

Continuing Commentary

Commentary on David C. Geary (1996). Sexual selection and sex differences in mathematical abilities. BBS 19:229–84.

Abstract of the original article: The principles of sexual selection were used as an organizing framework for interpreting cross-national patterns of sex differences in mathematical abilities. Cross-national studies suggest that there are no sex differences in biologically primary mathematical abilities, that is, for those mathematical abilities that are found in all cultures as well as in nonhuman primates, and show moderate heritability estimates. Sex differences in several biologically secondary mathematical domains (i.e., those that emerge primarily in school) are found throughout the industrialized world. In particular, males consistently outperform females in the solving of mathematical word problems and geometry. Sexual selection and any associated proximate mechanisms (e.g., sex hormones) influence these sex differences in mathematical performance indirectly. First, sexual selection resulted in greater elaboration in males than in females of the neurocognitive systems that support navigation in three-dimensional space. Knowledge implicit in these systems reflects an understanding of basic Euclidean geometry, and may thus be one source of the male advantage in geometry. Males also use more readily than females these spatial systems in problem-solving situations, which provide them with an advantage in solving word problems and geometry. In addition, sex differences in social styles and interests, which also appear to be related in part to sexual selection, result in sex differences in engagement in mathematics-related activities, thus further increasing the male advantage in certain mathematical domains. A model that integrates these biological influences with sociocultural influences on the sex differences in mathematical performance is presented in this article.

Sex differences may indeed exist for 3-D navigational abilities: But was sexual selection responsible?

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Abstract: Polygyny does not necessarily entail sexual selection of men. All factors that affect the operational sex ratio must be considered. Data from contemporary hunter-gatherers indicate higher mortality rates in men than in women, and lost female reproductive time. If sexual selection did occur in ancestral hunter-gatherers, it was probably men selecting women and not women selecting men.

According to Darwin (1888, pp. 331–40), sexual selection has two causes: (1) differing mortality rates between males and females, and (2) polygyny, where a minority of males monopolize a larger number of females. More recent authors have cited other causes: sex differences in age at maturity, in reproductive longevity, in migration schedules, in spatial distribution, and in mortality during the reproductive season (Kvarnemo & Ahnesjö 1996).

In short, sexual selection occurs when too many of one sex compete for too few of the other. We call this situation an imbalance in the “operational sex ratio” (OSR), that is, the ratio of males to females among individuals ready to mate.

Geary (1996t) argues that the existence of polygyny in preliterate societies should have tipped the OSR towards a shortage of women available for mating. Hence, men should have been competing for sexual access to women.

We can test this hypothesis by examining mating success in contemporary hunter-gatherers. To date, the most thorough study is that of Nancy Howell on the !Kung bushmen. She found that the sexual division of labor differentially affects male and female death rates: “gathering, as opposed to hunting, does not seem to be a highly risky business” (Howell 1979, p. 57). Thus, 91 males remain per 100 females over the age of 10 (Howell 1979, p. 247). Polygyny does exist, but at a rate of only 6% of all sexual unions (Howell

1979, p. 235). “A relative scarcity of husbands, then, is a regular and expected part of the !Kung marriage system” (Howell 1979, p. 247). About 75% of the women lose some reproductive time while waiting between partners and 10 to 20% lose from 5 to 15 years (Howell 1979, pp. 248–50).

One might expect that more men would take second wives until no women are left unmated. Such an outcome is prevented by socioeconomic constraints. “[H]aving two families simultaneously is difficult to manage, both economically (in providing for a large number of dependents) and socially (in avoiding the conflicts and irritations of polygamous marriages)” (Howell 1979, p. 272). Each additional wife, including her subsequent offspring, decreases the ratio of food-providing adults to food-consuming children (Howell 1979, pp. 53–54). Beyond a certain point, polygyny ceases to be a viable life strategy.

This picture is confirmed by data from other hunter-gatherers. The sexual division of labor universally assigns men the riskier food-procurement activities, notably hunting. Women are assigned food gathering, although they may also take part in fishing and the capture of small animals. Thus, among the Aka Pygmies the men are more likely than the women to die an early death, particularly from hunting accidents and falls from trees while collecting honey, palm nuts, and palm wine (Hewlett et al. 1986, pp. 60–61). This sex difference seems to widen further away from the equator. Among nineteenth-century Labrador Inuit 15 years and over, there were only 57 males per 100 females (Scheffel 1984). High male mortality rates have been reported from Inuit groups further north, although the demographic effects were often offset by female infanticide (Balıkcı 1967; Birket-Smith 1929, pp. 66–68).

Hunter-gatherers also face tighter constraints on polygyny as one moves further away from the equator. Women tend to become net food consumers, especially in winter when opportunities for food gathering are meager (Jochim 1976, pp. 141–53; Martin 1974, p. 13). The Arctic environment offers gatherers only occasional roots, berries, and bird eggs (Birket-Smith 1929, p. 133). Inuit are quoted as saying “Women do not hunt, they are not self-sufficient, and they are less independent than men” (Balıkcı 1967,

p. 621). Consequently, “monogamy is prevalent, as the support of several wives is possible only for the expert hunter” (Hodge 1959[1905], p. 809). In reviewing the literature, Kjellström (1973, pp. 114–15) gives an Inuit polygyny rate ranging from 0% to 25% at the time of European contact, the average being 10%.

At the other extreme lies Australia; its scarcity of large game animals ensures that female gathering contributes much more to the Aborigine diet than does male hunting. The Aborigines were also the only hunter-gatherers with very high rates of polygyny.

This seems to be the general picture. If sexual selection did occur in ancestral hunter-gatherers, it probably acted in the direction of men selecting women and not women selecting men. To be sure, it may have greatly varied in intensity, particularly between tropical and nontropical environments.

A final note: ancestral men and women could have been selected in differing ways without sexual selection being involved. Consider the sexual division of labor. Hunting requires travel over a wide territory with much solitary scouting and reconnoitering. Gathering necessitates continual social interaction among individuals concentrated within a smaller area. Over time, these differing task requirements may have favored men with better navigational abilities and women with superior social and linguistic skills.

Author's Response

Sexual selection, the division of labor, and the evolution of sex differences

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Abstract: Sexual selection traditionally involves male-male competition and female choice, but in some species, including humans, sexual selection can also involve female-female competition and male choice. The degree to which one aspect of sexual selection or another is manifest in human populations will be influenced by a host of social and ecological variables, including the operational sex ratio. These variables are discussed in connection with the relative contribution of sexual selection and the division of labor to the evolution of human sex differences.

Frost argues that sexual selection should be considered primarily in terms of the operational sex ratio (OSR), that is, the ratio of sexually mature males to females in any given population (Emlen & Oring 1977). In populations where there are more sexually mature females than males, he argues, male choice of mating partners should be the primary factor driving the dynamics of mating and reproduction, as opposed to male-male competition and female choice. It is argued further that in preindustrial societies more men are killed during hunting than women during gathering, resulting in an unbalanced OSR. As examples, the OSR – with fewer sexually mature men than women – of the !Kung and Inuit are described, among others, along with low polygyny rates in these groups. In fact, many women apparently go without mates in these societies, because many men are not willing to marry a second wife, owing to the associated costs (e.g., addition provisioning). In these circumstances, Frost argues, male-male competition is not necessary and male choice should prevail over female choice, given that men have a larger pool of potential mates to choose from than women do. Finally, Frost

suggests that the sexual division of labor, rather than male-male competition, might be responsible for the male advantage in certain domains of spatial cognition.

The issues broached by Frost are related to the mechanisms of sexual selection, the ways in which these mechanisms are expressed under different ecological conditions, and the relative contributions of sexual selection and the division of labor to the evolution of human sex differences. The former issue is addressed in the first section and the latter in the second (see Geary, in press, for further discussion).

R1. The mechanisms of sexual selection

Sexual selection “depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction” (Darwin 1871, vol. I, p. 256). In most species, these dynamics are expressed through female choice of mating partners and/or through male-male competition for access to mates or for control of those resources that females need to reproduce (Andersson 1994; Emlen & Oring 1977). Across species, it appears that female choice and male-male competition are relatively more common than their counterparts – male choice and female-female competition – because of a sex difference in the costs and benefits of reproduction (Trivers 1972). As an example, internal gestation and obligatory postnatal care (e.g., suckling) necessarily result in higher reproductive costs for female mammals than for conspecific males, and, at the same time, they create an important sex difference in the potential rate of reproduction (Clutton-Brock & Vincent 1991). Following mating, male mammals can rejoin the mating pool much more quickly than can conspecific females, and typically do so.

Thus, even when there are equal numbers of mature males and females in the population, the OSR is typically skewed, so that there are more sexually receptive males than females in the mating pool at any given instant (because suckling and gravid females have left the mating pool, Parker & Simmons 1996). The larger number of sexually receptive males than females, among other factors, creates the potential for both male-male competition over access to mates and female choice. Indeed, these dynamics appear to manifest themselves in more than 95% of mammalian species (Clutton-Brock 1989), where males compete for control of sexually receptive females or for control of those resources that females need to reproduce, and females are consistently more selective in their choice of mating partners than are males.

Nonetheless, sex differences in the rate of reproduction or the OSR are not enough to result in polygamy (polygyny or polyandry). The ecology of the species must have the potential to support polygamy, a potential that is determined by the extent to which “multiple mates, or resources critical to gaining multiple mates, are economically defensible . . . [and on] the ability of the animals to utilize this potential” (Emlen & Oring 1977, p. 215). The ability of animals to utilize any environmental potential depends in turn on the degree of parental care required for the successful rearing of young, in particular the freeing of one sex from such care. The resulting emancipation is a necessary prerequisite for polygamy because only then do members of the emancipated sex – typically males – have the time and energy to devote to mating effort. Even this is not enough. For polygamy to be realized, the resources that

support the species need to be clustered in space and, in most cases, members of the higher investing sex (in terms of parental investment) – typically females – need to be sexually receptive at different times and clustered together.

The groups described by Frost, such as the !Kung, live in ecologies with relatively little potential to support polygyny. In other words, the ecologies supporting these groups make it difficult for men to gain control of enough resources to support more than one wife, in most cases. In this circumstance, the relative monogamy of these groups is ecologically imposed and, given this, there is less to be gained by intense male-male competition in comparison with groups supported by more resource-rich ecologies, as noted by Frost (Flinn & Low 1986). Moreover, because provisioning by men very often increases the survival rate of offspring, these ecologies also press for some level of paternal investment. Once men invest in children, they become an important resource for women in their quest to keep their children alive. Paternal investment, in turn, sets the stage for both female-female competition and male choice (e.g., Johnstone et al. 1996), to the extent the men differ in their ability to provision women and their children. Good providers are in greater demand and thus have more potential mates to choose from than their less skilled peers; this in turn results in the potential for male choice. At the same time, women have much to gain – in terms of lower child mortality rates (e.g., Hill & Hurtado 1996) – by marrying a good provider, hence they compete amongst themselves for the investment of such men, creating female-female competition. In both cases, any associated sex differences would be attributed to sexual selection.

Even so, it is very unlikely, even under these conditions, that men will be more exacting in their choice of mating partners than women, on average. This is because the costs of reproduction will always be higher for women than for men – costs that include a nine-month gestation period, the risk of death during childbirth, and higher levels of postnatal parental investment (Hill & Hurtado 1996; Whiting & Edwards 1988). Furthermore, it appears that one function of sexual reproduction is to provide a variable immune system to offspring, as a defense against quickly evolving parasites (Hamilton & Zuk 1982; Møller 1997). Immune-system genotype (i.e., the major histocompatibility complex, MHC; Nei & Hughes 1991) appears to be signaled by means of olfactory cues (Potts et al. 1991) and across those species in which it has been assessed, females – including women – appear to be much more sensitive to these cues than are conspecific males (e.g., Wedekind et al. 1995). It appears then that mate choice is influenced, in part, by disassortative mating for immune-system genotype – which would result in a more varied immune system in offspring than with assortative mating – and that this is driven largely by female choice. The combination of female-driven MHC-dependent mate choices and the sex difference in reproductive costs indicate that female choice will nearly always be an important feature of mammalian reproduction and the associated criteria will almost always be more stringent than the criteria associated with male choice.

Frost implies that ecologically imposed monogamy, or at least very low levels of polygyny, plus an unbalanced OSR, are a general characteristic of preindustrial cultures and largely obviate the need for male-male competition. In a review of 849 cultures, Murdock (1967) found that polygyny was found in 83% of these cultures, although, as noted

by Frost, only a minority of men are polygynously married (typically < 20%). Nevertheless, there are considerable reproductive benefits associated with polygynous marriages. When monogamy is not ecologically or socially imposed, men typically compete for political influence or for control of those material resources that allow them to establish social dominance over other men (e.g., Chagnon 1979; Jaffe et al. 1993). In large part, the attainment of social dominance – by means of male-male competition – determines which men marry polygynously, which marry monogamously, and which men do not marry at all.

The reproductive consequences of the attainment of social dominance are most evident in cultures that produce excess wealth (i.e., wealth beyond subsistence needs) and do not legally restrict polygynous marriages, that is, when the group lives in a social and biological ecology that supports polygamy (Flinn & Low 1986). As noted by Betzig (1986), in each of the first 6 civilizations, socially dominant men had scores – sometimes hundreds – of wives and were generally ruthless in their elimination of sexual competitors, reproductive dynamics that are not restricted to large-scale states. In fact, it appears that across preindustrial societies about 30% of young men are killed as a result of male-male competition, most typically intergroup warfare (Keeley 1996). The net result is considerably more variability in the reproductive success of men than of women. For the Yanomamö Indians of Venezuela, for instance, about 2 out of 5 men have participated in at least one murder – typically in the context of intergroup conflict – and those who have killed have a higher social status than men who have not killed, along with $2\frac{1}{2}$ times as many wives and about 3 times as many children (Chagnon 1988). Keeley's (1996) review of warfare in preindustrial cultures indicates that the pattern found with the Yanomamö is very common and supports the position that male-male competition is and has been a very potent force in the dynamics of human reproduction.

R2. Intrasexual competition or the division of labor

The issue addressed in this section is whether the pattern of sex differences in spatial cognition and in other areas is better understood in terms of sexual selection or the sexual division of labor. In the target article, it was asserted that sexual selection, in particular male-male competition, was the most likely ultimate cause of the male advantage in certain spatial domains (Geary 1996t). As noted above, Frost, in contrast, suggests that the sexual division of labor, in particular hunting, might be the ultimate source of the sex differences in these spatial, and presumably other, domains.

Across species, differences in the physical size of males and females – physical dimorphisms – provide one indicator of the extent to which male-male competition has been involved in the evolution of sex differences. As an example, for monogamous primates – those showing relatively little direct male-male competition – there are few sex differences in physical size or in the pattern of physical development (Clutton-Brock et al. 1977; Leigh 1995). For primate species with polygynous or promiscuous mating systems – those with relatively intense male-male competition – there tend to be distinct physical differences between males and females. The most notable of these are dimorphisms in

body and canine size (Mitani et al. 1996), although during the course of hominid evolution, body size appears to have been a more important influence on male-male competition than canine size (Plavcan & van Schaik 1997; Wrangham & Peterson 1996). For extant primates, body size dimorphisms are consistently related to the intensity of male-male competition and not to the subsistence activities of the species (Mitani et al. 1996; Plavcan & van Schaik 1997), suggesting that many human sexual dimorphisms probably evolved by means of male-male competition rather than the sexual division of labor. There are, in fact, a number of other physical and behavioral sex differences that support this position.

By far the largest documented sex differences in physical capacities are for throwing distance and throwing velocity (Thomas & French 1985). As early as 4 to 7 years of age, more than 9 out of 10 boys show a higher throwing velocity than the average same-age girl, despite the fact that girls are physically more mature at this age (Tanner 1990). By 12 years of age, there is little overlap in the throwing-velocity distributions of boys and girls; the very best girls show throwing velocities that are comparable to the throwing velocities of the least skilled boys. The sex difference is somewhat larger for throwing distance. By 2 to 4 years of age, more than 9 out of 10 boys can throw farther than the average girl, and by 17 years of age only the very best girls can throw as far as the least skilled boys. At this age, men also have moderate to large advantages in visual acuity, throwing accuracy, and the ability to track and intercept (i.e., block) objects thrown at them; about 3 out of 4 males outperform the average female in these areas (Law et al. 1993; Velle 1987; Watson & Kimura 1991).

These sex differences are almost certainly related, at least in part, to differences in the structure of the skeletal system that supports throwing. For instance, relative to overall body height, boys have a longer ulna and radius (i.e., forearm), on average, than do girls – a difference that emerges in utero (Gindhart 1973; Tanner 1990). For neonates, the radii of 3 out of 4 boys are longer than the radii of the average girl, while for 18 year olds, the radii of more than 19 out of 20 men are longer than the radii of the average women. There are also sex differences in the timing and pattern of skeletal ossification in the elbow (Frisancho & Flegel 1983; Tanner 1990). These differences in skeletal structure and the associated throwing capacities, combined with a large male advantage in arm and upper body strength, indicate strong selection pressures for these traits in men. In fact, these sex differences are consistent with the view that the evolution of male-male competition in humans was influenced by the use of projectile (e.g., spears) and blunt force (e.g., clubs) weapons (Keeley 1996).

It might be argued, as Frost did, that these sex differences evolved as a result of the participation of men in hunting and not through direct male-male competition per se. Although it is not certain, a number of findings suggest that the sex differences just described (and many others, e.g., navigation skills; Geary 1995; 1996t; in press) evolved largely as a result of male-male competition rather than hunting.

First, although most of the physical sex differences described, such as throwing distance, are consistent with selection through both male-male competition and hunting, the male advantage in blocking thrown objects is only consistent with male-male competition. In other words, the

male advantage in tracking and dodging thrown objects would provide an advantage in the context of intergroup aggression that involved the use of projectile weapons but would not be necessary for skilled hunting.

Second, as described above, physical sex differences are not typically found in monogamous primates – those characterized by relatively little direct male-male competition – but are consistently found in species with polygynous or promiscuous mating systems – those characterized by relatively intense male-male competition (e.g., Clutton-Brock et al. 1977; Mitani et al. 1996). Moreover, physical dimorphisms are uncommon in socially monogamous species, even species with a sexual division of labor (Clutton-Brock et al. 1977; Clutton-Brock 1991). Human sex differences in sexual behavior and attitudes indicate that women are not as sexually promiscuous as chimpanzee and bonobo (*Pan paniscus*) females (Oliver & Hyde 1993), suggesting that the mating system of our recent ancestors was more likely to be polygynous than promiscuous. Either way, the pattern of human physical sex differences, combined with the high level of male mortality associated with male-male competition in preindustrial societies, suggest that there has been moderate to intense male-male competition throughout the course of human evolution.

Third, play appears to provide the practice necessary to develop the capacities needed for survival and reproduction in adulthood (Fagen 1981), and the pattern of human sex differences in play activities is consistent with the hypothesis that coalition-based male-male competition was an important feature of human evolution. Sex differences in rough-and-tumble play, or play fighting, are especially evident in species where conflict in adulthood is often resolved through physical aggression (Smith 1982). In polygynous primates, males engage in play fighting more frequently and more vigorously than conspecific females, a sex difference that is related, at least in part, to prenatal exposure to androgens (Collaer & Hines 1995; Wallen 1996). Although boys sometimes engage in play hunting, studies of the spontaneous play behavior of children reveal that boys more frequently organize themselves into groups and compete against groups of other boys and engage in this form of play three times more frequently than do same-age girls (e.g., Lever 1978).

More often, boys compete as members of teams and must simultaneously coordinate their actions with those of their teammates while taking into account the action and strategies of their opponents. Boys interviewed expressed finding gratification in acting as a representative of a collectivity; the approval or disapproval of one's teammates accentuates the importance of contributing to a group victory. (Lever, 1978, p. 478).

Most of these competitive games require many of the same physical, social, and cognitive capacities that are involved in coalition-based warfare. These games require (1) the formation of in-groups and out-groups, (2) the strategic coordination of the activities of in-group members as related to competition with the out-group, (3) the throwing of projectiles (e.g., a baseball) at specific targets, and (4) the tracking and reacting to the movement of these projectiles (Geary 1995). These activities can be exemplified by the game of baseball, played in modern America (and many other parts of the world) and by the game of Throw at Each Other with Mud, played by Sioux Indians 200 years ago (Hassrick 1964), among many other athletic games.

Throw at Each Other with Mud was a . . . gentle spring pastime where teams of boys attacked (each other) with mud balls which they threw from the tips of short springy sticks. Each boy carried several sticks and an arsenal of mud as he advanced. "It certainly hurt when you got hit, so you must duck and throw as you attack." Sometimes live coals were embedded in the mud balls to add zest to the game (Hassrick, 1964, p. 128).

Another skill often associated with intergroup conflict, as well as hunting, involves navigation in *unfamiliar* territory. Compared to those of girls, the play activities of boys more frequently involve larger play ranges and more exploration of these ranges. These activities, in turn, appear to facilitate the development of those cognitive skills associated with generating mental representations of the 3-dimensional topography of these environments, as noted in the original target article (Geary 1996t). For example, Matthews (1992) found that the play range of 8- to 11-year-old English boys covered from 1½ to 3 times the area of the play range of same-age girls. Whiting and Edwards (1988) report a similar sex difference for children in three separate groups in Kenya, as well as for children in Peru and Guatemala. Moreover, when exposed to an unfamiliar environment, boys are better able than girls to later draw an accurate map of this environment. In other words, boys are better than girls, on average, in mentally reconstructing the topography of an unfamiliar environment, specifically, retaining the general orientation and accuracy in the clustering of major features of the environment (e.g., routes; Matthews 1987).

None of this should be taken to mean that hunting was not an important influence during the course of human evolution; it probably was. In fact, to the extent that men differed in their hunting ability and to the extent that these individual differences influenced mating opportunities – as appears to be the case in many contexts – hunting was probably a feature of male-male competition (Symons 1979; see BBS multiple book review of *The Evolution of Human Sexuality: BBS3(2)* 1980). The real issue is whether the pattern of sex differences just described first emerged as a consequence of male-male competition or hunting.

My current view is that these and many other sex differences first emerged through male-male competition, and that the resulting male advantage in physical strength and aggression and the tendency of men to form coalitions was coopted for cooperative hunting; that is, these differences did not evolve through hunting but can nonetheless be used to hunt (Geary, in press). A similar pattern is found in the chimpanzee (Goodall 1986). Given the strong relation between physical sex differences and male-male competition in primates (Mitani et al. 1996), it is very likely that the male advantage in body weight, aggressiveness, and the tendency to form coalitions evolved in the chimpanzee as a result of male-male competition (Wrangham & Peterson 1996). These same capabilities, however, are often used in group hunts and result in male chimpanzees who are more efficient hunters than female chimpanzees. In the chimpanzee, meat obtained through hunting is often shared with estrous females and thus influences mating opportunities.

It seems likely that a similar pattern occurred in human evolution. Male-male competition resulted in sex differences in a number of physical, social (i.e., coalition formation), and cognitive (e.g., navigation) skills that could also be readily adapted to hunting. The male advantage in hunting probably created a sex difference in the foraging strategies of male and female hominids, as is found in the

chimpanzee (Goodall 1986). Gradually, males used meat obtained through hunting as a means of increasing their mating opportunities (as is again found with male chimpanzees) and females preferred mating partners who could provide this resource. Over time, provisioning as a form of mating effort appears to have evolved as a form of parental investment. Indeed, in many extant preindustrial societies, hunting is a form of male-male competition, as well as a form of parental investment, and skill at hunting is one criterion that women often use in their choice of mates (Hill & Hurtado 1996; Symons 1979).

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[Note: The letter 'r' before author's initials refers to the author's response references]

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