Sperm competition influences sperm size in mammals

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SUMMARY
Among mammals sperm competition leads to selection for increased sperm numbers but it is not known whether it also leads to changes in sperm size. Two contrasting theoretical predictions have been made. The first hypothesis relies on the assumption that there is a trade-off between sperm numbers and sperm size and predicts that, in species confronting sperm competition, there will be a concomitant decrease in sperm size as sperm numbers increase. In contrast, the second hypothesis suggests that longer sperm may outcompete rival sperm; if longer sperm may swim faster, they will reach the ova sooner and will be selected when sperm competition prevails. We tested these hypotheses in both primates and rodents. We report that males from species in which females mate promiscuously have longer sperm than species in which females mate with one male. In addition, we also found that sperm length is positively correlated with maximum sperm velocity. Our findings thus support the view that longer sperm may be adaptive in the context of sperm competition.

Sperm competition is ubiquitous among insects (Parker 1970; Thornhill & Alcock 1983; Smith 1984) and has recently been found to be widespread in birds (McKinney et al. 1984; Birkhead 1988) and mammals too (Birdsall & Nash 1973; Schwagmeyer & Woontner 1985; Moller & Birkhead 1989; Sherman 1989). Among mammals, males from species in which females usually mate with more than one male in any given oestrous cycle, show a number of reproductive features that are probably the result of selective pressures related to sperm competition. Thus, males in these species tend to have larger testes in relation to their body size (Harcourt et al. 1981; Kenagy & Trombulak 1986), copulate more often (Moller & Birkhead 1989), produce more sperm (Moller 1989), a greater proportion of their sperm is motile (Moller 1988), and their testes have a higher ratio of seminiferous tubules to connective tissue (Harvey & Harcourt 1984). The transfer of large numbers of sperm in competitive situations has been found to be an effective strategy since males who transfer more sperm per ejaculate (Martin et al. 1974), or who copulate more often (Lanier et al. 1979; Dewsbury 1984; Huck et al. 1985), are more likely to sire offspring. Males can exploit the advantage conferred by high sperm numbers by facultatively altering their sexual behaviour. Hence, males copulate more often after a female has mated another male and after periods of separation (Moller & Birkhead 1989). Similarly, human males seem to ejaculate more sperm after long periods away from their mates, irrespective of the time elapsed since they last copulated (Baker & Bellis 1989).

Some theoretical models have proposed that, assuming a fixed energy budget is devoted to gamete production, any increase in sperm numbers must be compensated by a decrease in the size of each gamete (Parker 1982, 1984). Since sperm competition favours high sperm numbers, a concomitant reduction in sperm size might be expected in species subjected to this selective pressure. On the other hand, one could postulate a different scenario: if long sperm were more likely to reach the ova first, both high sperm numbers and long sperm may be selected for when sperm competition prevails. To test these contrasting hypotheses we have analysed differences in sperm length between polyandrous (females mate with more than one male) and monandrous (females mate with only one male) species in two mammalian orders: primates and rodents. In the analyses presented here species were considered separately; however, analyses done combining all species from the same genera which shared the same mating system, revealed the same trends and were also statistically significant.

As reported in previous studies (Harcourt et al. 1981; Kenagy & Trombulak 1986), testes weight was found to increase with male body weight in both primates ($r^2 = 0.494$, $n = 19$, $F = 16578$, $p = 0.0008$) and rodents ($r^2 = 0.533$, $n = 27$, $F = 28507$, $p = 0.0001$), supporting the idea that large animals have large testes in order to counteract the dilution effects of large female tracts with high sperm numbers (Short 1981). It has been argued that the increase in sperm numbers with body size should have been accompanied by a decrease in sperm size, and a negative correlation between body weight and sperm size found when comparing all mammalian species for which data were available has been used to support this view (Cummins 1983; Cummins & Woodall 1985). In contrast, we found no relation between body weight and sperm size in either primates or muroid rodents (figure 1a, b).

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\[ y = 1.852 + 0.00036x; \quad r^2 = 0.000 \]

\[ y = 1.8971 + 0.0809x; \quad r^2 = 0.091 \]

Figure 1. Log male body weight against log sperm length for (a) primates \((r^2 = 0.00, n = 27, F = 0.00, \text{N.S.})\) and (b) murid rodents \((r^2 = 0.09, n = 32, F = 2.99, \text{N.S.})\). Key to symbols: inverted triangles, Prosimii; upright triangles, Ceboidea; circles, Cercopithecoidea; open squares, Hominoidea; closed squares, Muroidea. Most data on body weights come from Clutton-Brock & Harvey (1977), Kenagy & Trombulak (1986), and Moller (1988). Most data on sperm size comes from Cummins & Woodall (1985); some additional data come from the literature. When several measures were available for any given species, the mean value was used. Measurements derived from Retzius' illustrations have not been included, and neither have those measurements explicitly considered by the authors as being of 'suspect accuracy'.

when these were considered separately. Cummins & Woodall (1985) also found no relation in primates, but reported a negative correlation in rodents. The main difference between their analysis and ours is that while they included rodents from all suborders, some of which were poorly represented, we have restricted our analyses to murid rodents. It has to be emphasized that, on physiological grounds, there is a priori no reason to expect the opposite relation either, i.e. a positive association between sperm length and male body weight. Although large animals have large testes, the size of an organ is generally determined by the number of cells it contains rather than by the size of its cells. Thus, larger testes have more germ cells, but these need not be larger, nor do the gametes produced. Furthermore, most variation is sperm size is accounted for by the length of the tail (Cummins & Woodall 1985), which grows towards the lumen of the seminiferous tubule (Setchell 1982), where there are few spatial constraints whatever the size of the animal.

The lack of an allometric relation between sperm size and male body weight precludes the need to correct for differences in body weight in the analyses where sperm size was compared between monandrous and polyandrous species. *Erythrocebus patas* has been categorized here as polyandrous despite having single-sex units, because it reproduces seasonally and this makes harems difficult to defend during the breeding season. This situation results in frequent take-overs by outsiders and promiscuous mating (Cords 1987). On the other hand, *Pongo pygmaeus* has also been categorized as polyandrous, because males are unable to defend females' ranges and females mate promiscuously (Rodman & Mitani 1987).

Among primates, males in polyandrous species have longer sperm than males in monandrous species (figure 2a). When different primate taxa were considered separately, phylogenetic effects were revealed (figure 2b). Within each taxon, polyandrous species had longer sperm than monandrous species; *Theropithecus gelada* seems to be an exception to this general trend, as females mate with one male but males have relatively long sperm. In addition, the range in sperm size differed between taxa. While prosimians and New World primates showed a wide range in sperm size, cercopithecines and hominoids showed a more restricted range which did not overlap. Thus, all cercopithecine species had longer sperm than hominoid species.

Further analyses were done to take into account phylogenetic effects. The Comparative Analysis by Independent Contrasts (CAIC) produced by A. Purvis (Department of Zoology, University of Oxford, U.K.) was used for this purpose. Phylogenetic trees were constructed from Fleagle (1988) and Martin (1990). It should be mentioned that the use of CAIC is probably not entirely appropriate in this case, because the analysis of our data relies heavily on one categorical variable (i.e. mating system). This comparative analysis recodes an input column with \( k \) categories into \( k - 1 \) new columns, which are treated as continuous variables from then on. This has its drawbacks, rendering its use in cases such as ours questionable (A. Purvis, personal contact).
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Figure 2. Sperm length in primates: (a) Mean sperm length in monandrous versus polyandrous species (n = 28, Mann-Whitney U: U = 31, Z = -2.492, p = 0.01). (b) Sperm length within different taxa (circles, monandrous species; crosses, polyandrous species) (2-factor ANOVA, Mating System: df = 1, F = 9.594, p = 0.005, Taxon: df = 3, F = 4.984, p = 0.009, Interaction: df = 3, F = 1.746, N.S.). Prosimii: (1) Daubentonia madagascarensis; (2) Microcebus murinus; (3) Lemur mongoz; (4) Lemur calla; (5) Lemur macaco; (6) Galago crassicaudatus; (7) Galago senegalensis; (8) Nycticebus couang. Cebioidea: (9) Callithrix jacchus; (10) Cebus apella; (11) Saimiri sciureus. Cercopithecoidea: (12) Cercocebus galeritus; (13) Cercopithecus aethiops; (14) Erythrocebus patas; (15) Macaca arctoides; (16) Macaca fascicularis; (17) Macaca mulatta; (18) Macaca nemestrina; (19) Macaca speciosa; (20) Papio anubis; (21) Papio cynocephalus; (22) Papio spheniscus; (23) Theropithecus gelada. Hominoidea: (24) Hylobates lar; (25) Gorilla gorilla; (26) Pan troglodytes; (27) Pongo pygmaeus; (28) Homo sapiens. Information on mating systems was obtained from Smuts et al. 1987. Data on sperm size as in figure 1.

communication). Because the relation between the contrasts in sperm length and contrasts in mating system was non-linear, a binomial test of the number of positive pairs of contrasts was indicated; the contrast between monandrous and polyandrous species was found again to be significant (n = 22, p < 0.001).

Muroid rodents showed a much greater range in sperm size than did primates. In this mammalian group, sperm was also longer in polyandrous species than in monandrous species (figure 3). The ongoing debate concerning the phylogeny of this particular group of rodents, prevented us from making more sophisticated phylogenetic analyses.

Males confronting sperm competition may increase their sperm output in two ways: increasing the number of sperm per ejaculate or increasing the number of ejaculates. Theoretical models predict that, among vertebrates, the second alternative may be more beneficial (Parker 1984), as it allows greater flexibility, avoids the need for major physiological changes, and may bring additional advantages if males cannot predict when the females are fertile or when other males will mate. The available information on rodent species suggests that males in polyandrous species tend to copulate more often (Dewsbury 1981). If males confronting sperm competition can increase their reproductive success by increasing the number of times they copulate with a female and by increasing sperm size, as this study suggests, a correlation between these two variables should be expected. To test this hypothesis, we used Dewsbury's (1981) data on number of ejaculations before satiety on several species of muroid rodents, which ranges from 1 to 19. We found that species in which males ejaculate many times before reaching satiety with a given female, have long sperm (figure 4), strongly suggesting that both features are the result of selective pressures related to sperm competition.

As we suggested earlier, one of the possible reasons why longer sperm may be selected when sperm competition prevails, is that longer sperm may be able to swim faster and reach the ova sooner, thus outcompeting rival sperm. We plotted data on maximum sperm velocity for several mammalian species against sperm length and found a positive correlation between the two which was highly significant (figure 5). Further evidence comes from studies on Drosophila, where both long and short sperm can be found within ejaculates; long sperm have higher beat frequencies and higher wave propagation velocity than short sperm, and are thus more successful at fertilizing when the female remates again (Joly et al. 1991). Among mammals, differences in sperm length are mainly due to differences in tail length (Cummins & Woodall 1985), and detailed analyses of flagellar motion have reached the conclusion that the longer the sperm flagellum the greater the forces generated by its motions (Katz & Drobnis 1990). This implies that longer sperm are not only able to move faster, but are also able to penetrate the egg vestments more easily.

In conclusion, our results show that primate and rodent species in which males face sperm competition...
have longer sperm than monandrous species. We would like to argue that when ejaculates from different males mix in the female tract, sperm with long tails will swim faster and reach the ova sooner. This may be a crucial advantage among mammals where sperm have to swim actively in order to move forward along the upper sections of the female tract, and where the first male gamete to reach an egg is the one most likely to fertilize it (Cummins & Yanagimachi 1982). If male mammals do benefit from increased sperm numbers and from elongated sperm in competitive situations, it is likely that both features will evolve in response to the same selective pressures.

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