1984 Reply to M. Blute's "The sociobiology of sex and sexes today." *Current Anthropology, 25(2),* 193-212.

by JOHN TOOBY
Department of Anthropology, Harvard University, Cambridge, Mass. 02138, U.S.A. 14 x 83

Blute begins her involved reasoning from a correct theoretical perspective: that the sex chromosomes have conflicting selective interests (Cosmides and Tooby 1981, Dawkins 1982). Unfortunately, her application of this principle is dubious. Blute's central novel claim is that the Y chromosome parasitizes female parental investment (in species in which males are heterogametic) and that accordingly the X chromosome is selected to choose males with small, inert, or absent Y chromosomes. This argument is based on some fundamental conceptual errors concerning how natural selection operates which prevent her idea from working, even in principle. She fails to appreciate that (1) the cost of meiosis applies to autosomes, not just to the X chromosome, and (2) even if this were not true, the X chromosome in an egg or the mother gains nothing by mating with a sperm carrying a small, silent, or absent Y.

Blute's assertion that autosomes do not suffer the cost of meiosis (or of male parasitism of female investment) because the situation "will normally be reversed elsewhere" misconstrues how selection works. It is parallel to arguing that because, in aggressive encounters, wins exactly equal losses (summed over all participants), there is no penalty to losing. In analyzing how selection acts, one cannot average results across conditions (male, female) to argue that there is no negative result within a condition (female). This could only make sense if the "win" of a male with a given genotype were made inevitable by the "loss" of a female with an identical genotype. In fact, however, these two events are noncontingent. This is because a "loss" on the part of an allele in a female does not guarantee a "win" on the part of a male bearing the duplicate allele; she could be parasitized by a male of any genotype. Only under conditions of inbreeding does the "cost of meiosis" differ between the sex chromosomes and the autosomes.

Natural selection does not take place by interfering with the existence or replication of alternative genetic material per se (the supposed advantage to the X of the reduction, silencing, or elimination of the Y). Nor does it work through the differential occupation of somatic cells in the present generation. Instead, it takes place by the differential replication of alternative alleles into subsequent generations. A reduced, silent, or even absent Y chromosome does not in any way increase the proportion of X chromosomes in subsequent generations. So long as Mendelian ratios are maintained (a condition Blute does not depart from), a specific X chromosome in a mother has only a 50% chance of being replicated into a given offspring, regardless of whether the Y chromosome in the sperm fertilizing the egg is small, silent, nonexistent, or stands on its head. The same thing applies to any resulting XY son: 50% of its offspring pass on the X, 50% the Y, regardless of the size or activity of the Y. Even where the Y chromosome is absent entirely, the absence of the Y is just as much an allele as a Y, preventing the X from occupying 50% of the offspring. This absence of a chromosome is a gene that is passed from generation to generation, occupying the space that its "homologous" X could occupy. The concept Blute may be searching for is that of meiotic drive, when an allele increases its replication into offspring beyond 50%. Hamilton (1967) discusses the possible consequences of meiotic drive on sex chromosome morphology.

There are numerous other difficulties. For example, it is hard

to make credible how the absence of Y-chromosome DNA would lead to more extreme male structures (Blute's sexual-selection hypothesis), since the reduction of the Y only exposes more of the X to expression in males, an X which is doubly expressed in females. Also, it is hard to see how female parthenogenesis could be "overcome" by males, especially by "coercion" (how could behavioral "coercion" conceivably convert an already existing diploid egg into a haploid one?).

The "crisis" in evolutionary biology is really limited to the question of the function of sex, and this appears close to solution. The population cycling theory (and its pathogen variant) (Hamilton 1980) and the cross-locus dependent pathogen hypothesis (Tooby 1982, Price 1983) have the requisite qualities of intense selection pressure and ecological universality, as well as predictive success. In any case, given that sex does enjoy some advantage, the standard "sociobiological" theory relating sexual selection to parental investment remains powerful, elegant, and predictive.