Partible paternity, the secondary sex ratio and a possible Trivers-Willard effect.

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Abstract: Partible paternity, the belief that a child can have more than one biological father, is widespread in lowland South America. An analysis of demographic data sets from four lowland tribes (Aché, Barí, Ese Eja, and Surui) reveals a systematic variation in the sex ratios of live births with respect to the number of fathers to whom the births are attributed. Births attributed to only one father show a sex ratio that is unexceptional for South America; births with two fathers are highly male biased, while children with three or more are female biased. This pattern may be a manifestation of a phenomenon predicted by the Trivers-Willard hypothesis, which proposes that, in many circumstances, females in good condition might bias their offspring toward males, while those in poor condition would produce a preponderance of females. If, as suggested below, a woman with a husband and a single extramarital lover tends to be better cared for before and during a pregnancy than other women, this difference might result in the improved maternal condition required by the Trivers-Willard hypothesis for excess males, while women who accept two or more lovers might be preponderantly those who are already in distress, thus tending to produce female biased offspring.

In theoretical biology, the Trivers-Willard hypothesis (see below) posits a connection between the sex ratio at birth (secondary sex ratio) and the condition (health, nutritional status, etc.) of the mother. Since its publication (Trivers and Willard 1973) it has been repeatedly tested against human data (reviews in Hrdy 1987, Sieff 1990, Lazarus 2002, Cronk 2007,) with mixed results. Most of these human studies use data from complex societies with modern medicine and effective methods of birth control, while the original hypothesis refers to conditions where those evolutionarily novel, potential confounders are absent. Here, after a brief exposition of the Trivers-Willard hypothesis, we present secondary sex ratio data from four lowland tropical forest tribes in South America, all of them egalitarian, natural fertility populations. These four tribes have the beliefs and practices of partible paternity (also briefly described below) and we suggest that the peculiar correspondence of the partible paternity data and the sex ratio data is broadly consistent with the Trivers-Willard hypothesis, if two plausible suppositions are accepted.

The Trivers-Willard hypothesis proposes an environmentally provoked deviation from equality in the numbers of males and the numbers of females born to a hypothetical reproducing female. As R. A. Fisher (1930) showed, if there is an unequal operational sex ratio in a population, evolution favors parents who invest in producing a preponderance of the rarer sex. Thus the rarer sex becomes more common over evolutionary time. At equilibrium, this condition produces males and females in roughly equal numbers at the end of the period of parental investment, given the adjustment that if one sex is “cheaper” (e.g., smaller, more liable to mortality during the period of parental investment, etc.) than the other, then that sex will be more numerous at conception.

Expanding on Fisher’s reasoning, Trivers and Willard (1973) pointed out that, given the common circumstance that male variance in reproductive success is greater than female variance (i.e., a few males inseminate a great many females and some never mate at all, while the great majority of females do mate and produce at least some offspring) there is a selective advantage for a female to be able to bias her offspring toward one sex or the other, if the reproductive success of her offspring is predictable. “Predictable” may follow from nothing more complicated than the tendency of a robust, well fed mother to produce large, strong, healthy offspring—and for that advantage to be carried on throughout life, including mating success; while a mother in poor condition will tend to produce small, weak, sickly offspring who will be handicapped as adults.

What this line of reasoning comes down to for present purposes is this: “(A)n adult female in good condition who produces a son will produce more surviving grandchildren than a similar female who produces a daughter, while an adult female in poor condition who produces a daughter will leave more surviving grandchildren than a similar female who produces a son” (Trivers and Willard 1973:90.)

In this report, we analyze secondary sex ratio data from four lowland tropical forest peoples of South America: the Barí of Venezuela, the Aché of Paraguay, the Suruí of Brazil and the Ese Eja of Bolivia.1 . It is well known that lowland South American peoples typically have high sex ratios, when compared to worldwide averages (Millard and Berlin 1983,) and it is not surprising that all four peoples display a secondary sex ratio different from the 105 to 106 males per 100 females usually considered normal for human populations (cf. Tab. 1): Barí 109:100 (n = 739); Ache 134:100 (n = 314); Suruí 115:100 (n = 760); Ese Eja 69:100 (n = 105). As is to be expected for small population demographic data, these ratios differ markedly from one other, particularly in the case of the smallest example, from the Ese Eja. The sex ratio for the sum of these data is 112:100 (n = 1918.) That small overall deviation from the typically high South American ratio is not the subject of this report, however. Rather, we focus on the secondary father status of the individual births.

All four of our live birth data bases come from peoples holding to the beliefs and practices of partible paternity (Beckerman et al. 1998; 2002; Beckerman and Valentine 2002.) This ideology, common in lowland South America (Walker et al. 2010) holds that a child can have multiple biological fathers. Every man who has intercourse with the mother around the time of conception, or at any time throughout the pregnancy, contributes to forming the child. The associated behaviors (women’s liberty in sexual behavior, as long as they do not violate incest taboos; men’s tolerance of wives’ adultery) permit the mother to take sanctioned lovers during pregnancy. While a woman’s husband is held to be her child’s primary father, these lovers are considered to be secondary fathers of the child to whom they have contributed.2

The analytical result that motivates this report is the finding that the live birth sex ratio appears to be sensitive to the number of fathers to whom a child is attributed. The possibility of such a relationship among the Barí was raised a few years ago (Beckerman and Lizarralde 2013,) but did not reach statistical significance even at the [alpha] = 0.05 level, with the single data base then available. The accumulation of three additional data bases and subsequent pooled analysis suggests that the suspected relationship between multiple fathers and the secondary sex ratio is likely to be real3.

While there are major differences among the four data bases assembled here (Tab. 1, Tab. 2), as is to be expected with such small total numbers per tribe, the aggregated data suggest, especially when viewed as a 2x3 contingency table for the pooled data (Tab. 3), a general tendency for males to be mildly over-represented in live births attributed to a single father (with respect to worldwide sex ratios) as is common in lowland South America (109:100; n = 1461), strikingly over-represented in births attributed to two fathers (143:100; n = 364), and under-represented in births attributed to three or more fathers (75:100; n = 93).

A statistical analysis of the data of Tab. 2 yields a chi-squared value of 9.11 (df = 2; p = 0.01); a test using Fisher’s exact method extended to a 2 x 3 contingency table also produces a result of p = 0.01, both considerably bypassing the p < 0.05 level earlier chosen for the Barí data alone

Perhaps more interesting, for reasons discussed below, is that the overweighting of males among children with two fathers contrasts dramatically with the overweighting of females among children with three or more fathers. A comparison of the live birth sex ratios only of children attributed to two fathers (i.e., those with only a single secondary father) and children attributed to three or more fathers (those with two or more secondary fathers) produces a chi-square value of 7.47 (df = 1) significant at the p = 0.006 level. The difference is similarly significant at the p = 0.007 level by Fisher’s method, although the category of children attributed to two or more extra fathers has a small sample size (n = 93) and needs to be interpreted cautiously.

The live birth sex ratio results reported above are consistent with the predictions of the Trivers-Willard hypothesis, if one tentatively accepts the propositions 1) that a woman who has a single lover as well as a husband tends in some way to be in better condition before and/or during pregnancy than a woman with only a husband to support her (better nutrition due to increased provisioning by two men, and lower stress due to social support by two men, are obvious possibilities here); and 2) that a woman who takes two or more lovers in addition to her husband tends to be compromised in some way with respect to nutrition, health, or support.

There is unfortunately little ethnographic evidence bearing on the first of these propositions. Courtship prestations are probably a cultural universal, and Aché, Barí, and Ese Eja lovers do provide gifts of game and/or fish to women with whom they are having affairs.

While there are no data with respect to differential maternal condition before and/or during pregnancy for women in any of the four tribes under consideration here, there is evidence from two of them that children of pregnancies attributed to two fathers--a primary and a single secondary father—may be more robust than those who have only one father.

It has been shown in the cases of the Aché (Hill and Hurtado 1996; Beckerman 2002) and the Barí (Beckerman et al. 1998; Beckerman et al. 2002) that children with both a primary father (the mother’s husband) and a single secondary father have higher survivorship than children with only a primary father, or children with two or more secondary fathers. Better health is the most likely reason, although of course there are other possibilities. Whether this advantage (cf. Beckerman et al. 2002) translates into augmented reproductive success in adulthood is not known.

At the other end of the secondary fathers scale, data also suggest that too many secondary fathers may be associated with elevated risk to a child. Writing of the Aché, Hill and Hurtado (1996: 444) reported “Those children with one primary and one secondary father show the highest survival in our data set, and one secondary father is also the most common number reported during out reproductive interviews…children with three or more fathers appear to have fared worse than those with only one or two fathers.” This difference, however, did not reach statistical significance in their data (Hill and Hurtado 1996: 465.)

Exploring the same issue among the Barí, Beckerman et al. (2002: 37) found that “Comparing the odds of dying before 15 for a child with two or more secondary fathers and a child with no secondary father, the odds ratio was 0.632; ns. Comparing the odds of dying before 15 for a child with two or more secondary fathers and a child with one only, the odds ratio was 5.188, p = 0.0001.” They concluded that “women took several secondary fathers per child only when they were unmarried and distressed and were, in effect, supporting themselves by something like prostitution. Such women were likely to be chronically undernourished, as were their children.” While no skinfold measurements were taken, Beckerman and Lizarralde recall these few women and their children as leaner and less energetic than their peers.

Even though there are no data relating maternal condition before or during pregnancy to the number of fathers a woman provides for her child, there are some data consistent with the possibility that male infants with both a primary and a single secondary father may eventually have higher mating success than other males. If the survival advantage of the sons of single secondary fathers is a result of better health, and that health is related to higher birthweight, then that benefit might carry over into adulthood.

Hill and Hurtado (1996: 354-5; 371-2) found that, among the Aché, male fertility increased with adult body weight for most of the male population, with a negative relationship for the very heaviest males. They suggested that “(a)lthough large men may be at an advantage in intrasexual competition, as hunters they are not as effective as intermediate-sized males.”

Previously unpublished height data4 collected by Roberto Lizarralde among the Barí in 1963-64, for men whom we were able to track for their eventual completed fertility (construed as the number of children born to all their wives) showed a tendency for taller men to produce more children (Fig. 1; Tab. 3), without the drop-off for the very largest men reported by Hill and Hurtado.

In a parallel case that raises the possibility that this reproductive advantage to size may be widespread in lowland South America, Gregor (1979:15) reported that among the Mehinaku of Brazil, taller men had considerably elevated amorous success when compared to their shorter fellows: “In our village, the three tallest men had as many affairs as the seven shortest men, even though their average estimated ages were identical (thirty-seven).”

The data sets presented above are in no way decisive in considering the proposal that the human live birth sex ratio differences reported here are the manifestation of a Trivers-Willard effect, which is quite a difficult proposition to establish (cf. Clutton-Brock and Iason 1986.) Indeed, a conclusive exploration of the possibility would require a multigenerational prospective study involving ongoing biomedical measurements, including regular and frequent collection of blood, urine and saliva samples, along with uninterrupted ethnographic study of demography and life history, all conducted in a society effectively insulated from the acculturative effects of the modern world—a virtually impossible task. Such being the case, we have prepared this report in the hope that South Americanists who have, or may in the future collect, incremental data that bear on the issue will consider addressing the proposition suggested above. If additional data disconfirm our suggestion of a human Trivers-Willard effect, the live-birth sex ratio disparities reported above will be relegated to the status of a curiosity, an unexplained peculiarity of small-sample of anthropological demography. If they tend to corroborate it, that support will suggest interesting avenues of research into the evolutionary ecology of human reproduction.

Males Females

Number of Secondary Fathers Number of Secondary Fathers

0 1 2 or more 0 1 2 or more

Barí 288 91 6 267 74 13

Aché 67 83 30 55 45 34

Suruí 384 21 2 336 15 2

Ese Ejá 22 19 2 42 16 4

Totals 761 214 40 700 150 53

Table 1: Numbers and sexes of live births by tribe, cross tabulated with number of secondary fathers to whom the births were attributed.

Number of Secondary Fathers

0 1 2 or more

Barí 1.08 1.23 0.23

Aché 1.23 1.84 0.88

Suruí 1.14 1.40 1.00

Ese Eja 0.52 1.19 0.50

Table 2: Secondary sex ratios by tribe and number of fathers to whom births were attributed

Number of Secondary Fathers

0 1 2 or more

Males 761 214 40

Females 700 150 53

Table 3: Pooled numbers and sexes of live births, cross tabulated with number of secondary fathers to whom the births were attributed.

Figure 1

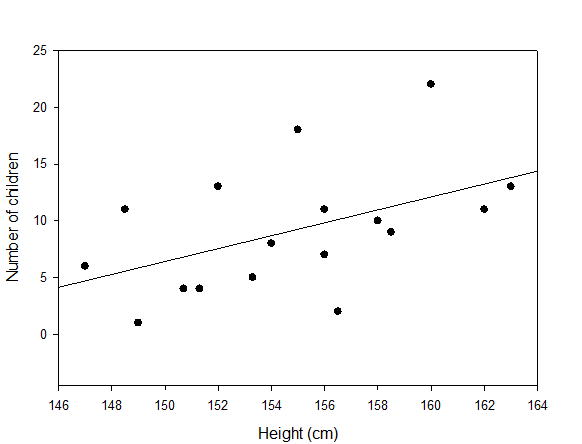


Figure 1: Scattergram of number of children born to Barí fathers vs. height in cm of the fathers; intercept = -78.8; slope = 0.57; r2 = 0.23; p = 0.05.

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1These live birth sex ratio databases were recorded for purposes other than the focus of this article. The Barí data came from reproductive history interviews conducted by Beckerman and R. Lizarralde in Venezuela with 114 post-reproductive women (or in a few cases of deceased women, their immediate family members.) These subjects were essentially all the post-reproductive Barí women then living in Venezuela. The field protocol, designed around the issue of whether children with secondary fathers had improved survivorship, was reviewed in Beckerman et al. (2002: 33-35.) The Aché data came from interviews of 338 Northern Aché over the age of ten. Field methods were elaborate and were discussed in Hill and Hurtado (1996: 86-94.) Peluso’s data from a Peruvian Ese Eja community were supported by 65+ months of fieldwork. The data set was not a sample set but rather a full data set that included all adult members of one community. Methods included structured and unstructured interviews that were used to create a data matrix that was triangulated via further interviews and participant observation. Further details in Peluso (2004) and Alexiades and Peluso (2009.) The Surui data were logged by Yvinec in the course of recording genealogies. When a child was attributed to more than one father, he noted the men identified. However, he did not inquire explicitly into the fatherhood of all children, and may have missed some cases of multiple paternity. His field methods wer described in Yvinec (2011.) He generously supplied these data, but, as a linguistic anthropologist, did not participate in the analytical or theoretical portions of this article.

2No systematic evaluation of the distinguishing characteristics of secondary fathers has been published. Among the Aché, Hill and Hurtado (1996: 442) suggested that “men who regularly supplied meat to the mother were also likely to be her lovers, and thus a secondary father of the child in question.” Among the Barí, Beckerman and Lizarralde (2013: 197-8) found that good hunters had more wives than ordinary men. It could be argued that this predilection for good hunters as husbands might have extended to a preference for good hunters as lovers as well. Nor has there been any clarification of why secondary fathers were rare (named for under 20% of the full sample.) Beckerman and Lizarralde (2013: 209-10) discussed possible explanations for this infrequency among the Barí, but no general explanation has been offered.

3All these databases recorded sex of live born and number of secondary fathers after the birth of the child in question. It is conceivable that for some reason women might be more prone to identify secondary fathers for a male rather than a female child, although we have no evidence for such a tendency, and it would leave unexplained the under-representation of males in those children attributed to two or more secondary fathers. Nevertheless, the possibility merits further field research.

4In response to popular reports soon after contact that the Barí were giants, Roberto Lizarralde took the heights of quite a few of them with a tape measure in his early fieldwork. The figures used here refer only to measured men whose eventual completed reproductive success we were able to track. Many of the others died in post-contact epidemics