively.

Genetic Relatedness of Co-fathers

The distributions of genetic relatedness for co-father pairs and random pairs of men appears in figure 1. The average genetic relatedness for co-father pairs in this sample was .0388 (SD = .096), compared to .0234 (SD = .073) for pairs of men who were not co-fathers. This difference was statistically

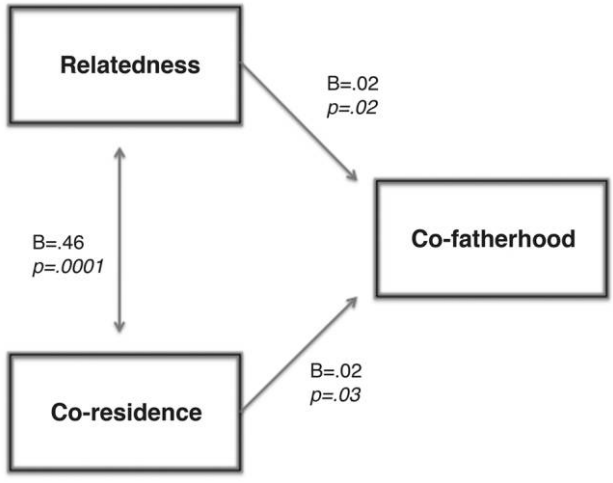

Figure 1. Partial correlations among relatedness, co-residence, and co-fatherhood among Ache men.

significant ($t(12,244) = -3.13$, $P = .002$). Co-fathers are statistically less likely than chance to be unrelated, although 70% of co-father pairs are still unrelated. Co-fathers are over twice as likely to be cousins or half brothers than expected by chance, and 4% of all co-father pairs are full brothers (fig. 2).

Co-fatherhood, Genetic Relatedness, and Co-residence

Results of the single predictor models showed that the relatedness matrix significantly predicted co-residence (B = .25; $P = .0001$). Relatedness also predicted co-fatherhood for this subset of the sample (B = .03; $P = .003$). Finally, co-residence predicted co-fatherhood (B = .03; $P = .004$).

When co-residence was regressed on both co-fatherhood and relatedness, the effect of relatedness remained highly significant (B = .24; $P = .0001$), and the effect of co-fatherhood also remained statistically significant (B = .02; $P = .02$). Together, co-fatherhood and relatedness were associated with 6.1% of the variance in the co-residence similarity matrix. Regression of co-fatherhood on co-residence and relatedness showed that the effects of co-residence (B = .02; $P = .03$) and relatedness (B = .02; $P = .02$) both remained statistically significant, indicating that both variables contribute unique variance to co-fatherhood status.

Discussion

The results of our analyses show that men with more secondary fatherhood also had more primary fatherhood. Data on relatedness reveal that co-fathers were more closely related, on average, than were men who were not co-fathers. Co-fathers were also more likely to reside together than men who were not co-fathers. These results offer insight into male and female reproductive strategies related to partible paternity,

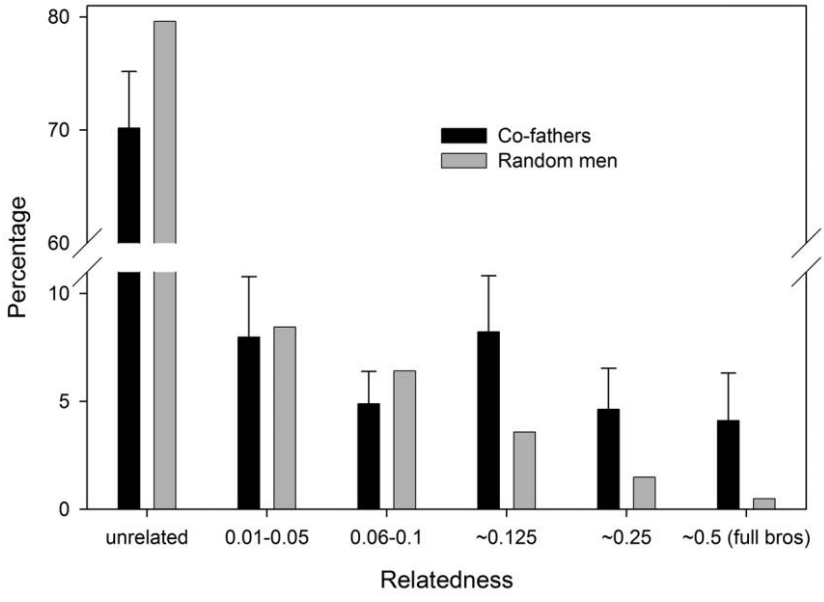

Figure 2. Comparison of observed relatedness between co-father pairs against baseline relatedness of random pairs of men alive at the same time. Error bars represent bootstrapped 95% confidence intervals.

and they permit testing of the aforementioned hypothesized benefits to men and women within Ache society.

Female Strategies and Ache Partible Paternity

The findings reported above concerning relationships among co-fathers, co-residence, and kinship suggest some benefits to females of the practice of partible paternity among the Ache. As already mentioned, it appears that the Ache did not have explicitly formulated rules or prescriptions concerning shared paternity. It is possible that the absence of emphasis on unilineal descent groups, as well as considerable residential flexibility among the Ache, account for the lack of formal rules or restrictions on choice of fathers. In any case, fluidity of band composition and the absence of regulated co-fatherhood, as well as female control of paternity assignment described above, gave Ache women considerable latitude in selecting mates and co-fathers for their offspring. Thus, women are expected to have made strategic decisions regarding co-paternity in ways that maximized potential benefits to themselves and their offspring.

The fact that co-fathers were more closely related, on average, than men who were not co-fathers suggests that women selected men who were more likely to invest in their offspring—nepotistically, if not paternally. Aside from the issue of biological paternity, there are theoretical (Alexander 1979, 1987; Hamilton 1964) and empirical (see, e.g., contributions in Chagnon and Irons 1979) grounds for expecting individuals to invest more in kin than non-kin. Sufficiently low paternity certainty of an unrelated co-father may lead to lower levels of investment than would be the case if a co-father were a relative of the biological genitor. By selecting as co-fathers men who are close kin, women would have been increasing the investment in themselves and their offspring, and, by granting some degree of paternity probability, may have increased levels of investment beyond that from nepotism alone. Also, choosing co-fathers who are closely related may have increased the probability of cooperative relationships and decreased the probability of conflict between men who share paternal stakes in the same offspring. While relatedness between co-fathers is consistent with the *multiple investors* hypothesis, we cannot rule out the *gene shopping hypothesis* for co-fathers of women's children who were not close relatives of one another.

The fact that co-fathers were more likely to reside together suggests that women selected men who were more able to invest in her and her offspring. Proximity to a woman and her offspring increased the opportunity for direct investment by co-fathers. One important type of relationship among the Ache is referred to as the *bykuare* (ones who provided the essence of the child), who supplied a pregnant mother with meat that then inspired the child's name (Hill and Hurtado 1996:67, 442). These men were described as being especially concerned with a co-child's welfare. Thus, women were likely to have received direct nutritional provisioning from some secondary fathers.

Our results concerning patterns of residence and relatedness of co-fathers are most consistent with the predictions of the *multiple investors hypothesis* that women strategically chose individuals as co-fathers in ways that increased the probability and amount of investment in their offspring. Indeed, as re-

ported above, having a secondary father was associated with increased offspring survivorship. Enlisting multiple potential investors can be viewed as an insurance or bet-hedging strategy. High adult male mortality due, in part, to warfare created a female-biased adult sex ratio among the Ache (Hurtado and Hill 1992). Male scarcity, combined with high rates of divorce, leads paternal investment to be scarce and unreliable, not only because men themselves are scarce but also because in contexts of female-biased adult sex ratio men increase mating effort at the expense of parental effort (Guttentag and Secord 1983; Pedersen 1991). This suggests the possibility that, by obtaining co-fathers for offspring, women were in essence hedging their bets on male investment should a primary father die or desert while offspring are still dependent.

Public recognition of co-fatherhood through participation in *couvade* rituals, investment in the welfare of women and their children by secondary fathers, and increased offspring survivorship associated with having co-fathers are all evidence against the *sex for resources hypothesis* (Shapiro 2009). While potential co-fathers did sometimes exchange resources for sexual access, it appears that among the Ache, benefits to women went beyond short-term exchanges to include long-term affiliation among co-fathers, women, and their children.

Male Strategies and Ache Partible Paternity

The findings concerning attributed fatherhood in the current sample are consistent with the prediction of the *mate competition* hypothesis that men with more secondary fatherhood would also have more primary fatherhood. Results suggest that men named as secondary fathers may be valuable or desirable mates; these men had more putative paternity of offspring of more women than men who were not named as co-fathers. However, the exact reason for their higher mating success is unclear. Possibilities include phenotypic indicators of "good genes" (e.g., sexual attractiveness), high levels of investment or willingness to invest in a female and her offspring, success in male-male competition (social status), or social selection (skilled hunters or men valuable as coalition members allowed/permitted greater sexual access to women). In any case, it appears that some men capitalized on the culturally legitimated extramarital sex attending partible paternity through greater potential reproductive success.

In a previous publication we had stated that Ache co-fathers tended *not* to like one another, were not likely to be close kin, and were traditionally enemies at club fights (Walker, Flinn, and Hill 2010), but these statements were not based on systematic data. We know that Ache men sometimes mentioned that they wanted to club some men who had sex with their wives and that some co-fathers were despised. However, our analyses here have led us to conclude that more often co-father relations were more likely to be affiliative given their higher levels of relatedness and higher probability of co-residence. These findings are consistent with the *male alliance hypothesis*. The sharing of mates and fatherhood may have reduced male-male mating competition, thus reducing the corrosive effects of mate competition on social cohesion and male coalitions so important to success in intergroup conflict. Warfare was a major cause of mortality for pre-contact Ache. Among adult males, external warfare accounted for 36% of all deaths (Hill and Hurtado 1996:163). Shared paternity between close kinsmen could have created or intensified alliances and cooperative relationships.

Conclusion

The current study focused on examining some important aspects of partible paternity among pre-contact Ache. Findings provide support for certain hypotheses regarding benefits to both women and men and evidence against some others. In particular, our results support the *multiple investors* hypothesis of female benefits. Co-fathers appear to have been chosen in ways that increased the likelihood and opportunity for male investment. That co-fathers were more likely to be close relatives to one another is inconsistent with, but does not rule out, the hypothesis that some women benefited from securing diverse genes for offspring. Results are also inconsistent with the hypothesis of transient benefits to women of exchanging short-term sexual access for resources from men. Regarding male benefits, our findings are consistent with the *male alliance* hypothesis. Fatherhood shared between related and co-resident men suggests that relations among co-fathers were often amicable, rather than antagonistic. Results also support the *mate competition* hypothesis. Patterns of primary and secondary fatherhood suggest that some men use partible paternity to their advantage in increasing potential reproductive success through multiple mates.

In closing, we think an important point needs to made about partible paternity, given its recent connection with certain misleading ideas about human sexuality that have gained some public appeal. Contrary to the arguments of some authors (e.g., Ryan and Jethá 2010), the existence of partible paternity in some societies does not prove that humans are naturally promiscuous any more so than the existence of monogamy in some societies proves that humans are naturally monogamous. Human mating dynamics are not well captured with simplifying terms such as "monogamy" and "promiscuity." Oversimplified views on the nature of human sexuality are perhaps ideologically satisfying, but they are empirically deficient. Phenomena such as partible paternity call for the development of increasingly sophisticated theory that takes into account the flexible, ecologically-contingent nature of human reproductive strategies.

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