



**Explaining Biased Sex Ratios in Human Populations: A Critique of Recent Studies
[and Comments and Reply]**

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Explaining Biased Sex Ratios in Human Populations

A Critique of Recent Studies¹

by Daniela F. Sieff

Recent studies attempting to test evolutionary explanations of biased sex ratios in human populations are here critically reviewed. It is suggested that closer attention to a broad range of ecological and social factors that may affect differential investment in sons and daughters might contribute to better evolutionary understanding of the patterns observed.

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Variations in the sex ratio—the number of males per hundred females—at birth have been reported for a number of human populations, and recently attempts have been made to explain these variations and differential postnatal care of sons and daughters in terms of evolutionary theory. Evolutionary sex allocation models propose that parents will allocate resources among male and female offspring in such a way as to produce the greatest net effect on their own fitness (usually measured in terms of surviving offspring or grandoffspring) per unit of resources expended (Charnov 1982). After a brief overview of the evidence for bias in sex ratios in human populations and some of the proximate mechanisms that have been suggested to account for it, I shall outline the several evolutionary theories available for explaining this bias and then critically review recent studies attempting to test them. Finally, I shall suggest that closer attention to a broad range of ecological and social factors that may affect differential investment in sons and daughters might contribute to better evolutionary understanding of the patterns observed.

Sex-Ratio Biases in Human Populations

The average sex ratio of human births is approximately 105 (Cavalli-Sforza and Bodmer 1971), but there is variation both within and between populations. Among the many variables associated with statistically significant biases in the human sex ratio at birth (reviewed by James 1987a, Blaffer Hrdy 1987) are race (in the United States of America, the Caribbean, and West Africa, blacks have a lower sex ratio than whites), birth order (later-born children tend to be female), sexes of existing offspring (the probability of having a son rises with the number of prior sons and falls with the number of prior daughters), war (sex ratios rise during wartime and immediately thereafter), handedness of the parents (the chances of having a son are significantly greater when both parents are right-handed), smoking (the sex ratio is lower among offspring of women who smoke), and timing of fertilization (high sex ratios following from conception either early or late in the fertile period). Teitelbaum and Mantel (1971), analyzing data from the American census for 40,000 births, found a lower sex ratio for the lowest social class than for the highest. Rostron and James (1977), using Scottish census data, failed to replicate this result and pointed out that, since Teitelbaum and Mantel's study did not control for parity and later-born offspring are significantly more likely to be female, their results could have been due to parity differences rather than socioeconomic status.

The magnitude of bias is generally small. For example, the variation of sex ratio due to parity falls between 103.2 and 102.6; the average sex ratio for offspring of women who smoke is 101.89, whereas that for offspring of nonsmoking women is 103.3. The average sex ratio for current births to nulliparous mothers is 102.6–102.9; the corresponding figure for mothers with no sons and four daughters is 90.2–97.4 and that for mothers with

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four sons and no daughters 108–114.6. Even when these more substantial biases are found, however, they are difficult to interpret from an adaptive perspective because the data are often presented as averages and background data that might help to suggest (albeit post hoc) evolutionary explanations are rarely available.

Data from traditional societies provide additional evidence for bias in sex ratios at birth. Using census data, Chagnon, Flinn, and Melancon (1979) have argued that the Yanomamo infant sex ratio of 128 reflects the secondary sex ratio rather than female-biased infanticide; Hurtado and Hill (1987) report a secondary sex ratio at birth of 117 for the Cuiva foragers of Venezuela, and Hill and Kaplan (1988), using carefully cross-checked data from reproductive histories, have shown a birth sex ratio of 116 for the Ache hunter-gatherers of Paraguay. The most striking biased sex ratios so far reported are those for Orthodox Jews. Census data from Russia between 1867 and 1884 show an average sex ratio of 137 for the Jews, whereas the surrounding groups had a sex ratio of 105 (Guttentag and Secord 1982). (Because sons and not daughters were taxed, any underreporting of births would probably have affected males.) A recent study of the sex ratio at birth among Orthodox Jews in Israel found a similarly high ratio of 131 (Harlap 1979).

The proximate mechanisms of bias in sex ratios at birth are not well understood. The idea that males are more susceptible than females to environmental stress is common (e.g., Tanner 1962; Cavalli-Sforza and Bodmer 1971; Stini 1975, 1982; McMillen 1979; Clutton-Brock, Scott, and Dickman 1985), but the evidence is more ambiguous than is generally supposed (Stinson 1985). A review of studies on spontaneous abortions that sexed offspring by karyotype showed an average sex ratio of 111, not significantly different from the average at birth (Stinson 1985). Although karyotyping was used to circumvent the difficulty of sexing fetuses, it has been argued that contamination by maternal tissue biased the results towards females and that a more accurate estimate of the sex ratio of chromosomally normal abortions is 123 (Hassold, Quillen, and Yamane 1983). Studies of stillbirths report sex ratios ranging from 92 to 124 (Stinson 1985). It has been argued that much of this variation may reflect a secular trend towards decreasing sex ratio of stillbirths attributed to improved obstetric care (Teitelbaum 1971, Ulizzi 1983).

Nutritional stress may contribute to male-biased infant mortality pre- and postnatally, although James (1987a, b) argues that the effects are relatively weak in humans. Studies on wood rats (McClure 1981), golden hamsters (Labov et al. 1986), and domestic mice (Wright, Crawford, and Anderson n.d.) have shown that mothers in poor condition produce litters biased towards females. Gosling (1986) has reported sex ratios in *coyppu* biased in accordance with the mother's nutritional condition; mothers with high levels of fat aborted small female-biased litters but not large ones or small male-biased litters, and mothers with only a small amount of fat aborted no litters.

Social stress may also affect the sex ratio at birth.

Golden hamsters exposed to attacks and chases late in pregnancy produced significantly smaller and significantly female-biased litters (Pratt, Huck, and Lisk 1989). Finding no significant difference in the number of females per litter in the dominant, control, and subordinate groups, the researchers concluded that the female-biased sex ratios were due to relatively high male mortality in utero. For nonhuman primates there is some evidence that high-status females are significantly more likely to attack lower-status conspecifics if the latter are carrying fetuses of a specific sex (Sackett 1981, Silk 1983, Small and Smith 1984). Among wild spider monkeys (*Ateles paniscus*), high-ranking females produce offspring with a sex ratio of approximately 100, whereas low-ranking ones produce almost entirely daughters; McFarland Symington (1987) argues that differential mortality of male and female embryos in utero is a likely cause. She hypothesizes that if the sex ratio at birth is due to in utero mortality, low-ranking mothers will abort more frequently and therefore show longer interbirth intervals, and when high- and low-ranking mothers are compared for the interbirth intervals following only daughters this is in fact the case. A problem with this interpretation, however, is that low-ranking mothers might be expected to have longer interbirth intervals in any case because of reduced access to food.

James (1985, 1986, 1987a, b) has suggested that biases in the sex ratio can be explained by hormone levels at the time of conception. A high level of maternal gonadotrophin at conception correlates with a female bias, a high level of estrogen with a male bias. The gonadotrophin level rises sharply at ovulation, and therefore high sex ratios will be expected to result from insemination early or later in the fertile period (James 1983). James (1985) uses the evidence that dominance rank in females is correlated with high gonadotrophin levels to argue that this steroid may be driving the female-biased sex ratios among the offspring of high-ranking female baboons (Altmann, Hausfater, and Altmann 1988) and rhesus monkeys (Simpson and Simpson 1982, but see Berman 1988). A challenge to James's theory, as he himself points out, is the male-biased sex ratio among offspring of high-ranking red deer mothers (Clutton-Brock, Albon, and Guinness 1986). One way to examine this apparent contradiction would be to look at the interaction of rank, hormone levels, and timing of mating for females. Among semi-free-ranging Barbary macaques at Affenberg Salem, high-ranking mothers produce offspring with a high sex ratio and low-ranking mothers offspring with a significantly low sex ratio (Paul and Kuester 1987). Barbary macaques are seasonal breeders, and as the majority of macaques become pregnant at first estrus these researchers conclude that differential abortion cannot account for the sex bias at birth. They suggest that it could be explained by the timing of fertilization, whereby high-ranking females are more attractive and continue to mate for longer after ovulation or begin to mate earlier. In the absence of behavioral data, it is difficult to evaluate this argument. It does, however, suggest that although high-ranking females might be ex-

pected to produce offspring with a low sex ratio because of their high gonadotrophin levels, the timing of fertilization may be more important in influencing the sex ratio. As James himself argues, more research is needed before any conclusions can be drawn. One further point with regard to the hormonal hypothesis is that although correlational data suggest that steroid environments influence sex ratios, there is little experimental evidence to show how this occurs (Levin 1987).

Some bias in human sex ratios may be induced post-natally through differential care (Dickemann 1984, Scrimshaw 1984). This may take extreme forms such as infanticide and pedicide or less extreme ones such as the differential allocation of food and health care. Selective neglect, passive or active, is well documented for human societies (see Blaffer Hrdy 1987 for a review of the human sociobiological literature and Chen, Huq, and D'Souza 1981, Miller 1982, Jeffry, Jeffry, and Lyon 1984, Bairagi 1986, Ginsberg and Swedlund 1986, Das Gupta 1987, LeVine 1987, and Boswell 1989 for examples from demography).

Evolutionary Explanation of Sex-Ratio Biases

Fisher (1930) has argued that because every individual has one mother and one father, parental investment in sons and daughters should be equal within a population. If parents invested equally in sons and daughters but the population had a biased sex ratio, then parents who produced offspring of the rarer sex would leave more grandoffspring; only a sex ratio of 100 would be evolutionarily stable. If, however, one sex had consistently higher mortality before the end of the period of parental investment, then offspring of that sex (in mammals, usually sons) would not receive a full quota of that investment, with the result that the average cost of each son conceived would be less than the average cost of each daughter. According to Fisher, it would only be by producing a surfeit of sons at birth that parents could equalize their investment. An alternative way to equalize investment, however, would be not to produce more sons but to invest more in each son who survived. Clutton-Brock and Albon (1982) point out that Fisher's argument applies to the population average and individual parents may deviate from the mean of equal investment. They go on to say that it overlooks the fact that competition or cooperation between relatives may be greater than between two random members of the population and this will alter the costs and benefits of sons versus daughters. Finally, they argue that if sex differences in mortality (or reproductive success [see Trivers and Willard 1973]) that occur after the period of parental investment are influenced by such investment, selection will favor parents who invest more in individuals of the sex with the higher mortality.

Trivers and Willard (1973) have proposed that if variance in reproductive success is greater for one of the sexes and if the offspring's reproductive success is influenced by parental investment, then parents will bias

their investment as their resources permit. Among polygynous mammals, variance in lifetime reproductive success is typically greater in males; males in good physical condition outreproduce females in good condition, whereas females in poor condition may outreproduce males in poor condition. If maternal condition affects the condition of offspring, then parents who are in above-average condition will produce disproportionately more sons, whereas females who are in poor condition will, on average, leave more grandoffspring by biasing their investment towards daughters.

Two separate ideas are encompassed by the Trivers and Willard model (Clutton-Brock and Albon 1986). The first is that parents will invest resources where those resources most benefit the offspring's reproductive success. When the variance in reproductive success is greater in males and when the success of a male depends on the investment received from his parents, parents will invest more heavily in individual males because this will give them a greater return per unit of investment (Trivers 1982, Maynard Smith 1980, Clutton-Brock and Albon 1982). The second is that the cost to the mother's future reproductive potential of producing a son versus a daughter will vary with maternal condition. Consequently, it is necessary to take into account the effect of a given unit of investment not only on the offspring's reproductive success but also on the mother's future reproductive success (Clutton-Brock and Iason 1986). For example, in many polygynous mammals the preweaning investment in individual sons is greater than the investment in individual daughters (Reiter, Stinson, and Le Boeuf 1978, Clutton-Brock, Guinness, and Albon 1982). Under these conditions it is only females who are in good condition who can afford the cost of producing a son, and therefore they are expected to bias their investment towards sons; parents in poor condition who rear sons will suffer a relatively greater cost to their future reproductive success and consequently will bias their investment towards daughters. Trivers and Willard suggested that this idea could be applied to human societies with wealth or socioeconomic status as the measure of parental condition.

Maynard Smith (1980) argues that if the sex ratio at conception is fixed at unity, parents may benefit by differentially abandoning their offspring when the sex can be determined. This abandonment will be evolutionarily stable only if it occurs after a very small fraction of total investment. That primates have a relatively long gestation period for their body size (Harvey, Promislow, and Read 1989) might suggest that once gestation had been completed it would not be adaptive for human parents to abandon offspring. In humans, however, prenatal investment is a relatively small percentage of total investment, and so abandonment might still be favored (Prentice and Whitehead 1987).

The relative costs and benefits of rearing sons versus daughters will be affected by any sex difference among offspring in the extent of cooperation or competition with parents and kin (Hamilton 1967, Clark 1978). If such competition or cooperation occurs over direct ac-

cess to mates, then it is called local mate competition/enhancement, and it usually applies to males; if it occurs over resources that influence reproduction, it is called local resource competition/enhancement, and it usually has a greater impact on females. Where there is greater competition between relatives of one sex (including parents and offspring), parents will produce fewer of the more competitive and hence more reproductively costly sex. Alternatively, if one sex helps either its parents or its siblings, then this sex becomes relatively cheaper to rear, and the sex ratio will be biased in its favor. In some species (e.g., red-cockaded woodpeckers [Gowaty and Lennartz 1985]), the effects of any such competition and cooperation are independent of parental rank and access to resources. Here the theory predicts a populationwide sex-ratio bias in favor of the more cooperative sex, and the costs and benefits of cooperating and competing offspring can be incorporated into a Fisherian model. In other species (e.g., bonnet macaques [Silk 1983], spider monkeys [McFarland Symington 1987], savanna baboons [Altmann, Hausfater, and Altmann 1988]), parental status influences the potential for cooperation and competition, and here parents of different status will follow different strategies.

Because sons and daughters provide different kinds of help at different ages and because the type and extent of competition may depend on the age, sex, and birth order of the offspring, it is necessary to quantify the net reproductive effects of various combinations of offspring. For example, daughters may help mothers in sibling care and therefore be a benefit while they are unmarried and the mother still has young children to care for. In virilocal societies an adult (married) daughter will, however, no longer be able to provide much help to her family, whereas an adult son may still provide some help.

Fisher's and Trivers and Willard's theories and the idea of local mate/resource competition/enhancement are not necessarily alternatives; each describes a set of factors that influence the reproductive costs and benefits of selective investment by sex, and these factors may be operating simultaneously to produce the observed sex-ratio patterns (Clutton-Brock and Albon 1982, Clutton-Brock and Iason 1986, McFarland Symington 1987). Differential offspring mortality during the period of dependence, sex differences in the parental costs of producing reproductively successful offspring, and the extent of competition and cooperation among kin will all influence patterns of individual sex allocation, which in turn will affect populationwide sex ratios. Overlaid on these population patterns are variations in the ability of individual parents to afford different investment costs, and this may result in intrapopulation sex-ratio variation. Moreover, high-status individuals may be able to manipulate lower-status individuals and therefore alter the latter's costs and benefits. For example, Silk (1983) has argued that in primate species with female philopatry, food competition results in weaned daughters' imposing a cost on other females in their group. High-ranking mothers can enhance the reproductive success of their daughters by reducing (through harass-

ment) the number of other females born into the group, thereby decreasing the amount of resource competition that their daughters will encounter. In contrast, they are much less capable of enhancing the reproductive success of their dispersing sons. High-ranking females will therefore produce offspring with low sex ratios, whereas low-ranking females will produce offspring with high sex ratios.

Tests of Evolutionary Hypotheses

Models of sex allocation assume that it is possible to measure parental investment and to detect the end of the period of dependence upon that investment. Trivers (1972) defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of survival (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." To date few studies have been able to measure parental investment in a specific child in terms of the cost to the parent's ability to invest in other offspring. Instead, researchers have either measured absolute investment such as the length of the nursing period (e.g., Clutton-Brock, Guinness, and Albon 1982) or employed proxy measures such as the length of the inter-birth interval (e.g., Lee and Moss 1986). The latter measure may, however, be inappropriate for a species in which postweaning dependence is considerable. For example, cheetahs are dependent for long periods on their mothers while their hunting skills are developing (Ewer 1973). In some species postweaning maternal investment may be biased towards a particular sex, and in this case resource competition may become important. For example, among white-tailed deer a daughter will stay near her mother and may impose a feeding cost and therefore a reproductive cost on her long after the period of lactation is over (Verme 1983, Caley and Nudds 1987). In humans the extremely long period of dependence makes the problem of measuring total parental investment in terms of Trivers's technical definition particularly acute. Moreover, with postmortem inheritance it could be argued that parental investment continues after the death of the parents, making any identification of an end to the period of dependence an arbitrary one.

Another problem in measuring parent investment is that the same absolute unit of investment entails different reproductive costs to the parent at different stages of the parent's life (Charnov 1982); equally, the fitness effect of a unit of investment will be different for a recipient depending on its age and sex (Clutton-Brock and Albon 1982, Clutton-Brock and Iason 1986). For example, Borgerhoff Mulder (1989a) has shown for the Kipsigis agropastoralists of Kenya that investment of cattle has a greater effect on sons' reproductive success than on daughters'. The primary factor accounting for variation in male reproductive success is degree of polygyny (Borgerhoff Mulder 1987), and as bridewealth payments consist of livestock this explains the importance of cattle for sons' reproductive success. Given this significant

positive correlation between wealth and polygyny, Borgerhoff Mulder argues that investment of cattle exclusively in sons supports Hartung's (1982) prediction that parents will transfer wealth to offspring of the sex for which that wealth will have the greatest benefit in terms of reproductive success. She goes on to say, however, that this seeming neglect of daughters may simply result from a failure to measure other aspects of investment. Daughters of wealthy parents are on the average younger at menarche and have greater age-specific fertility (Borgerhoff Mulder 1989b), and this suggests that early investment of food in daughters may be important to their reproductive success. This study highlights the difficulty of deriving a common currency of investment—of quantitatively comparing gifts of cattle with food eaten during childhood. Borgerhoff Mulder's more pragmatic approach is to quantify the fitness consequences of investment by measuring the effect of a particular unit of parental investment on the reproductive success of sons and daughters. Ideally it would also be necessary to quantify the degree to which that unit of investment alters the parents' own future survival and reproduction. Furthermore, as Borgerhoff Mulder points out, to quantify parental investment in accordance with Trivers's definition it is also necessary to measure the help that sons and daughters give their parents and the degree to which that help affects the parents' own reproductive success. For example, daughters leave the natal home at marriage, after which they rarely contribute to its resources. Daughters who run away from their marital homes return to their parents and become economically dependent on them. The relative labor contributions of sons and daughters may also differ. Cattle invested in sons may be offset by sons' contributions to their families through work. If sons' labor provided more resources for their families and consequently increased parents' lifetime reproductive success, then this effect would need to be included in the assessment of parental investment.

Yet another problem in measuring parental investment is that parents of different status may have different types of investment strategy that are difficult to compare quantitatively. For example, Hewlett (1988a) reports that among the Aka pygmies of the Central African Republic high-status and low-status males offer different types of parental investment. Whereas low-status males spend a considerable amount of time in direct contact with their infants, high-status males spend less time with their infants and more time talking to other males and maintaining their status. Although it is difficult to see how one could quantify "talking" as parental investment or separate the reproductive benefits of increased status to the male himself from the benefits to existing offspring, Hewlett argues that high-status males do not necessarily contribute less to their offspring.

A final problem is that males and females typically begin reproducing at different ages. If one sex (in mammals, generally the female) begins reproducing earlier, then parents may leave more descendants if they bias their investment towards that sex. (Over generational

time, it will still, of course, be possible for sons to out-reproduce daughters through polygynous matings.)

Operationalizing measures of parental investment and collecting quantitative data on the effect of parental investment on parents' and offspring's reproductive success are crucial to studies of sex-ratio variation in humans. As Clutton-Brock and Iason (1986) have warned with regard to studies of the subject in nonhumans, current ignorance of the comparative effects of parental investment on the fitness of sons and daughters and of the costs of rearing the two sexes mean that almost any sex-ratio bias will be capable of being interpreted adaptively.

Clutton-Brock, Albon, and Guinness (1986) have argued that for a sex-ratio bias to be described as adaptive according to Trivers and Willard's model, certain conditions need to be fulfilled. Most important, it is necessary to show that parents produce offspring with low sex ratios when their relative lack of resources will result in daughters' having greater reproductive success than sons, whereas mothers in better condition produce offspring with high sex ratios when the resources available to them will make their sons more reproductively successful than their daughters. In order to show this, it is necessary to plot the effect of maternal rank on the reproductive success of sons and daughters. To date only one study (Clutton-Brock et al. 1986), of red deer, has been able to provide these data.

Weaker support for the hypothesis comes from results showing a sex-ratio bias according to maternal rank without any information about the reproductive success of sons and daughters of high- versus low-status mothers. Such results have been obtained for golden hamsters (Pratt, Huck, and Lisk 1989), spider monkeys (McFarland Symington 1987), and bonnet macaques (Silk 1988). Among baboons (Altmann, Hausfater, and Altmann 1988) and, arguably, rhesus monkeys (Meikle, Tilford, and Vessey 1984, but see Berman 1988), sex ratios are biased according to maternal status, but in these female-bonded primate species high-ranking mothers have offspring with a low sex ratio rather than the high one predicted by the Trivers and Willard formulation.

In polygynous, sexually dimorphic species, selection for large size in males imposes faster growth rates on males and makes them more susceptible to food shortage, both in utero and postnatally (Clutton-Brock, Albon, and Guinness 1985). Consequently, only mothers in above-average condition have sufficient resources to produce surviving sons. There is quantitative evidence from a number of species (e.g., African elephants [Lee and Moss 1986], American bison [Wolff 1988], elephant seals [Reiter, Stinson, and Le Boeuf 1978], Galapagos seals [Trillmich 1986], red deer [Clutton-Brock, Guinness, and Albon 1982], and humans [Tanner 1978, Prader 1984]) that male offspring are typically gestated longer, born at a heavier weight, and suckled more frequently or until a later age. Clutton-Brock et al. stress that the relationship between maternal condition and offspring sex ratio may be the result of sexual selection for large male size (in selection on the offspring) rather than selection for parental control of sex allocation. Even so, the fact

that only mothers in good condition can afford to produce successful males means that male mortality rates will be greater where mothers are in poor condition, resulting in a low sex ratio as Trivers and Willard predict.

In the first attempt to apply the Trivers and Willard hypothesis to humans, Dickemann (1979a, b, 1982) has sought to explain the prevalence of female infanticide among high-status families in India, China, and feudal Europe in terms of differential parental investment. She argues that because high-status males are likely to mate polygynously, high-status families can produce more grandchildren if they concentrate their investment in sons rather than in daughters (Alexander 1974). These highly stratified human societies, however, contain an element that is not explicitly part of the Trivers and Willard model: reproductive benefits can be gained by daughters' marrying hypergynously, and therefore families compete to marry their daughters to high-status males. Hypergynous marriage may yield an immediate benefit to the daughter's reproductive success, as she will have more resources available to her and therefore potentially increased fertility. It may also result in a longer-term reproductive advantage, whereby women married to high-status men will have high-status and therefore polygynous sons who will inherit their fathers' resources (Dickemann 1982). In his discussion of marriage payments in South Asia, Tambiah (1973:65) writes that the dowry that accompanies a virgin at marriage is associated with the ideal of monogamy but that in cases of polygamy the size of the dowry results in the "stratification of women according to the economic assets they bring." Inheritance rights of sons vary with their mothers' marital status.

For the long-term advantages of hypergyny to be an important influence on parental investment strategies, wealth differences must be comparatively stable over time (for example, in a system of heritable family estates). If there is little assurance that wealthy families will remain wealthy in years to come, then there is little reason for parents to invest a large amount of their currently available resources in order to secure their daughter's marriage into a wealthy family. Rather, marriages will be contingent on the resources that a man can offer his wife for immediate use, and bridewealth rather than dowry will be expected (Goody 1973; Borgerhoff Mulder 1988, n.d.). Moreover, if wealth is stable, parents who are relatively wealthy when their children are born can expect to be relatively wealthy when the children are older and need the resources (e.g., for education, marriage payments, attracting a mate, or gaining status); if wealth is comparatively unstable, then it will be harder for parents to predict the resources that will be available for their offspring, and biased sex ratios will not be expected.

Given these complications, there are three possible ways in which the female infanticide among high-status groups could be seen as adaptive:

First, there is the simple prediction from the Trivers and Willard model that is stressed by Dickemann as driving the system (Dickemann, personal communica-

tion): that high-status sons have a high probability of being both maritally and extramaritally polygynous, whereas daughters are limited by their physiology to a lower number of offspring, and therefore high-status parents will increase their reproductive success by producing offspring with a sex ratio biased in favor of males. The problem with this hypothesis is that it is, as Kitcher (1985) points out, insufficient to explain female infanticide; the use of a wet nurse to reduce the period of lactational amenorrhea would be an alternative to female infanticide if parents were simply trying to maximize the number of sons that they produced.

Second, female competition (dowry and seclusion to ensure virginity) increases the economic cost of raising high-status daughters. The concentration of wealth in a relatively small percentage of families means that the intensity of dowry competition increases with status. The cost of a dowry may be relatively greater for families of high rank looking for even higher-ranking husbands than for families of lower rank (Dickemann, personal communication). Given limited wealth, parental reproductive success may be increased by investing economic resources in a potentially polygynous son, and consequently female infanticide will be an adaptive parental strategy.

Third, in the long run it may be advantageous for parents of relatively high but not the highest status to endow a few daughters selectively—to provide large dowries for a few daughters rather than small dowries for all daughters. Thus it could be that among the upper-middle status groups sons are unlikely to be polygynous but the importance of making a good marriage results in greater variance in female reproductive success. Therefore parents may kill some daughters in order to invest heavily in others (Borgerhoff Mulder, personal communication).

These three possible interpretations of the dynamics of Dickemann's model are not mutually exclusive, and they could be examined with detailed demographic and economic data. Whether high-status families leave more grandoffspring through female infanticide is an empirical question (see Kitcher 1985), and it is likely that different high-status groups are following different strategies. For example, at the very pinnacle of the hierarchy, it may be advantageous for parents to kill nearly all their daughters because of the greater reproductive success of sons and the economic cost of raising daughters. For families of slightly lower status, it may be more advantageous to invest heavily in a few daughters in order to ensure them hypergynous marriages, and in this situation limited female infanticide will be an adaptive parental strategy.

One final point raised by Dickemann's study is that in humans it is not necessarily true that for a given level of parental condition each individual son will benefit equally. Only inheriting sons will necessarily expect to have increased reproductive success, and with the unigeniture that is characteristic of many highly stratified societies (Goody 1973) noninheriting sons, even high-status ones, may have lower reproductive success than

daughters. In these circumstances it may benefit parents who already have a son to bias investment towards daughters. A preliminary analysis of demographic data from the Krummhörn region in Germany between 1720 and 1874 lends some credence to this idea (Eckart Voland, personal communication). Where land is limited and relatively unavailable for purchase, unigeniture means that "apart from the heir, every surviving son creates more costs and problems . . . than he brings in terms of fitness gains," and Voland suggests that this may explain the absolutely and relatively greater chances of survival for daughters of wealthy peasants than for their brothers.

Some quantitative support for the Trivers and Willard hypothesis comes from Boone's (1986, 1988a, b) study of the 15th- and 16th-century Portuguese nobility. Using genealogies from the 25 highest noble lineages recorded in the *Peditura Lusitana*, he differentiates four status groups and finds that males in the top three have more reported surviving offspring than either high-status females (though this difference is not statistically significant [Boone 1988b]) or lower-status males and that females born of the lowest status have significantly more surviving offspring than low-status males. He then argues that parents differentially biased their postnatal investment towards the sex with the highest reproductive benefits, with high-status parents biasing that investment in favor of sons. Firstborn high-status males inherited large estates, while younger brothers often went into religious military orders. Daughters of the highest-status nobles were effectively removed from the breeding population by entrance into convents, and the cost of this was likely to be less than investment in a son through the estate. Among the lower-status nobles, Boone argues, the dowries invested in daughters represented a greater parental investment than the investment of land in sons, thereby fulfilling the conditions of Trivers and Willard's model.

One problem with Boone's conclusion is the absence of any quantitative measure of parental investment—any indication of the value of an estate compared with the cost of a dowry, entrance into a convent, or a religious commission. Another problem is that if nobles of all statuses were marrying lower-class women, we might expect all noble groups to have higher reproductive success through sons than through daughters. Moreover, as Boone (1988a) himself points out, he has no reproductive records for women who married out of his population into Castilian, Burgundian, and Austrian courts. Of women born into his sample who eventually married, only 32% remained within it. If the women marrying into the sample came from poorer areas and those marrying out of it went to wealthier ones, then Boone's treatment of his sample as a bounded social system could have produced biased results (Dickemann, personal communication). More generally, this problem highlights the necessity of delimiting the actual marriage (and mating) pool rather than restricting analysis to a subset of the breeding population (Dickemann, personal communication).

Voland's (1984, 1988, 1989) studies of 17th–19th-century Germany also provide some support for Trivers and Willard's model. The society in question was stratified, with landowners, smallholders, farm laborers, and tradesmen. The only class in which female childhood mortality was greater than male was the landowning class, which suggests that highest-status parents favored sons (though reanalysis of Voland's data has shown that this effect is not significant [Brittain, Morrill, and Kurland 1988]). The higher mortality of boys in lower-status groups could have resulted either from their greater susceptibility to nutritional stress or from differential care, either of which would be in accord with Trivers and Willard's prediction. A closer look at the data reveals, however, that sex and status biases in infant mortality do not fit the model as closely as they might. For example, the bias in favor of sons among landowners was substantial mainly among firstborns, and this raises the intriguing question why landowners showed markedly less such favoritism towards later-born children.

Another problem, as Voland himself points out, is that it is among smallholders that sons have the highest risk of death and daughters the greatest chance of survival. A simple interpretation of the Trivers and Willard hypothesis would predict highest male mortality in the lower-status groups. Voland argues that because daughters of smallholders had a greater chance of hypergynous marriage than daughters either of farm laborers or of tradesmen, there were greater benefits to smallholders in biasing investment in favor of daughters. Only about 15% of the smallholders' daughters' marriages were hypergynous, however (Voland 1989), and Boone (1988b) has questioned whether hypergyny in fact results in more descendants.

One further problem with Voland's study is that it presents no data on the reproductive success of offspring in the different status groups, with the result that his conclusion that sex differences in infant mortality are "adaptive" is less than fully convincing. The only discussion of the effect of class on offspring's reproductive success is based on the marriage patterns within this sample of the population. No independent measures of the resources available to each class are presented, nor is it made clear whether there were opportunities for offspring to marry outside these categories, for example, into the families of wealthy merchants.

Cronk's (1989a) study on the Mukogodo of Kenya presents evidence of low-status parents' biasing their investment in favor of daughters. The Mukogodo are looked down upon by neighboring Maasai and Samburu pastoralists because they have only recently given up their hunting-gathering-beekeeping subsistence pattern and own fewer livestock than their neighbors. Cronk shows that there are more marriages of Mukogodo women to non-Mukogodo men than vice versa and that Mukogodo men typically have to pay more bridewealth for non-Mukogodo women than non-Mukogodo men pay for Mukogodo women. He argues that this makes marriage chances better for Mukogodo women than for

Mukogodo men and that, in conformity with a critical assumption of the Trivers and Willard hypothesis, Mukogodo women, on average, have significantly more surviving offspring than Mukogodo men. The finding that at the end of 1986 there were significantly more female children aged 0-4 than male children (98 versus 66; chi-square = 5.734, $p < 0.025$) suggests that parents are biasing their investment in favor of daughters. Further, albeit weaker, evidence lies in the fact the Mukogodo take daughters to the local Catholic health clinic significantly more than do neighboring ethnic groups. (No data are available on the likelihood of Mukogodo daughters' becoming ill compared with daughters of both other ethnic groups and with Mukogodo sons; it is conceivable that daughters were discriminated against in terms of food allocation and consequently became ill more often.) Finally, that the data on the reproductive success of men versus women come from reproductive histories of adults while the evidence of investment favoring daughters comes from current children presents some problems in the interpretation of the results, though they do offer exciting opportunities for further research (Cronk, personal communication).

Betzig and Turke's (1986) study on Ifaluk is the only one to date to have examined parental behavior towards different-sex offspring through the use of association data. These researchers report that a significantly greater proportion of the associations of high-status parents of both sexes are with sons rather than with daughters. Conversely, low-status parents spend a significantly greater proportion of their time associating with daughters. On the face of it, this observation is consistent with Trivers and Willard's prediction, but it must be treated with caution. First, as Betzig and Turke point out, it is difficult to know what kind of interaction an association involves and whether the benefits flow from parent to child or from child to parent. Consequently, it is hard to estimate how investment in associations affects the survival and reproductive success of offspring. Second, there may be differences in work patterns for individuals of different status that result in high-status parents' associating more with sons. Finally, because Betzig and Turke pooled all associations observed rather than taking an average for each parent-child dyad, their data are nonindependent, and this casts doubt on the significance of their results.

Brittain, Morrill, and Kurland (1988) test the hypothesis that "parental circumstances lead to differential treatment of infants" using both data collected in situ and demographic records for the French West Indies. As differences in prosperity between families are small, they examine changes in prosperity over time, predicting that if parents were biasing investment adaptively, then periods of poverty would be followed by relatively greater male child mortality. As indices of prosperity they use age of men at marriage (commonly used in this fashion by demographers [e.g., Smith 1984]) and sex ratio at birth. That the sex ratio responds to stress with a bias at birth towards females is, however, still controversial

(Stinson 1985). Moreover, using the sex ratio at birth as a measure of parental prosperity assumes the general phenomenon to be tested, namely, that parents bias investment in favor of offspring of different sex in accordance with their condition. Brittain et al. find no significant relationship between either index of wealth and child mortality by sex and conclude that parents are not behaving in accordance with Trivers and Willard's predictions. It is difficult, however, to see why males born during a poor period would necessarily have lower reproductive success than those born during a more prosperous period; they would only be at a reproductive disadvantage if, as a result of having been born during that period, they were unable to accumulate as many resources as males born during a more prosperous period, and there is no evidence to support this assumption.

According to Fisher (1930), parents will produce more offspring of the sex with higher mortality during the period of parental investment, and Chagnon, Flinn, and Melancon (1979) argue that the high neonatal sex ratio (129) among the Yanomamo is best explained as compensation for high male juvenile mortality. Pointing out that male bias is not concentrated among village headmen or in important lineages, they reject the Trivers and Willard hypothesis. These researchers argue that the elevated male juvenile mortality is due to warfare and report that by the age of 15 years the sex ratio is more balanced (108). Kaplan and Hill (1988a) dismiss the idea that higher male mortality might explain the high sex ratio at birth among the Ache, reporting that all of the male warfare deaths they recorded took place when males were no longer dependent on their parents and were net contributors to the family's food resources. That males were net contributors does not mean, however, that the likelihood of their death was independent of parental investment. If sex differences in mortality were affected by the amount of parental investment that had been received during the period of dependence, then selection would favor parents who invested more in the sex with the higher mortality. Because one way of increasing investment is to produce more offspring of that sex (Clutton-Brock and Albon 1982), the Fisher hypothesis cannot be ruled out as an explanation of the Ache data.

Possible New Directions

Attempts to test an evolutionary explanation of biased sex ratios in human populations have largely focused on the Trivers and Willard hypothesis, and because they have suffered from a paucity of data on the effects of parental investment on the reproductive success of offspring and parents the empirical support for it has proved weak. Better evolutionary understanding of sex-ratio biases in human populations might come from more systematic examination of a variety of ecological and social factors other than parental resources that may affect differential investment in sons and daughters,

among them the degree of cooperation or competition with parents and/or siblings.

ENHANCEMENT OF THE REPRODUCTIVE SUCCESS OF PARENTS AND/OR SIBLINGS

Offspring that provide help to their parents or siblings repay some of the costs of parental investment, and if they enable their parents or siblings to have greater lifetime reproductive success their net reproductive cost will be lower (Bulmer and Taylor 1980, Hughes 1981, Emlen, Emlen, and Levine 1986, Gowaty and Lennartz 1985). Depending on the timing and type of help provided, overall or parity-specific bias in favor of the helping sex will be expected. Offspring may reduce their net costs to their parents through direct care of younger siblings, contribution to the resources available to the family as a whole, or aid to siblings in acquisition of resources or mates.

Direct care of siblings. Where daughters provide direct help to their mother in looking after siblings (Weisner and Gallimore 1977), a mother will have greater lifetime reproductive success if she has a daughter early in her reproductive career. Turke (1988) has shown that this is the case on Ifaluk, although no sex-ratio bias is found at birth or in child survival. A recent demographic study has suggested that neglect of children may be strongly influenced by their birth order; in the Punjab only second- and later-born daughters suffer disproportionately high child mortality, and although the data as presented cannot be statistically tested it is striking that, regardless of landholdings, firstborn daughters suffer lower childhood mortality than firstborn sons (Das Gupta 1987). It may be that among firstborns, who are subject to small size, the higher male mortality is purely a consequence of sex-specific risks of low birth weight, but it is also possible that mothers are selectively caring for firstborn daughters and that this contributes to the mothers' lifetime reproductive success. Here the benefits of daughters are parity-specific, and an overall sex-ratio bias towards daughters will be predicted only where daughters of all parities provide more help than their brothers. In India this is unlikely because after marriage, which is usually virilocal, daughters have fewer opportunities to help their parents than sons. Jeffrey, Jeffrey, and Lyon (1984) report that mothers in a village in Uttar Pradesh describe a married daughter as "spittle which has been spat out, and no longer belongs to her parents."

Contribution to family resources. Among marmots the offspring of young (in contrast to older) mothers show a low sex ratio at weaning (Armitage 1986). Female marmots are highly philopatric, and the sex-ratio bias of young mothers has been explained by the fact that marmots form matrilineal groups that cooperate to defend resources; a mother will benefit from having daughters early in her reproductive career, as they will help her defend the territory and thereby increase her lifetime reproductive success. Hill and Kaplan (1988) have suggested that one

explanation of the high sex ratio at birth (116) and the greater survival of males to 15 years among the Ache might be that sons are cheaper to rear because they make a larger contribution to the family's food resources. Foraging data show that from the age of 16 years sons produce substantially more food than daughters, and because sons marry later they have a longer period with no dependents in which to contribute to the natal family's resources. A problem with this explanation, as Hill and Kaplan point out, is that bride service is common; a daughter may bring a husband into her home to add to the resources of her natal family, whereas a son may move at marriage to his wife's home.

Smith and Smith (n.d.) point to the differential subsistence contributions of the two sexes in explaining why, despite a significant male bias in childhood sex ratio (approximately 119) and the fact (calculated from mean age at marriage, mortality schedules, and cohort size) that Inuit parents invest an average of 26 years of effort in each son versus 18 years in each daughter, approximately equal numbers of sons and daughters survive to adulthood. The Inuit themselves report that boys are more highly valued because they will eventually contribute to the family's food supply. This preliminary study concludes that if sons do in fact contribute more to the family's food resources, they will be of greater reproductive value to their parents not because they produce more grandchildren but because they contribute to the survival and reproduction of their parents and siblings (Hughes 1981). Although this would be extremely difficult to test in a historical population, studies of time allocation and productivity returns are possible for extant traditional societies (Hill, Hawkes, and Hurtado 1987, Hawkes, O'Connell, and Blurton Jones 1989, Blurton Jones, Hawkes, and O'Connell 1989).

Behavioral and demographic data from Bangladesh have shown that daughters are given less food and medical care relative to sons in wealthier families than in poor families (Bairagi 1986), and it is suggested that the parental bias results from the greater work opportunities available to sons. It could also, however, be due to the greater reproductive success of high-status sons as the Trivers and Willard theory predicts. Indeed, both hypotheses might apply simultaneously, and their effects could in theory be separated with the aid of demographic data. It should be possible to determine whether high-status sons were more valuable to parents because of their greater fitness through small-scale demographic analysis of the reproductive success of offspring of parents of different status. If the benefit of sons lay in their resource contributions, then high-status parents who had more sons would be expected to have larger completed family size than high-status parents who had predominantly daughters.

Using parish registers for historical Western societies, Johansson (1984) presents data suggesting that while in 17th-century Britain there was no consistent sex bias in child mortality, by the 19th century every European country for which data are available shows marked ex-

cess female mortality throughout childhood and adolescence. During the period of agricultural modernization childhood mortality in rural areas fell more rapidly for boys than for girls. The explanation Johansson offers is that the commercialization of agriculture increased wage-earning opportunities for men, causing women to be relatively devalued and neglected. If this analysis is correct, then it is possible to interpret the sex-biased mortality in an evolutionary framework: in environments where males had greater wage-earning capacity, they would have been the cheaper sex to produce because they would have needed less parental support before becoming independent and/or because they were able to contribute more resources to the family, and parents would have biased their investment towards sons. Despite Johansson's conclusion that "there seems to be little room for either biology or sociobiology in this story" (p. 468), her economic argument is consistent with evolutionary theory.

A similar relationship between economic opportunities and sex-specific mortality is found in an analysis of demographic data from Massachusetts between 1860 and 1899 (Ginsberg and Swedlund 1986) showing a relatively lower death rate for females in the more industrial than in the more agricultural counties. Ginsberg and Swedlund argue that the opportunities for women to earn wages in industrial areas resulted in women's making an important contribution to family resources and consequently not being discriminated against as they were in agricultural communities. They point out that they have no direct evidence of differential care, but the sex-biased juvenile mortality does support their hypothesis.

Interestingly, analysis of fertility in China also suggests that son preference is stronger in rural than in urban settings. Arnold and Zhaoxiang (1986) do not present data on the economic opportunities for sons and daughters in these settings, but the sexual equality promoted by the Communist party would be expected to have increased the opportunities for women in the industrial and commercial centers relative to those in the more traditional agricultural areas, thereby providing a possible explanation of the rural-urban variation.

To date the only comparative study among humans analyzing the relationship between sex-biased parental investment and the relative contributions of sons and daughters is the preliminary study of Hewlett (1988b). Using data from ten populations of tropical-forest hunter-gatherers, he reports a statistically significant positive relationship between the percentage of calories obtained by adult males and the juvenile (under 15 years) sex ratio and considers this support for the hypothesis that male children are favored in societies in which males contribute more to subsistence.

Help to siblings in acquiring resources and mates. Lion litters of two or three cubs have birth sex ratios biased towards males (Packer and Pusey 1987), and cheetah mothers provide disproportionately more solid food for litters that contain two or more surviving males

(Caro n.d.). In both of these felid examples, the bias in allocation of resources to sons probably reflects the fact that brothers help each other to gain access to territories and therefore to enhanced mating opportunities. This cooperation between brothers means that when a mother has a chance of producing several surviving offspring she should bias her investment towards sons, although the overall population sex ratio will not necessarily be biased (Clutton-Brock and Iason 1986).

A similar phenomenon may occur in humans. For example, among the Yanomamo, Chagnon and Bugos (1979) have documented that closely related kin help each other during fights to a greater extent than more distantly related individuals. It may be that an individual with several brothers has a relatively greater chance of survival than a single son, and this could explain the observed high sex ratio. Chagnon, Flinn, and Melancon (1979) also suggest that an individual's ability to secure mates depends on number of close kinsmen and size of lineage, and it may be that the high sex ratio results from brothers' having more opportunities to help each other in mate acquisition, which would increase the reproductive payoff per male raised. Although Chagnon (1982) stresses the importance in the acquisition of mates of full brothers, half-siblings, and first-generation parallel cousins, his analyses of the effect of number of kin on male reproductive success do not differentiate between close and more distant kin.

Hewlett (1988a) has shown for the Aka that brothers form the basic hunting unit and a man with brothers is preferred by prospective wives as more economically reliable. Men with brothers do not travel as far to find their wives, marry earlier, and are more likely to become village leaders. Hewlett specifically claims that high-status males are males with more resources and defines "resources" as "brothers." To date, he has not presented data on the variation in the secondary sex ratio or on sex-specific childhood mortality in different families, but it might be expected that once a woman had produced a son she would bias her future investment towards sons.

COMPETITION FOR RESOURCES WITH PARENTS AND/OR SIBLINGS

If either sons or daughters compete disproportionately with their kin, then they will reduce the potential reproductive success of those kin more than offspring of the less competitive sex. Since the more competitive sex is more expensive to rear, parents will bias their investment against this sex (Hamilton 1967, Clark 1978, Grafen 1984, Johnson 1988, Gowaty n.d.). Competition may occur between offspring and mothers, fathers, or siblings.

Mother-offspring competition. Sex ratios at birth in *Antechinus* are biased in accordance with the mothers' reproductive value (Cockburn, Scott, and Dickman 1985). There is an almost complete dispersal of sons within three weeks of weaning, while daughters are highly philopatric. In some populations females give

birth to two litters in a lifetime, and here sex ratios for the first litter are biased towards males, for the second litter towards females. Cockburn et al. conclude that mother-daughter competition is the cause of the bias and that this example provides evidence for facultative adjustment of sex ratios according to life-history pattern.

Father-offspring competition. In societies in which the father provides the resources for his son's bridewealth, conflict may arise as to whether those resources should be used for the father's or for the son's reproduction, and under these circumstances it may be beneficial for the father to have sons late in his reproductive career. Although anecdotal reports of this form of competition are common for East Africa (e.g., Hakansson 1987), it may be that in bridewealth systems based on pastoralism the benefits of a son's labor outweigh the costs of competition over bridewealth.

Competition between siblings. In a situation in which resources are not infinitely partible, competition between siblings over those resources may decrease the value of additional children of the more competitive sex (Hamilton 1967, Grafen 1984). For example, land is a resource that becomes inviable if divided into units below a certain size. Consequently, where land is limiting, the equal division of land among offspring may be less efficient than unigeniture as a parental investment strategy (Goody 1973). The unequal division of resources results in a disproportionately high gain to the inheriting child (usually a son). This, in turn, may increase sibling competition, and unless alternative strategies are open to noninheriting sons parents will gain decreasing fitness returns from producing each additional son. In reality this situation may be comparatively rare in humans, as such alternative strategies are often available (see Boone's work cited above).

Summary

It is an axiom of evolutionary theory that parents will allocate resources to offspring of different sexes in order to maximize parental reproductive fitness. Three hypotheses have been proposed to explain parental biases: Fisher's theory of equal investment at the end of the period of dependence, Trivers and Willard's hypothesis that parents will bias their investment in terms of the resources available to them and the effects of those resources on the offspring's reproductive success, and the hypothesis of local mate/resource competition/enhancement, which stresses the contributions offspring make to the reproductive success of their parents and/or siblings and the reproductive costs imposed on parents and/or siblings by competition. These hypotheses are not mutually exclusive and may apply simultaneously. Better understanding of the evolutionary basis for sex-ratio bias in human populations can be expected to result from closer attention to a broad range of ecological and social factors that may affect parental investment.

Comments

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It seems to me that we might learn more about sex allocation and other evolutionary problems by looking for facts that *don't* seem to fit the theory (cf., e.g., Darwin 1859, Alexander 1974, Hamilton 1964, Axelrod and Hamilton 1981, Hamilton and Zuk 1982). I can think right away of two:

1. Why do powerful men ever leave their status, riches, and harems to sisters' sons rather than to their own? In several highly stratified Standard Cross-Cultural Sample (Murdock and White 1969) societies, inheritance is matrilineal, or bilinear, rather than patrilineal (see codes in Murdock and Provost 1973 and Murdock and Wilson 1972). At the top of some despotic groups, where harems are large, resources are abundant, and the power to defend both is great, succession is through the female rather than through the male line (see codes in Betzig 1986 and Murdock and Wilson 1972; see also Betzig and Turke 1986). What might determine such exceptions?

2. Why do powerless parents ever favor sons over daughters (see Kitcher 1985)? Hartung (1982) found a significant correlation between proportion of women married polygynously—a fair approximation of variance in male fitness (Low 1988)—and male bias in inheritance, also for Standard Cross-Cultural Sample groups. And Whyte (1978) coded 28 (30%) of 93 sample societies as having an overall preference for male children, 54 (58%) as having no preference for either sex, and only 11 (12%) as having a preference for daughters. But in every human society there are important reproductive, and so economic, differentials (Chagnon 1979), and as societies grow more stratified, the have-nots should increasingly outnumber the haves. Other things being equal, the Trivers and Willard (1973) model predicts that the majority should come to favor female-biased inheritance and prefer producing daughters to sons. What other things might not be equal?

I wish I could answer these questions. Anyone who tries to may shed more light on sex allocation than the rest of us have so far.

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Sieff has provided a useful and thoughtful review of an important topic in evolutionary biology. Her suggestion that we look more closely at hypotheses other than the Trivers-Willard is especially good. Although my article on female-biased parental investment among the Mukogodo (Cronk 1989a) deals only with that hypothesis, my dissertation (Cronk 1989b) includes preliminary tests of

some of the other possibilities that Sieff mentions, including the idea that Mukogodo daughters may help their fathers, their brothers, or both to obtain more wives by attracting bridewealth payments. The results of these tests do not support the local-resource-enhancement hypothesis. First, a regression of total number of wives against number of daughters who survived to age 15 from men's first marriages in a sample of 220 Mukogodo adult men reveals no significant relationship between these two variables (Pearson correlation coefficient = 0.111, regression coefficient = 0.041, $t = 1.652$, $p[\text{two-tailed}] = 0.100$). Another way to approach this question is to see whether the mean number of wives for men with some daughters surviving to age 15 from a previous marriage is greater than that for men with no such daughters. In fact, there is a slight but insignificant bias in favor of the latter (\bar{X} [no daughters] = 1.333; \bar{X} [some daughters] = 1.320; $t = 0.13$; $p[\text{two-tailed}] > 0.25$). Second, no statistically significant relationship was found between men's numbers of full sisters surviving to age 15 and their total numbers of wives ($N = 330$; Pearson correlation coefficient = -0.095; regression coefficient = -0.045; $t = -1.731$; $p[\text{two-tailed}] = 0.084$).

Why is there no relationship between the number of daughters or sisters men have and their marital success? First, Mukogodo herds are so small that it is probably rare for a man to be able to use bridewealth just obtained from a new son-in-law to obtain another wife either for himself or for one of his sons. Most men probably have to use most or all of the bridewealth they receive to pay off old debts, to acquire cash, to establish and maintain social relationships based on livestock sharing, or simply to support their families. Of course, these negative findings imply neither that Mukogodo females could not be enhancing their families' resources in other ways nor that the hypothesis of local resource enhancement is irrelevant to all human societies. However, the Trivers-Willard hypothesis still appears to be the best available explanation of the female-biased childhood sex ratio and patterns of parental investment among the Mukogodo.

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For Sieff, it is "an axiom of evolutionary theory" that parents should attempt to maximize their fitness by differentially allocating resources among their male and female offspring. Thus, while her review provides useful and often insightful critiques of particular studies, she never examines the fundamental assumption that the explanation for biased sex ratios is in all cases natural selection. While any study must be based on assumptions, by failing to consider alternatives Sieff leaves the impression that only technical difficulties stand in the way of a Darwinian explanation for human sex ratios. I am not convinced.

Natural selection is a theory about heritable character-

istics; the currency of "success" is offspring because more offspring means more copies of the characteristic in subsequent generations. The question is, then, what are the heritable units being selected? Clearly "sex ratio" is not a phenotype subject to selection but rather a population measure. Biased sex ratios may come about through many specific mechanisms leading to prenatal and/or postnatal differential mortality by sex. As Sieff notes, in the case of secondary sex ratios these proximate mechanisms are not well understood. Biased childhood sex ratios often seem due to differential parental care, although sex-specific mortality is known to vary for other reasons (Lopez and Ruzicka 1983). Does the proximal cause matter?

For example, in the literature reviewed by Sieff a reproductive benefit can be seen when the first child in a family is a female who then assists the mother in child-rearing. But what if families produce daughters first by chance? Even if these families end up with more surviving offspring because of the help provided by their daughters, if "producing daughters first" is not a heritable characteristic, then *nothing* is evolving by natural selection. Rather, given the lack of correlation between specific genotype and reproduction, gene frequencies will drift randomly.

A different but related problem can be illustrated by Cronk's (1989a) study. He argues that females have greater reproductive value than men among the Mukogodo partly based on their ability to marry higher-status non-Mukogodo men. The offspring of these out-marrying females are presumably no longer Mukogodo; therefore, their optimal reproductive strategy will be different (at least from their mothers'). Again, what has evolved? Mukogodo parents of females might have more grandchildren than those with male offspring, but a hereditary bias for producing females could not increase through natural selection because there is no consistency across generations.

What alternative explanation might account for differential parental investment in males or females? Interestingly, the "possible new directions" Sieff advocates are convergent with current theory in population studies. The theory of wealth flows (Caldwell 1982) explains continuing high fertility as a result of the economic returns of children to the family. Under differing circumstances, male or female offspring might make greater contributions to familial resources (several studies reviewed by Sieff make this point). As a consequence of increased resources, survival and further reproduction of family members might well be enhanced. However, without evidence of the heritability of the sex-biasing behavior, natural selection loses its privileged explanatory position and the economic motivation of parents is a sufficient explanation for the behavior.

It might be argued that biological heritability of the behavior is irrelevant to causation by natural selection (e.g., Alexander 1974) or that the human brain has evolved to maximize fitness (Lumsden and Wilson 1981). Logically these views are simply opinions, speculations, or hypotheses. It is exactly the specific inher-

itance of parental genes by offspring that generates the power and inevitability of Darwin's mechanism.

Present evidence seems more consistent with the assumption that human motivation has been broadly shaped by natural selection so that humans generally strive to survive and reproduce. However, variation in sociocultural behavior seems not to be tightly constrained by short-term differentials in reproduction; consequently, studies such as those reviewed by Sieff will rarely provide the detailed understanding of behavior that anthropologists aspire to attain.

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Fisher's (1930) theory of sex-ratio selection stands as one of the major accomplishments of modern evolutionary biology. His resolution of the problem of how natural selection acts on population sex ratios was a critical catalyst for the theoretical shift from group- to individual- and gene-level adaptation (Fisher 1958 [1930], Williams 1966). Subsequent refinements in sex-allocation theory by Hamilton (1967) and Trivers and Willard (1973) provoked renewed theoretical and empirical interest (e.g., Werren 1980, Charnov 1982, Bull 1983, Karlin and Lesard 1986). One can hardly pick up an issue of *Animal Behaviour* or *Theoretical Biology* that does not have an article on sex ratios among nonhuman species.

The application of sex-ratio/sex-allocation theory to human populations appears legitimate and potentially fruitful, albeit extremely complex (Alexander 1974, 1979). Sieff's article comes at a particularly appropriate time, as a sufficient number of studies of sex ratios among human populations have accumulated to warrant an overview and general critique. Although she provides useful criticisms of specific studies, we were expecting a synthesis of the major problems confronting sex-allocation research. We believe that one shortcoming of her review is a minimal discussion of the empirical feasibility of testing hypotheses from sex-allocation theory with data from human populations. We focus our comments on this problem.

Sieff compiles an admirable collection of six statistical factors and eight possible proximate causes associated with sex-ratio biases. Three major theories of sex allocation are discussed (Fisher, Hamilton, and Trivers and Willard, with emphasis on the latter). The hypotheses derived from these evolutionary theories are as follows:

1. Each sex contributes 50% to the next generation's gene pool, so selection will favor equal allocation of "parental expenditure" between offspring of the two sexes on a populationwide basis (Fisher 1930).

2. If one sex is more costly per individual to produce, then parents will raise fewer individuals of that sex (Fisher 1930).

3. Higher mortality of one sex during the period of parental investment reduces the cost per offspring initi-

ated of that sex, hence primary or secondary sex ratios will be biased in favor of that sex (Fisher 1930).

4. Competition among relatives for mates ("local mate competition" [Hamilton 1967]) reduces the reproductive value of that sex to its parents (and other relatives), hence the sex ratio will be biased against that sex.

5. Greater competition among relatives of one sex for resources raises the cost of that sex, hence the sex ratio will be biased against that sex (see 2 above [Fisher 1930, Clark 1978]).

6. Differential reproductive potential of the two sexes according to maternal condition or status will favor parental abilities to manipulate sex ratios accordingly (Trivers and Willard 1973).

7. Differential cooperation among relatives (i.e., one sex is more "altruistic") causes that sex to be less costly to produce (Trivers and Willard 1973).

8. Manipulation by conspecific competitors may affect sex ratios (Silk 1983).

9. Sexual specialization in resource use (i.e., sons and daughters utilize resources differently [Chagnon, Flinn, and Melancon 1979, Borgerhoff Mulder 1989a, Flinn n.d.]) may cause sex-ratio adjustments according to the type of resources parents control.

Some additional theoretical factors not discussed by Sieff include selfish sex chromosomes (Alexander and Borgia 1978, Trivers 1986), sexual specialization in parental investment (i.e., parents invest more in offspring of same or opposite sex [Flinn n.d.]), kin recognition (e.g., confidence of paternity) differing by sex of offspring (Flinn n.d.), mate-exchange systems (Chagnon, Flinn, and Melancon 1979), sibling and other kin coalitions (Alexander 1974), status advertisement (Alexander 1989), and selection for random assortment (Williams 1979). There is also a host of nonevolutionary explanations of sex ratios among human populations (e.g., Divale and Harris 1976, Schiefenovel 1989).

Clearly, this is a very complex phenomenon. As Sieff cautions, a major problem confronting anthropologists using evolutionary theories to explain sex-ratio biases is that "almost any sex-ratio bias will be capable of being interpreted adaptively." What, then, are the empirical criteria necessary for supporting an evolutionary explanation of a sex-ratio bias? Sieff notes that we need to measure the costs and benefits of parental and other kin investment, an extremely difficult undertaking. Unfortunately, there are additional problems.

First, rather than simply admitting that various explanations of sex-ratio biases are "nonexclusive," we need to design research projects that will test the relative effects of different factors (e.g., local mate competition, differential mortality, differential altruism, differential resource utilization). Such an undertaking may be empirically impossible (cf. Irwin 1989).

Second, a complete explanation of any evolutionary phenomenon has several components (Tinbergen 1951, Daly and Wilson 1983). It would be particularly useful in the case of sex-ratio biases to connect evolutionary theory with proximate causes. For example, what particular function (evolutionary reason) was the selective force

favoring the association between timing of fertilization and sex ratio?

Third, the modern world differs from that of previous human evolutionary history in a number of potentially significant ways (e.g., Irons 1983). Nutrition, population density, mating systems, and resource control are critically important factors in evolutionary theories of sex allocation, and yet they have all changed dramatically in recent history. It is extremely difficult to verify that current patterns of sex allocation are adapted to current conditions. Moreover, because proximate mechanisms for sex-ratio manipulation must operate on probabilistic predictions of future conditions, actual behavior may never match theoretical expectations, particularly with small samples over short periods of time.

Fourth, the effects of knowledge transfer, or cultural information, on sex allocation may be very difficult to test empirically. For example, a critic of Dickemann's (1979a) evolutionary explanation of female preferential infanticide among Rajput Brahmins claims that wet-nursing of female infants would be a more adaptive solution (Kitcher 1985). This, however, assumes that all knowledge is available for cultural choice; an equally plausible analogy is that Yanomamo warfare is not adaptive because it does not utilize more effective weapons, such as nuclear bombs. Decision making is always constrained by available knowledge. The human imagination has limits. Studies of sex allocation among humans must consider relevant historical constraints on behavior affected by cultural knowledge.

Our guess is that while these problems are not insurmountable, they await resolution by a future, more sophisticated generation of anthropologists and biologists. Our primary concern with studies of sex allocation is whether adaptive explanations can be adequately verified.

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According to recent sociobiological theories, evolution has specifically selected for biological mechanisms which regulate sex ratios at conception and/or which ensure that parents preferentially invest resources in the sex most likely to leave high numbers of offspring. As a result, sex ratios and parental investment are presumed to be evolutionarily adaptive in many, if not all, cultures.

The problem with this hypothesis is that the proximate mechanisms regulating differential human parental investment are primarily the human brain and human intelligence. Certainly, this is true in cases of differential deployment of nutritive and economic resources during postnatal growth and development. It is also true when parents copulate at specific times in order to take advantage of biologically based rhythms

of sex determination and when they practice selective abortion or infanticide.

The human brain and intellect, however, are not specialized organs of reproduction. They regulate a range of human behaviors including not only reproductive strategies such as mate selection and child care but also self-survival strategies such as foraging and other economic activities, protection from predators, and the seeking of social status. If cultures around the world consistently practice differential parental investment in ways that ensure long-term reproductive success, this can only mean that conflicts between self-survival strategies and reproductive strategies never exist or that when they do exist the intellect grants priority to reproductive strategies.

That conflicts between self-survival strategies and reproductive strategies do exist is obvious from modern cultures. Many elderly Americans, for instance, choose to deploy their economic resources for their own health care rather than invest in the education and health care of their descendents. Modern career women often delay childbearing to ages at which fertility can no longer be taken for granted in order to pursue career success. I suspect that earlier generations of women who entered convents rather than brothels were also choosing self-survival and status over reproductive success. The same may have been true of men who entered the priesthood.

Other considerations suggest that from an evolutionary standpoint the neural control of differential parental investment by sex should be subsidiary to other neurally regulated behaviors. For one, no animal can reproduce unless it first survives. This consideration alone would suggest that self-survival rather than differential parental investment would be the primary function of the human intellect. For another, until recently the human life-span was short, human reproductive intervals long. In preagricultural societies, even those fortunate enough to live a full life-span were unlikely to have more than five or six surviving offspring. Many women died young. Under such circumstances, women who practiced infanticide according to sex of offspring might have had fewer surviving offspring than those who welcomed and nurtured any healthy children to whom they gave birth.

The human brain is least efficient when called upon to delay immediate gratification for the sake of future benefits or to make complex decisions based on large amounts of information. The practice of differential parental investment by sex of offspring would strain these neural capacities to their limits. To make informed judgments, parents would have to calculate numbers of potential descendents some 30 years or more in the future based on numerous potential and often unpredictable social and environmental impacts. Such calculations are simply beyond the intellectual capacities of most of us.

Thus, if societies do practice differential parental investment in order to ensure the greatest long-term reproductive success, these practices must be based on group traditions rather than on individual predictive powers. Why, however, would cultures devise parental-

investment strategies designed to ensure the greatest reproductive success of every individual? The most critical of all basic evolutionary principles is that selection works on individual genes, not on groups. If anything, one would expect influential members of a social group to propagate cultural traditions which ensure their own success at the expense of that of others.

If, as Sieff implies, it is difficult to explain all parental-investment strategies on the basis of a few parameters, one reason may be that individuals often fail to act in their own best reproductive interests. Sociobiological theories are theories of ultimate causation. Ultimate causes act through proximate mechanisms. Sociobiological theories need to take into account that the brain is a fallible organ which often places self-interest and social success above reproductive success and which is primarily designed to deal with relatively short-term situations. In this regard, the occasional (or frequent?) failure of individuals and cultures to act in their own best long-term reproductive interest matches the failure of cultures to act adaptively in many other contexts for the same reasons (Barkow 1989).

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Sieff's paper underlines how nascent our understanding of sex-ratio biases in human groups really is. Univariate and multivariate statistical studies have sought to uncover biological and sociodemographic influences on the phenomenon, but causal answers remain elusive, despite over 300 years of work (Chahnazarian 1988). I would like to address three issues raised in the piece.

First, it is worth remembering that the statistical average of 105.5 males per 100 females at birth is derived from large, national populations. Anthropological tests of hypotheses about proximate causes and evolutionary consequences, however, tend to occur within the context of small communities. In such groups, the force of small numbers will generally result in deviations from the expected sex ratio at birth through chance alone. Furthermore, the sex ratio of a birth cohort will change throughout the life cycle in response to a wide variety of factors, including differential mortality and migration, in the presence or absence of biased "parental investment." Given that vagaries in sex ratios will result through stochastic processes alone as well as through culturally determined behaviour, how do parents decide on the wisest course of "investment" when it is usually impossible to predict which children will survive the reproductive period to produce the optimum number of viable offspring? If such decisions are made, then we need long-term research that (1) charts the decision-making strategies pursued by parents and kin groups over the life span of their children and (2) evaluates the effects such decisions have on the size and composition of the next generation. It is important to know whether

parental-investment strategies are, indeed, being carried out.

Second, Sieff correctly points out that "deriving a common currency of investment" and measuring "parental investment in a specific child in terms of the parent's ability to invest in other offspring" are major stumbling blocks to research into the relationship of reproductive success to parental investment. Certainly another fundamental problem resides in developing an operational definition of "investment" in the human context. Can praise, affection, advice, and other less tangible expressions of nurturing be considered "investments" in the same way as food, inheritance, time allocation, and productivity returns? How can such nebulous but crucial aspects of kin relations be worked into evolutionary models based on cost/benefit analysis?

Finally, more benchwork is needed in a wide variety of cultural settings on how sex ratios fluctuate over the course of the life cycle, what factors influence those fluctuations, and what effects such fluctuations have on other demographic parameters, such as the potential for finding suitable mates and producing offspring. Until we have a strong foundation of basic research on such proximate issues, I believe it is premature to draw conclusions about ultimate questions like the evolutionary basis for sex-ratio bias in human populations.

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Sieff has written a thought-provoking paper about an evolutionarily important set of facts concerning the secondary sex ratio, but two observations might have been more clearly spelled out.

First, the chance of discovering facts about a particular population or successfully testing hypotheses on the causes of variation in the sex ratio at birth depends in large part upon the size of the data collection that can be reliably observed. The number of births needed to make a contribution depends in part upon the degree of variation between populations, but generally speaking we need about 1,000 births, accurately recorded, to detect differences. If we are studying a group like the approximately 500 !Kung Bushmen of my own studies, we expect about 20 births per year, and we would have to observe for about 50 years to get an adequate sample. If we want to distinguish younger and older mothers, of high and low status, with varying numbers of previously born children in different sex-ratio combinations, the size of the study population may need to be enormous. And if we are only interested in noncontracepting populations, there may be no readily available data collections to test our theories on.

Second, the size of the effect that might be important for evolutionary consequences is probably very small. One understands that the discussion of advantages of having male or female children for particular parents is

overstated in Sieff's theoretical discussion for the purposes of simplicity. But the outcome of the processes discussed may only shift the probability of the next child's being male from something like .51 to .52, a difference too small for the individuals directly involved to know whether it is working or not. We can only measure the probability on groups of individuals, and there are no reliably observed large populations in which the sex ratios are greater than about 110 males per 100 females. The cases cited by Sieff need to be examined in much more detail with regard to their methodology, possible sources of error and bias, and the size of their populations before they can be interpreted as evidence that large variations exist in sex ratio at birth.

I am sure that Sieff is right that there are variations and that these variations are important. She does a good job of considering theories of the possible contributions to those variations, but a quick reading might leave the impression that the strength of the causal factors is much greater than it is.

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To test the evolutionary sex-allocation models that Sieff reviews, the fundamental hypotheses must be clearly specified in testable form, and the data must be appropriate and of sufficiently high quality to convey accurate information about sex ratios. Most of the sex-ratio literature with which I am familiar is about sex ratios of very dubious empirical status. Sieff's essay does not address this problem, instead treating every study as if the data employed were perfectly straightforward and needed only to be interpreted in terms of evolutionary theory.

In human populations, even when the data are otherwise of high quality, the standard sex ratio (for European populations) of 105/6 is only found by aggregating a large number of births over a long period of time. The smaller the population and the shorter the time period, the wider the range of values for the secondary sex ratio. If one were content to work with data from small towns over one- or two-month periods, any value within a range of 80 to 120 could be found, and thus any hypothesis about sex ratios could be proved. I have never seen a demonstration that animal data are free from similar problems.

Even more serious is the difficulty of gathering *accurate* data on sex ratios. For example, with regard to the 19th-century data on Russian Jews, when the civil registration system was first set up many Jews were reluctant to participate in it for a variety of religious and social reasons. Those who were least reluctant were concerned about the future security of their heirs' property, hence the overwhelmingly male bias of the ratios (a bias that diminished over time). Since many religious Jews were also convinced that censuses violated the laws of God, those who participated in early censuses were also males concerned with the possible relationship between census data and proof of residence and other legal matters.

It is common for registration systems to display male-biased ratios at the beginning (because property-owning parents are most willing to register male babies) and then begin to reflect the normal range of values as nearly all parents accept the necessity of registering children of both sexes.

Sieff correctly specifies that reproductive success should be measured in the form of surviving offspring or even grandoffspring, and this tells us that secondary sex ratios can only be weakly related to the main hypotheses and should perhaps be disregarded. Testing a hypothetical relationship between sex-selective parental investment and reproductive success calls for a conclusive demographic demonstration of some reasonably stable relationship between the patterns of parental investment of a group of parents at one time and the differential reproduction of the favored gender at a later time. To my knowledge, no such demonstration has ever been provided for a human population. (If one exists for an animal population, it is not clear from this essay.) In those European historical populations for which we have data, tertiary sex ratios (by age 20, for example) are highly variable at the local level and not at all under the control of the household-level decisions that parents make.

Indeed, to this day historical demographers have never used the available historical or modern data to ask whether grown sons or daughters were more likely to have children of their own and, if so, how many. This is the critical empirical question that none of the literature reviewed here addresses. What there is a great deal of evidence for is that parents can and did calculate whether sons or daughters were likely to be of more economic and social use to them *in the short run*. In traditional agrarian populations, particularly during the evolution of modern commercialized agriculture, for many families boys were economically more valuable than girls and slightly better treated.¹ Even though European parents in the agrarian sector may have acted in such a way as marginally to favor the survival of boys during the 19th century, this is not the same thing as saying (1) that they did so because they could rationally anticipate that their sons would have more surviving offspring than their daughters or (2) that they were compelled to behave as if they knew this by a genetically coded behavioral program.

The kind of historical parental rationality with respect to reproduction that has been studied most closely thus far is that exhibited by economically extraordinary parents in Europe, and it is very clear that they did not use their superior social or material advantages to guarantee their own long-term reproductive success. Over the period 1600 to 1900 (and later), ruling-class European land-owning families transmitted the right to inherit and re-

1. The demographic evidence for the hypothesis that excess female mortality in 19th-century Europe was a temporary manifestation of culturally influenced forms of economic stress during agricultural modernization (and not some timeless manifestation of evolutionary biology) has recently been reviewed and updated (Johansson 1990).

produce to no more than one son and one daughter per generation (on average). (They had almost twice as many children surviving to reproductive maturity.) Since 10–30% of their married children did not have children, upper-class populations shrank steadily over time (Johansson 1987). On the whole, such families preferred to gamble on their own extinction rather than face the virtual certainty that too many equally endowed and married surviving children would dilute their assets and thus diminish their status and power. In almost every generation, upper-class families understood that their behavior was causing their overall numbers to decline, but they did nothing about it.

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Sieff's article touches a difficult problem with important relations to social and cultural behaviour. Biased sex ratios in human populations can be studied from various points of view. The sex ratio of any population depends on four factors: (1) the primary sex ratio, i.e., the sex ratio at conception, (2) the secondary sex ratio, i.e., the sex ratio at birth, (3) differential sex-age mortality, and (4) migration. Sieff does not deal with the first and the last of these and gives limited attention to the second. It is evident that through allocation of resources to offspring of different sexes parents can affect only differential mortality—what might be called the tertiary sex ratio, i.e., the sex ratio at death. It can but need not be limited to children. The sex ratio at death in economically, socially, and demographically developed countries has been higher than the secondary sex ratio; it reflects excess male mortality that recently reached ca. six years (median value; an unweighted average does not make much sense here) and is steadily increasing. This is inexplicable on a biological basis alone, and therefore Sieff's conclusion is correct: "Better understanding of the evolutionary basis for the sex-ratio bias in human populations can be expected to result from closer attention to a broad range of ecological and social factors."

Migrations are a topic of a great importance, but they cannot help to elucidate the questions Sieff raises. Interest in the primary sex ratio developed only after it had been shown that the secondary sex ratio differed at a high level of statistical significance from 100. A few hypotheses have been formulated, but for obvious reasons they cannot be tested. A. A. Chuprov's 1912 hypothesis that the primary sex ratio is much higher than the secondary one (as much as 150) seems to be in contradiction with recent findings. New data on the sex ratio of stillbirths and of spontaneous abortions (using a method based on the analysis of chromosomes) seem to indicate that the primary sex ratio is close to the secondary one.

The founder of demography, John Graunt, in the mid-17th century, was probably the first to describe the biased sex ratio at birth. Various hypotheses have been

offered to explain why, in countries with reliable evidence of demographic events, this ratio has always been significantly higher than 100, but it has remained a mystery. If we reject the 18th-century religious interpretation of Johan Susmilch, we are reduced to the bare description of the facts. The secondary sex ratio in countries with reliable data is 104–108, with a median value of 106 (Pavlík 1982). Any value within this range can safely be accepted, e.g., the secondary sex ratio of 104.6–107.1 for the Czech Socialist Republic after the Second World War. (Czechoslovakia has some of the best evidence of demographic events, and special attention has been given to newborns.) Values outside this range must be interpreted with caution. Evidence of sex-differential child mortality is abundant, and the mechanisms of registration biases are well known. One of these has to do with application of the internationally accepted definition of "live-born child," which may already be sex-biased. Late registration exists in many countries; the omission of children who died before registration may be frequent and sex-biased. We cannot rule out the possibility of inaccuracy in reporting sex of the newborn; the census data used for this purpose are of especially poor quality. Testing for statistical significance should always be required, but it cannot compensate for inadequate primary evidence.

With all this in mind, I would strengthen Sieff's hypothesis that all biases in the secondary human sex ratio (outside the range mentioned) are induced postnatally through differential mortality. I would argue that the secondary sex ratio in developed countries has not changed in spite of the enormous decrease in fertility during the last two centuries. (It is extremely difficult to measure the secondary sex ratio in less developed countries and to obtain reliable data.) The reasons for the existing secondary sex ratio are basically biological. Information on non-human populations is still scarce and rather confusing, as Sieff's article shows. Further research is badly needed here as well. Sieff has assembled the available evidence in an important field and identified directions for further research. Demography, studying the reproduction of human populations as a collective process, can help to suggest and to assess hypotheses.

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Like the review of sex-ratio research written nearly 20 years ago by Teitelbaum (1972), this one has an introduction defining the live-birth sex ratio, a review of factors purported to explain differences in sex ratios, an extensive bibliography (with citations near the date of publication), and a very short, tentative, cautionary end ("Most of the numerous factors listed have been studied independently, without provision of any control for the possible effects of other variables" [Teitelbaum

1972:106], "Better understanding of the evolutionary basis for sex-ratio bias in human populations can be expected to result from closer attention to a broad range of ecological and social factors that may affect parental investment" [Sieff]. I do not imply that Sieff has merely repeated Teitelbaum. On the contrary, the papers complement one another quite well and show how research about human sex ratio may have evolved from facts to theory.

After briefly demonstrating the mathematical importance of sex ratio to demographic, biological, and genetic models, Teitelbaum (1972:91-95) mentions "Fisher's theory of the role of natural selection in determining the sex ratio." He recognizes that "it is essentially a non-genetic argument" until we empiricize the concept of "parental expenditure." Thus Sieff extends Teitelbaum (and Fisher) by adding two more theories of explanation from the popular paradigm and familiar language of sociobiology: parental-investment bias and offspring contributions to kin success. Despite the impressive number of studies over many species reviewed by Sieff, parental investment still eludes the quantification required for a decisive test of the theories. This particularly holds for the human examples confounded by cross-cultural variables.

I admire the efforts of Teitelbaum and Sieff to make sense of measurements sometimes easily collected from a variety of sources but very difficult to explain in a comprehensive manner. Their immense and intense reviews of the literature testify to the work of many others. Sieff observes, though, that "the magnitude of bias is generally small." In the end, I wonder if all the professional investment by so many theoretical "parents" will produce trivial or significant results. Teitelbaum (1972:97) noted the wasted expenditure in using sex ratio as a genetic trait or a mutation rate. Maybe sex ratio and sociobiology will fare better over time.

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This is an exemplary paper. Sieff has managed to pack an incredible amount of information on sex-ratio theory and the results of recent empirical studies into a very limited space without sacrificing clarity. In addition, she has taken a critical but very evenhanded approach to evaluating the recent spate of research on human sex-ratio variation. While focusing on studies guided by evolutionary biology, she has taken pains to point out some clear links to past work with a more economic or sociological orientation (by Goody, Tambiah, et al.). While I could quibble with a few of Sieff's interpretations, I think that virtually all of the problems I see are simply attributable to the condensation required in a review article on such a complex and active area of research.

I will offer two brief suggestions. First, the problem of devising a "common currency" for measuring parental

investment is a difficult one, but I think there is some room for hope. Specifically, since most forms of parental investment require parental labor, which labor is therefore unavailable for investment in other offspring, the labor time or energy embodied in various forms of parental investment (whether these be cattle, food, money, or child care) is arguably the best approximation to a *measurable* common currency (and proxy for the generally unmeasurable ultimate currency of fitness) that we are going to find. Embodied labor time has clearly been successful as a common currency and fitness proxy in other areas of behavioral biology (foraging strategies, spatial organization, etc.). It is not a perfect currency, to be sure (i.e., it is not perfectly correlated with fitness effects), but it may be good enough for many purposes—and perhaps often what parents themselves consider most in evaluating alternative investments of their resources.

Second, that resources must be "infinitely partible" in order to favor equal allocation to offspring is an overstatement. Resources need only be partible into at least as many portions as there are offspring. More generally, optimal allocation of parental resources depends not just on partibility but also on the shape of the fitness function relating resource inheritance to offspring survival and reproduction. If this function is positively accelerated (i.e., exhibits increasing marginal returns per unit invested), then selection will favor unequal division (e.g., unigeniture) even if resources are smoothly partible. Determination of the fitness functions for different types of parental investment under different socioeconomic regimes is a crucial and difficult task facing future students of human sex-ratio variation.

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With her comprehensive, well-thought-out, and argumentatively stringent review, it is to Sieff's credit to have illustrated that human parental-investment strategies should be (and probably are) rather sophisticated, with the result that no single formula can explain all of the observed sex-related investment differences. We agree with her that the adaptive value of differential parental investment becomes understandable only with in-depth knowledge of the socio-ecological and cultural conditions of the particular society. To support this conclusion, we should like to present a few preliminary trends from our family-reconstitution study of the Krummhörn, in northwestern Germany (table 1). We believe that these data may contribute a further component to the sex-ratio puzzle (Siegelkow and Voland n.d.). Farmers in the Krummhörn, with 116.2, have the highest sex ratio at birth, but the sex ratio at 15 is only 91.4. In between lies a differential parental investment in favor of farmers' daughters that was completely unexpected with regard to direction and degree. Female infant mortality amounts to 5.4%, extremely low both for the

TABLE I

Selected Data on Reproductive Patterns, Krummhörn (Germany), Marriage Cohort 1689–1820, First Marriages Only

Subpopulation	N	Live Births		Infant Mortality		Sex Ratio		% of Surviving Children (15 Years and Older) Locally Married	
		Boys	Girls	Boys	Girls	Age 0	Age 15	Male	Female
Farmers	45	129	111	.194	.054	116.2	91.4	43.5	69.9
Smallholders	131	343	305	.152	.131	112.6	114.1	46.1	59.6
Landless	225	545	512	.139	.117	106.4	97.3	50.6	54.5

SOURCE: Siegelkow and Voland (n.d.).

NOTE: Data from completely known families only.

Krummhörn population and for 18th- and 19th-century villages in a regional comparison (Knodel 1988). The figure is clearly below the corresponding value for farmers' sons ($p < 0.01$). What, in our opinion, must be viewed as parental manipulation appears to correlate with the local marriage probabilities of the surviving children.

Farmers' apparent preference for daughters is surely related to three decisive constraints: (1) there was virtually no population growth in the Krummhörn in early modern times (Engel n.d.), and consequently fitness maximization was possible only through "displacement" of competitors. (2) Land was scarce, and for geographical reasons (location on a peninsula) farmsteads could not be increased. (3) Long-term reproductive success was correlated with landownership (Voland 1990). Ultimogeniture secured long-term reproductive chances for only one son. Other sons had to be paid their share of the inheritance, thus weakening the economic power of the farm, and nevertheless were condemned to emigrate or at best to marry beneath their social status. The prospects for daughters were different, since farmer parents had a real opportunity for maximizing their fitness by the "genetic invasion" of other farms through the marriages of their daughters. Our figures on endogamy prove this (Voland and Engel 1990). Moreover, this strategy was culturally facilitated, since a daughter's share amounted to only one-third of that for sons (Agena 1938). Thus, girls seem to have been cheaper to produce, and if so the Krummhörn farmers were investing according to Fisher's theorem.

But are we not succumbing to the temptation of opportunistic post hoc explanations? If the figures in table 1 had shown a preference for sons, we would admittedly have been inclined to view the Krummhörn as confirmation of the Trivers-Willard hypothesis. Clutton-Brock and Iason (1986) are right when they point out that with a little imagination almost any sex ratio can be interpreted as adaptive. After reading Sieff's review, however, evolutionary anthropologists will no longer so readily succumb to this danger. Only if, as Sieff argues, we do not lose sight of the specific socio-ecological constraints in analyzing demographic variation will

sociobiology—originally praised for its precise hypotheses—avoid degenerating into an opportunistic "so-so-biology."

Reply

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Responses to my article can be divided into three broad categories: conceptual, methodological, and data-oriented. First, several commentators argue that sex-biased parental investment is not amenable to analysis from an evolutionary perspective (Fix and Gibson) or that an evolutionary approach has little to add to an economic one (Fix and Johansson). Comments in the second category raise methodological problems in measuring sex-allocation strategies. For Herring, Howell, Pavlík, and Johansson I underestimate the role of random variations in small populations and rely too heavily on data of questionable accuracy. Flinn and Sattenspiel, Herring, and Sheets emphasize how difficult it is to devise a valid measure of parental investment, while Smith suggests a solution to this problem. Betzig focuses on cases that do not seem to fit evolutionary expectations. Finally, Cronk and Voland and Siegelkow present new data. As the conceptual criticisms are fundamental, I address them first.

Fix's argument is that natural selection works on heritable characteristics and sex ratio is a population measure rather than a phenotype. Moreover, sex ratio is not faithfully heritable (that is, offspring do not inevitably produce offspring in the same sex ratio as their parents did), and Fix believes that natural selection can have no explanatory power in such cases. However, sex ratio can be as much a phenotype as the size of a mother's litter or the weight or color of her offspring. Population sex ratios are an aggregate of individual sex ratios, and individual parents do differ. Furthermore, if biased sex allocation is to be advantageous for parents

we would expect it to be a facultative trait that responds to parental condition and the nature of available resources. There are several examples of this from the non-human literature. In some haplodiploid wasp species in which sibling mating is common, the primary sex ratio is markedly female-biased (Hamilton 1967, Werren 1980, Trivers 1985). Because one male can fertilize several sisters, a parent producing a 1:1 ratio would waste investment in superfluous males (local mate competition). However, when a female lays eggs in a host that already houses the eggs of another female, it is advantageous for her to bias her sex ratio towards sons that will mate with the first female's daughters. Strong evidence of this comes from the parasitic wasp *Nasonia* (Werren 1980), among which the offspring of females that are second to lay their eggs in a particular host have a male-biased sex ratio that is a close fit to the ratio expected if these females are to maximize their reproductive success (Werren 1980). Other examples of facultative adjustment of sex ratios (in wood rats, golden hamsters, domestic mice, and coypu) are discussed in my article. In fact, evolutionary theories of sex allocation require that sex ratio be a facultative trait rather than one whereby offspring produce the exact same phenotype as their parents. What is required for natural selection of biased parental care is that there be a heritable component to the ability to alter sex ratios facultatively in accordance with prevailing conditions. Whether this ability is transmitted genetically or through learned behavior makes no difference with regard to designating this trait an adaptation (Caro and Borgerhoff Mulder 1987).

Gibson questions whether parents can be biasing their investment adaptively. She argues that because, in humans, the proximate mechanism for decisions concerning differential investment is the brain it is inevitable that sex-biased parental-investment strategies will clash with survival strategies and that the parents' survival strategies will prove more important. While the idea of tradeoffs between survival and reproduction is well developed in evolutionary biology (life-history theory addresses this issue), it is difficult to understand why sex-biased reproductive strategies per se should clash with survival strategies.

Gibson also suggests that "the human brain is least efficient when called upon to delay immediate gratification for future benefits or to make complex decisions based on large amounts of information." She writes that "the practice of differential parental investment by sex of offspring would strain these neural capacities to their limits." Cheetah mothers, however, appear to be able to delay immediate feeding gratification for future reproductive benefits depending on the sex of their offspring. Caro (1989) has shown that pairs or triplets of males have a greater chance of both obtaining and retaining a territory than do singletons. At certain times of the year females collect in male territories, suggesting that territorial males have enhanced access to females. Caro has also shown that cheetah mothers with pairs or triplets of males in their litters hunted more often and provided these litters with more food than mothers with non-

male-biased litters (Caro n.d.). Moreover, cheetah mothers with two or three male cubs spent significantly less time feeding from carcasses and had significantly smaller average belly size than females with only one son in their litters (the effect of total litter size per se was not significant). This suggests that at kills mothers may be restraining themselves from eating in order to raise more than one surviving son. It is difficult to conceive that cheetah mothers can delay immediate gratification and differentially invest in male and female offspring whereas human mothers cannot.

Johansson criticizes the evolutionary approach but recognizes that the hypotheses are ones that can be empirically addressed with sufficiently high-quality data. Along with Herring, she argues that in order to test the evolutionary hypotheses conclusive data on the relationship between patterns of parental investment and offspring reproductive success are needed. I agree entirely, and in fact this was one of the main issues that I was trying to emphasize in this paper. I disagree, however, with Johansson's view that there is no evidence of a relationship between patterns of parental investment and offspring reproductive success in my paper, and I am sorry not to have been clearer in presenting what evidence there is. In the study I cited, Clutton-Brock, Albon, and Guinness (1986) have shown that in red deer dominant mothers have a significantly male-biased sex ratio compared with subordinates. They have also found a significant positive relationship between sons' breeding success and maternal rank but not between the latter and the breeding success of daughters. Further, sons of high-ranking mothers are reproductively more successful than daughters, whereas daughters of low-ranking mothers are more successful than sons. The strong effect of early growth on male breeding suggests that dominant mothers are able to invest more resources in their sons, thereby producing the reproductively successful males that the subordinate females cannot afford to produce. More recently, Borgerhoff Mulder (1989a) has shown that among the Kipsigis male polygyny (which accounts for the greatest amount of variation in male reproductive success) is correlated with cattle holdings, whereas there is no relationship between a female's reproductive success and the number of cattle belonging to either her parents or her spouse. Given that parents pass on their cattle to their sons, this is good evidence of a relationship between parental investment and offspring reproductive success.

Johansson goes on to argue that in 19th-century European agrarian societies, parents who favored sons paid more attention to economic benefits than to anticipated reproductive success through sons. This was essentially my point, except that I extended the argument by suggesting that the economic benefits of sons would be expected to mean more surviving offspring and grand-offspring for parents who favored sons in accordance with local resource enhancement. This is an empirical issue, and the hypotheses can be tested with demographic data.

Betzig's observation that in stratified societies we do

not find as much female-biased investment as Trivers and Willard's theory predicts might also be illuminated by examining the potential of local resource enhancement/competition. The exceptionally high degree of sociality in humans and their extended resource exchange networks mean that humans have unprecedented potential for local resource enhancement. Again, this is an empirical issue, and the effect of offspring contributions on parental reproductive success can be separated from the reproductive success of offspring themselves through detailed demographic analysis.

Both Johansson and Herring assert that adult sex ratios may be independent of parental strategies. Johansson states that in historical populations household sex ratios at age 20 are highly variable and "not at all under the control of household-level decisions that parents make." Since she does not suggest what factors might be influencing these sex ratios, it is difficult to evaluate her argument. Herring writes that stochastic events will result in parents' being unable to predict the survival chances of children and bias their investment accordingly. Although this argument has more validity, it is difficult to see what processes are truly independent of parental care (Simmons et al. 1982). Disease is often influenced by nutrition, and in most extant traditional societies medical care is at least a theoretical possibility. Earthquakes, hurricanes, brushfires, and wars are stochastic events that can affect mortality, but even in these circumstances parents may have to make decisions about which children they are going to try to save.

Four comments (Herring, Howell, Pavlik, Johansson) stress the problem of chance variations in small-sized populations and of inaccurate historical data. While I agree that these problems may be acute, there are ways, at least in extant populations, of reducing inaccuracy to a minimum. Howell estimates that a sample of approximately 1,000 births is necessary for statistical analysis and implies that in small populations the fieldworker is unlikely to observe sufficient births for such analysis. However, in contemporary studies of traditional populations researchers are using reproductive interviews to record the number and sex of offspring born. Although reporting biases may be inevitable in retrospective data, the advantage of working with a small population is that each reproductive history can be checked, rechecked, and cross-checked with other members of the community, thereby producing a high level of accuracy (e.g., Hill and Kaplan 1988a, b). It is also likely that an anthropologist who spends up to a year in the study population will become aware of whether children who die in childhood are in fact being omitted (e.g., Cronk 1989b).¹

Several commentators emphasize the problem of measuring parental investment (Flinn and Sattenspiel, Herring, and Sheets). Again, I agree that this is a serious problem, but one potential solution would be to follow Smith's suggestion and use parental labor as a measure. If parental labor were recorded by focal follows rather

than by instantaneous scans, Herring's less tangible expressions of nurture, such as praise, affection, advice, and even punishment and criticism, could also be recorded. More problematic, however, is allocation of labor to tasks that could benefit several offspring. For example, it would not be sufficient simply to measure time spent hunting, tending cattle, gathering food, collecting water, or cooking. It would also be necessary to measure how the resource was allocated and the effect of that particular resource on the offspring's survival and reproduction.

An important issue brought up by Flinn and Sattenspiel is that it may be "empirically impossible" to test the relative effects of different factors. Although this is conceivable, no human study has yet even attempted to test the relative effects of different factors. Rather, researchers have approached their data with one particular theory in mind and have failed to consider other potential influences. McFarland Symington (1987) has managed to examine the relative influence of (a) the differential cost of sons and daughters, (b) maternal rank, and (c) local resource competition in spider monkeys, and although such an undertaking is unquestionably difficult, it is premature to imply that it is impossible or even requires "a more sophisticated generation of anthropologists and biologists" than the present one. What is needed, however, is more empirical research that considers alternative factors that might be influencing parental-investment strategies, and it is exciting to see Cronk and Voland and Siegelkow presenting new data that do this.

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