

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

LAURA BETZIG

Evolution and Human Behavior Program, University of Michigan, Ann Arbor, Mich. 48109, U.S.A. 20 VII 89

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 haroms 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 bilineal, 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.

LEE CRONK

Department of Anthropology, Texas A&M University, College Station, Tex. 77843-4352, U.S.A. 8 VIII 89

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 [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 [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 [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.

ALAN G. FIX

Department of Anthropology, University of California, Riverside, Calif. 92521, U.S.A. 8 VIII 89

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-