

DO PRIMATES EXPERIENCE SPERM COMPETITION?

Sperm competition can occur whenever sperm from more than one male attempt to fertilize the limited ova of a female. This process can lead to evolution through sexual selection and has been proposed as the selective force behind such diverse adaptations as prolonged copulation, the structure of genitalia and accessory organs, and even semelparous courtship strategies (Smith 1984). Several authors have argued that sperm competition occurs among primates, including humans (Short 1977, 1979; Harcourt et al. 1981; Harvey and Harcourt 1984; Smith 1984; Kenagy and Trombulak 1986; Verrell 1992), and has resulted in the evolution of males with disproportionately large scrota and testicles (Smith 1984) and disproportionately long penes (Margulis and Sagan 1991; Verrell 1992) in those species in which females routinely mate with more than one male. These arguments are now widely enough known that they appear in introductory behavioral ecology texts (Krebs and Davies 1984) and at least two general-audience texts on human evolution (Margulis and Sagan 1991; Diamond 1992). When used to reconstruct human social systems, these arguments have suggested that the mating systems of human ancestors involved regular female promiscuity (Smith 1984; Margulis and Sagan 1991).

In this note, we review the evidence on which the arguments were originally based and conclude that it is so incomplete, and the possibility of spurious relationships so great, that no conclusions about the importance of sperm competition in primates, let alone humans, can be supported at this time. More important, we maintain that present inferences regarding the consequences of sperm competition are inadvertently male centered in that they have ignored important aspects of female reproductive structure and function. We do not deny the possibility of sperm competition among primates, but we are unconvinced by current analyses and question whether sperm competition is a likely selective agent responsible for the evolution of male genitalia in this taxon. Furthermore, we feel that currently incomplete analyses may lead to insupportable sociological conclusions.

The evidence on which the argument for sperm competition among primates is based is correlative in form. Various authors have pointed out that primates with multimale breeding systems generally have larger testicular mass than do primates in which only one male usually mates with a female (Harcourt et al. 1981; Smith 1984; Kenagy and Trombulak 1986). Harcourt et al. (1981) further demonstrate that testis weight scales allometrically with body weight and that multimale breeding primates have a higher regression coefficient than do single-male primates of the same body size. Others have extended the evidence by claiming parallel patterns with regard to penis size (Margulis and Sagan 1991; Verrell 1992). Most of these analyses specifically report that the largest extant primate (*Gorilla go-*

rilla) has relatively tiny testicles and penis, whereas the smaller *Pan troglodytes* has relatively enormous testicles and a large penis. The former species lives in single-mating male groups; the latter has regular multiple-male mating.

The conclusion drawn from these observations is that males that mate with females who will mate with other males experience sperm competition and benefit if they have larger testes and longer penes to deposit a greater volume of sperm closer to the site of ovulation. Males that monopolize a female do not experience such competition and can evolve more conservative genitalia (Krebs and Davies 1984). This argument has been applied to humans with the specific interpretation that, since human testes and penes seem large, human ancestors must have experienced sperm competition, that is, ancestral females must have regularly mated with more than one male (Smith 1984; Margulis and Sagan 1991). This extension ignores the fact that human testis weight is that predicted for a single-male mating group of human size (Harcourt et al. 1981).

The problem with these arguments is that they assume that the size of male genitalia is an adaptation that has come about exclusively through male-male interactions like sperm competition. In fact, the very function of the genitalia is to produce and deliver sperm to the female, suggesting that the nature of the female's reproductive tract (i.e., the vagina and the cervix) may be an important constraint on the evolution of male genitalia. The gorilla and chimpanzee illustrate this point. The male gorilla weighs an average of 170 kg and has a combined testicular weight of 30 g (Smith 1984) and a penis length of only 2.5 cm (Short 1979). The male chimpanzee weighs an average of 47 kg and has a combined testicular weight of 120 g (Short 1981) and a penis length of 8 cm (Smith 1984). The vagina of a female gorilla is approximately 10 cm long (T. Bowsher, personal communication; the value of 70–80 cm given in Smith [1984] is inflated by an order of magnitude), while that of the chimpanzee is about 17 cm (T. Bowsher, personal communication) and is made functionally much longer by the genital swelling or tumescence at the time of receptivity. For example, maximal swelling has been reported to range up to 1,400 cm³ (Yerkes and Elder 1936). A male gorilla having genitals the size of a chimpanzee's might injure a female gorilla during intercourse. A male chimpanzee with the genitals of a gorilla would produce so little sperm in proportion to the vaginal volume of the female that it might never succeed in fertilization, especially given the improbability of his penis even reaching the external opening of the vagina.

Harcourt et al. (1981) recognized that increased primate body size would itself favor increased testicle size because of a vaginal dilution effect. They made the implicit assumption, however, that all female primates have the same relation between body size and vaginal size. Not only is this false, but the internal arrangement of the female reproductive tract varies from species to species (Atkinson and Elftman 1950). Given that vagina size changes independently of body size (e.g., chimpanzee vs. gorilla), that the relative position of the uterus, vagina, and cervix vary among species, and that the actual site of fertilization may also vary, simple analysis of testicle or penis size alone reveals little about the likelihood that sperm will actually reach eggs. Some species like the gorilla may have small testicles because vaginas are small and little dilution occurs. They may have small penes because vaginas are short and fertilization occurs near the outside of the

body. Other species like the chimpanzee may require large testicles to compensate for large vaginal dilution effects and long penes to place sperm near a distant cervix. Whether these patterns vary with the type of mating system is as yet unknown, but the consequences of this dilution effect due to vagina size (not overall body size) may be important selective forces on sperm production and penis length independent of sperm competition.

The forces shaping vagina size are also unknown. If vagina size evolves in response to penis size, the patterns and arguments involving sperm competition still make sense. On the other hand, vagina size may be constrained by the space available within the female's body, the postures held during mating or parturition, the location of the birth canal, or some other unidentified feature that may be completely unrelated to type of mating system. This means that correlations between testicle or penis size and mating system are potentially spurious, and more detailed analyses that include the structure of females (i.e., the true reproductive function of the male's genitalia) need to be conducted.

Since the relation between genital size and mating systems among primates is consequently unclear, attempts to identify the human ancestral mating system through an analysis of human genital size (Smith 1984; Margulis and Sagan 1991) are premature at best. Furthermore, such attempts are necessarily fraught with social consequences and must therefore be based on uncontroversial evidence. For example, Margulis and Sagan (1991) claim that women in tropical climates may be expected to prefer men with larger penes. While their reasoning is not entirely clear, they preface this claim with the argument that, because of sperm competition, large-penis ancestral men fathered more large-penis sons than did less endowed males. Since their entire argument rests on the assumption that penis size is only important when sperm competition occurs, their statements concerning the preferences of "tropical" women can be interpreted to mean that sperm competition is more prevalent among these women, that is, they are more promiscuous. Furthermore, several authors (Short 1979; Harcourt et al. 1981; Smith 1984; Margulis and Sagan 1991) base their analyses of human testis size on the reported value of about 20 g per testis. None of these authors are explicit about who their "humans" are. Short previously (Short 1979, 1980) pointed out that this weight applies to European men and that the equivalent weight for Chinese men is almost exactly one half as great. Applying the logic of Margulis and Sagan, this indicates that contemporary Chinese must be descendants of highly faithful females, unlike contemporary Europeans, and certainly quite different from tropical women. Short (1980) reached the conclusion that so little was known about human variation that no conclusions about the significance of this trait could be drawn.

In a comprehensive review of the subject, Eberhard (1985) evaluated several contemporary arguments for the evolution of genital form among animals. He rejected the sperm competition argument as an explanation in species (like mammals) in which the penis cannot directly remove or otherwise interfere with sperm already in the female's reproductive tract. For example, in the present case, it may be that larger testes result in more sperm, but it is difficult to imagine how incremental increases in penis length would be favored during evolution because the result, if not the function, of ejaculation is to propel sperm beyond the penis.

Penes of different length may have equivalent delivery abilities depending on ejaculatory force, not to mention the position of the male and female at the moment of sperm release.

As an alternative, Eberhard (1985) argued that penis structure in most animals has evolved through the action of female choice. Such choice may be obvious and involve rejection of suitors, interruption of matings, refusal to accept sperm, and so on, or it may be more cryptic and involve differential use of sperm after its acceptance. Eberhard further argued that a common function of the female reproductive tract may be to discriminate against the sperm of undesirable mates by making fertilization difficult. This approach explains the common observation that the vaginal environment is hostile to sperm (Smith 1984) and leads to an entire rethinking of the case in primates. For example, the genital swelling of female chimpanzees is almost always viewed as a stimulus to make the female particularly attractive to the male at estrus (Short 1979). While this is undoubtedly a consequence of the tumescence, might not the function (and selective advantage) of the trait be an increase in the volume and length of the female tract, giving the female greater control over paternity in this multiple-mating species? Applying Eberhard's arguments, increased vaginal depth would allow females to control paternity by determining penetration and thus dilution effects. Females could therefore select among males, perhaps on the basis of desirable behaviors (Smuts 1985), choosing the sperm of preferred males even in species in which females routinely mate with multiple partners. Thus, intersexual processes, possibly on their own and possibly in concert with sperm competition, determine male genital structure. This argument is consistent with the observation that human females who mate outside their pair bond actually do so to promote sperm competition (Bellis and Baker 1990). It raises the possibility that the important evolutionary question is what determines vaginal depth rather than what determines testicular size or penis length.

In summary, current analyses of the relation between male genitalia, mating-system structure, and sperm competition among primates make an interesting story that may be superficially convincing and may eventually be supported. Unfortunately, current analyses have neglected any investigation of female genital structure, and the fact that this varies among primates, and that this variation is not a simple function of body size, suggests that the correlations on which the story is based need further analysis. In particular, the sperm-diluting effects of vagina volume and the distance from the exterior of the female's body to the point of fertilization in various species need further investigation. Furthermore, there is an existing and competing explanation for the evolution of genital structure through the action of female preferences that must be addressed. Application of sperm competition arguments to humans is premature at best, misleading at worst, and can lead into perilous territory that may have unintended or insupportable applications.

ACKNOWLEDGMENTS

We thank B. Brown, who first pointed out to us that the response of a female gorilla to a mate equipped like a chimpanzee would probably not be positive. We also thank P. Gowaty for her comments and suggestions.

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Submitted January 6, 1994; Revised October 26, 1994; Accepted November 9, 1994

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