



News and views

Monomorphism, male-male competition, and mechanisms of sexual dimorphism

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Reconstructing sociosexual variables such as mating system and social organization from fragmentary fossils and other sources of data remains a major challenge in understanding the evolution of behavioral and morphological diversity within the primate order. Often, a particular mating system can lead to the evolution of novel behavior (e.g., “competitive” paternal care in tamarins; Garber, 1997) or contribute to the evolution of a particular morphology (e.g., relatively larger sagittal crests in male gorillas with large harems; Caillaud et al., 2008). Indeed, within paleoanthropology, numerous hypotheses concerning the evolution of major adaptive traits in humans—bipedalism, language, increased reliance on stone tool-use—often rely on a particular inferred mating system. For example, Lovejoy (1981) proposed that monogamy was the ancestral mating system in *Australopithecus afarensis* and from this went on to craft a creative hypothesis for the evolution of bipedalism. Similarly, Deacon (1997) suggested that male-female pair-bonding helped foster the evolution of language by allowing males and females to vocalize their monogamous commitment to other group members. Increased reliance on stone tools has also been linked to a particular mating system and social organization, with a concomitant reduction in canine size (e.g., Wolpoff, 1976). These examples, and others like them, suggest particular sociosexual behaviors and mating systems were a potential driver of the evolution of unique human characteristics within the order Primates. It is not surprising, then, that any hypothesized mating system inferred from fragmentary fossil data is likely to draw scrutiny; this has particularly been the case for hypotheses

regarding hominin mating patterns, as witnessed by the recent debates concerning levels of sexual dimorphism in *Australopithecus afarensis* (e.g., Reno et al., 2003, 2005; Plavcan et al., 2005; Lee, 2005; Scott and Stroik, 2006; Gordon et al., 2008). One of the reasons for the vigorous debate is precisely because the mating system—as determined from the pattern of dimorphism—has been tied to the evolution of so many other novel life history, sociosexual, and morphological traits in the human lineage.

In this commentary, I do not intend to review the statistical or methodological debates concerning how best to estimate dimorphism from fragmentary fossils. Rather, I want to say a few things about socioecological mechanisms that produce a relationship between mating system, male-male competition, and sexual dimorphism. I will focus on body mass, but my arguments would equally apply to other intrasexually selected traits, including canine size (dimorphism in body mass can also arise due to other non-sexually selected factors, but I do not address this issue here; see Lovejoy, 1981; Slatkin, 1984; Cartmill and Smith, 2009: 214–215). Plavcan (2000) has shown that measures of strong intrasexual competition (e.g., mating system, high operational sex ratio, male-male aggression) correlate with polygyny. Thus, inferring polygyny from strong levels of sexual dimorphism is justifiable, however “...the converse—the absence of dimorphism—does not necessarily indicate monogamy, polyandry, or an absence of intense male mate competition” (Plavcan, 2000: 340).

My starting point is where Plavcan left off. I want to discuss two mechanisms that can lead to a disjunction between mating system, mating competition, and sexual dimorphism. While my discussion is based on the socioecology of extant primate groups, it is particularly relevant to the assessment of sexual dimorphism in the fossil record of primates. To be clear, my goal here is not to review *all* of the mechanisms that can hinder the evolution of sexual dimorphism in light of male-male competition. I only want to touch upon two socioecological mechanisms—sexually-selected stabilizing selection and extra-group reproduction—that are, for the most part, not discussed with respect to the evolution of size differences (or lack thereof) between primate males and females. In particular, I do not discuss the genetic (or phylogenetic) correlation between the sexes as a factor that can hinder sexual dimorphism, as these models have been proposed and/or discussed elsewhere (e.g., Lande, 1980; Leutenegger and Cheverud, 1982; Slatkin, 1984; Cheverud et al., 1985; Fairbairn, 1997; Lawler et al., 2005; Gordon, 2006a,b). Moreover, the factors that I discuss can operate

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independent of any significant genetic correlation between the sexes, as discussed below. While some of the discussion below might seem obvious, to my knowledge there has been no formal discussion of these two factors in terms of their influence on primate sexual dimorphism.

When does intrasexual selection on males lead to sexual dimorphism?

The only means through which sexual dimorphism is achieved via sexual selection is when intrasexual *directional* selection acts on one sex and not the other in the context of mate acquisition. Of course, directional selection is only one of the many types of selection that can change the shape and/or position of a distribution of trait values (e.g., a set of body mass values among males). Formally, directional selection acts on the first moment (the mean) of a distribution, and pushes the mean value of the distribution to larger (positive directional selection) or smaller values (negative directional selection). Selection can also act on other moments of the phenotype distribution, such as the variance, or higher moments such as skewness (Rice, 2004). In primates, the evolution of sexual size dimorphism usually occurs when directional selection acts to increase the mean phenotype of a male relative to that of a female. The underlying functional relationship between fitness and phenotype in this case is attributed to the fact that relatively larger body mass and size is associated with the ability to produce relatively greater muscle forces and other associated biomechanical advantages that can be used during male-male competition. However, the environmental context of male-male competition is likely to influence whether larger size translates into acquiring more mates.

As an example, consider Verreaux's sifaka. These creatures are arboreal, gregarious, folivores that reside in social groups with roughly equal adult sociometric sex ratios. Verreaux's sifaka are characterized by promiscuous mating and intense male-male competition. Mating competition can be divided into two basic types: 1) *Agonistic episodes* in which male sifaka primarily bite, cuff, or grab their opponents during combat, and this is accompanied by lunging, threat displays, and a variety of dominant and submissive gestures between interactants in the trees or on the ground; male combat can be both fierce and bloody; and 2) *Endurance episodes*, which involve sustained periods of arboreal chasing and lunging between adult males who may engage in these interactions until visibly exhausted (see Richard, 1992; Lawler et al., 2005). Given the appreciable degree of male-male competition and the multi-male/female mating system, one would expect to see appreciable levels of dimorphism in body mass and canine size. However, this species is monomorphic in body size (Fig. 1A) and canine size (not shown). Adult males are not significantly larger than adult females. Why is this the case? The distribution of male fertility as function of body mass for adult males is shown in Fig. 1B. As one can see, the fitness function is concave, indicating the operation of stabilizing selection acting on male body mass. The functional basis for this type of selection begins to make sense considering the nature of arboreal mating competition: selection may favor an overall optimal male size for quick movements in the trees; larger males are likely less agile, while smaller males are likely less competitive (Lawler et al., 2005).

Crow (1958) noted that the standardized variance in relative fitness is proportional to the strength of selection. Thus, large variations in male reproductive success (standardized by the mean reproductive success squared) result in lots of opportunity for sexual selection. In this population, there is large variation in male reproductive success (i.e., male fitness) (Lawler et al., 2005), and this variation in relative fitness covaries with the squared deviations of body mass from the mean body mass (e.g., Fig. 1). That is, intrasexual selection operates on the variance in male body mass

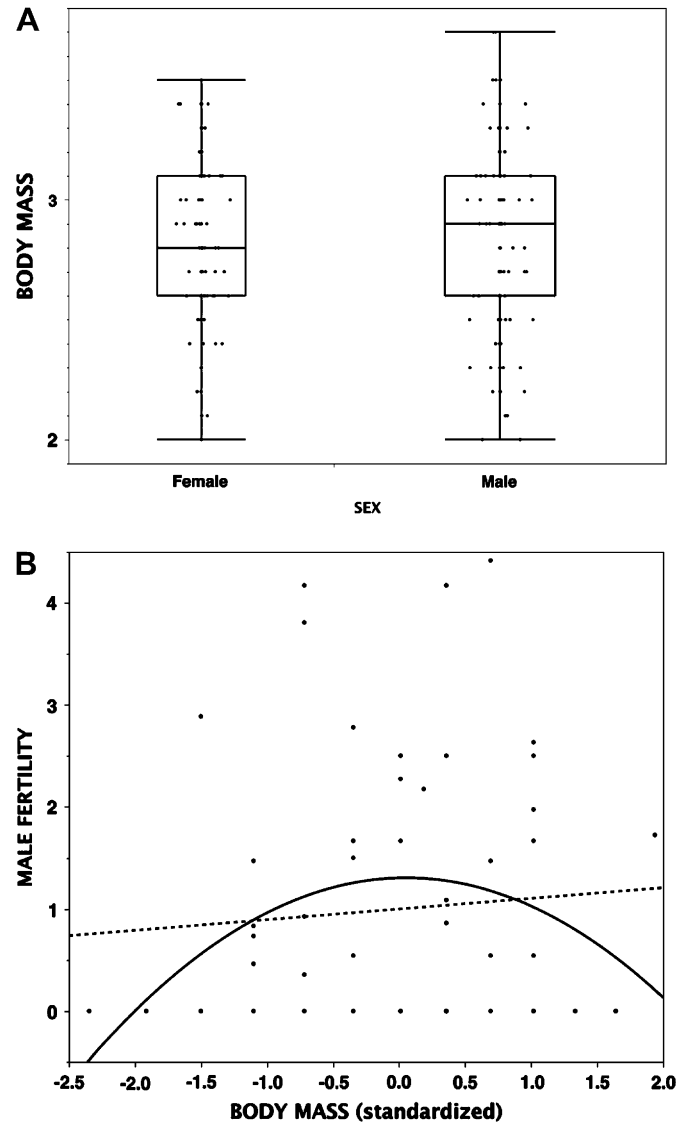


Figure 1. Box and whisker plots of adult male ($n = 136$) and adult female ($n = 108$) body mass (A) and the relationship between male fertility and male body mass (B). In A, the mean of adult male and female body masses is not significantly different (t -test = 0.104, $df = 241$, $p = 0.917$). In B, stabilizing selection is operating on body mass as shown by the significant fit of a 2nd order polynomial ($\text{body mass}^2 = -0.31$; $p = 0.028$); the linear slope is not significant ($p = 0.84$).

and not the mean. In short, these data provide empirical support for the idea that stabilizing selection acting on males mitigates selection for large male body size, in spite of multi-male/female mating and fierce male-male competition. Selection favors intermediate-sized males, perhaps due to their agility advantage over larger and smaller males during arboreal locomotor contests (Lawler et al., 2005). This process will operate independent of the strength of the genetic correlation between the sexes because the response to selection will generally not involve large changes in average body size in males and females, only the variance in body size will be affected. Of course, a full analysis of sexual dimorphism should document patterns of natural selection and sexual selection acting on both sexes, since it is also necessary to understand the selective pressures that act on female body mass (Plavcan, 2001); however, Shuster and Wade (2003: 18–29) showed that the strength of selection acting on males during mating competition is theoretically much stronger and acts faster than other types of selection

acting on females, as well as natural selection acting on males during non-mating episodes.

Sifaka provide just one empirical example of what is possible. Any scenario in which intermediate-sized males have a reproductive advantage over other males in the context of mate acquisition will result in intrasexual stabilizing selection. As an example, some researchers have suggested that *A. afarensis* retained some degree of arboreality (e.g., Susman et al., 1984); in this regard, selection for intermediate body mass might be favored during male-male competition assuming, of course, that such competition took place in the trees. Other researchers have suggested a different pattern of locomotion in *A. afarensis* that indicates terrestriality and generally precludes “agile” arboreality (e.g., Ward, 2002; Lovejoy, 2005a,b), but this does not negate my more general point: if intermediate-sized males are favored during mating competition whether in the trees or on the ground, then no directional selection will act on males and males cannot evolve a larger size than females. For example, terrestrial grappling in australopithecines may favor short limbs (as opposed to long limbs) and thus limit the amount of directional selection on limb length, and by implication, body size (Carrier, 2007). Finally, it is important to note that *A. afarensis* or any other primate species could manifest dimorphism due to differential exploitation of niches, as noted in Lovejoy (1981: endnote 85), but this possibility is peripheral to my general point regarding male mating competition. Recent studies concerning avian mating competition have begun to consider agility and maneuverability as intrasexually-selected traits (Székely et al., 2004; Raihani et al., 2006); continued exploration of this idea in primates will go a long way towards teasing out the relationship between male-male competition and sexual dimorphism (e.g., Lindenfors, 2002). Independent of speculations about the nature of male-male combat in ancestral primate lineages, the empirical evidence presented above reveals one mechanism that creates a disjunction between dimorphism levels and male-male competition. Thus, one potential explanation for monomorphism in light of intrasexual competition is the operation of stabilizing selection on males.

What effect do extra-group fertilizations have on the opportunity for sexual selection?

Genetic studies have revolutionized the analysis of mating systems. Such studies have provided a realistic picture of the degree of reproductive skew that takes place within a population. As noted above, the variance in relative fitness is proportional to the opportunity for selection (e.g., Crow, 1958; Shuster and Wade, 2003). Given this, it is important to quantify patterns of reproduction in wild populations in order to determine when selection can act. A mating system characterized by no variance in relative fitness among males will not provide any opportunity for selection to act on males. A common pattern, first noticed in birds (Gowaty, 1985), is that extra-pair males often sire offspring with females who are not their social mate. For gregarious primates, this phenomenon translates into extra-group fertilizations (EGFs) where some males leave their resident social group (if they have one) and mate with females of a nearby social group (Lawler, 2007). The effect that extra-group reproduction has on the opportunity for sexual selection to occur varies by circumstance. However, a few simple rules emerge. If there is a positive covariation between male mating success within a social group as well as outside a social group, this will increase the opportunity for sexual selection. In other words, if males sire offspring both within their own group as well as in an adjacent group (thereby co-opting the mates of some other male), then reproductive skew in the population is increased and so is the opportunity for sexual selection. However, a negative covariation between mating success within a group and outside a group

(i.e., males who are unsuccessful at mating in their own group but successful at obtaining EGFs) will reduce reproductive skew, and thus reduce the opportunity for sexual selection (Webster et al., 1995; Jones et al., 2001). I want to focus on cases where EGFs result in a reduced opportunity for intrasexual selection (note that I am not stating that EGFs eliminate the opportunity for selection).

Consider a hypothetical scenario of a primate population consisting of 25 groups, with four adult males and four adult females in each group (see Fig. 2). The variance in reproductive success, as well as the covariation between reproduction and body mass (i.e., selection on body mass), is calculated below with respect to different scenarios of mating and reproduction. Under total polygyny, male M_A mates and sires offspring with the four females, while the other males have zero reproductive success. If this situation holds across all 25 groups, then the variance in male reproductive success is 3.03. Under the conditions of partial polygyny, the M_A male mates and sires three offspring with three females, while the M_B male mates and sires an offspring with one female. Across all 25 groups, the variance in reproductive success is 1.52. Finally, consider a case of partial polygyny with the addition of extra-group reproduction. In this scenario, 13 groups experience partial polygyny (as just described), while 12 groups experience EGFs from non-resident males (Fig. 2). Across all 25 groups, the variance in reproductive success is 1.01. In short, the variance in reproductive success (which approximates the standardized variance, since the mean reproductive success across all groups is around 1) decreases from total polygyny to partial polygyny to partial polygyny + EGFs.

By assigning some body mass values to each male it is possible to examine the covariation between reproductive success and body mass. Here I make the assumption that body mass has something to do with reproductive success, thus body mass experiences directional selection. In this scenario, M_A males have a body mass of 102 (arbitrary units), M_B males have a body mass of 100, and M_C males have a body mass of 98. This assignment gives a slight advantage to M_A males, who, under total polygyny, do all the mating. Looking at the covariation between body mass and reproductive success across the three mating scenarios described above, the values decrease from 2.53 (total polygyny), to 2.02 (partial polygyny), to 1.26 (partial polygyny + EGFs). In short, the strength of directional selection acting on male body mass is reduced by about 50% due to partial polygyny + EGFs.

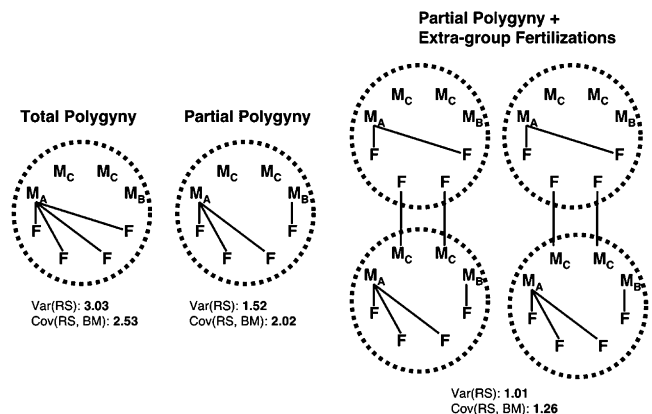


Figure 2. Variance (Var) in male reproductive success (RS) and covariance (Cov) of male reproductive success and body mass (BM) across 25 groups under three different mating systems: total polygyny, partial polygyny, and partial polygyny with extra-group fertilizations. Each group has four males and four females. See text for discussion.

Several consequences regarding total polygyny versus partial polygyny + EGFs emerge from this discussion with respect to the evolution of sexual dimorphism. Assume that female body mass is initially 100 units and is not under selection, and further, that body mass itself is uncorrelated both between the sexes and with other traits. Under these assumptions, it is possible to calculate the ratio of male to female body mass across each set of 25 groups after 100 generations. The mean body mass for the 100 males across 25 groups is 99.5. Thus, male body mass also starts out around 100 units. The covariance value for body mass and partial polygyny + EGFs can be expressed as a least squares regression slope, which is a measure of the strength of directional selection; this value is 0.45. Assuming that body mass is 50% heritable, this means that male body mass will change 22.5 units in 100 generations. Contrast this with the situation of total polygyny, where the regression slope is 0.90. Under total polygyny, male body mass will increase by 45 units in 100 generations and the ratio of male to female body mass will be 145 to 100. In contrast, under partial polygyny + EGFs, male body mass will increase 22.5 units and hence the ratio of male body mass to female body mass will be 122.5 to 100. Note that if there was a high genetic correlation between the sexes, then female body mass would track male body mass (also resulting in no dimorphism), until it is offset by other selective pressures acting on females (Lande, 1980). Of course, I built-in the fact that directional selection will act on male body mass, but my point is simply to illustrate the diluting effect that EGFs can have on the strength of sexual selection acting on males.

With respect to gregarious species, the behavioral mechanisms that create reproductive skew are often considered to occur within the social group, not outside it. Increasingly, numerous studies have documented the effects of EGFs on reproductive success within a population (Webster et al., 1995; Jones et al., 2001; Shuster and Wade, 2003; Lawler, 2007; Ostner et al., 2008). These studies reveal that EGFs have varying effects on the distribution of reproductive success of males. In some cases they increase reproductive skew and in other cases they reduce it. Males who mate both within their resident group as well as in adjacent groups will enhance the variation among male reproductive success. However, female-biased sex-ratios within groups can lead to a trade-off between a male's ability to pursue EGFs as well as guard within-group females. In such cases, a negative covariation between within-group fertilizations and EGFs can occur, resulting in a decreased opportunity for selection (Webster et al., 1995). Negative covariation can also occur in groups with equal sex-ratios, whenever a male's social mates are mated by non-resident males (Webster et al., 1995; Jones et al., 2001). The behavioral and ecological circumstances that create opportunities for EGFs include a high degree of home-range overlap, little costs to monitoring females in an adjacent group, and female preference for neighboring males (Lawler, 2007).

Prior to the simulation studies of Webster et al. (1995) and Jones et al. (2001), it was assumed the extra-group fertilizations would always increase the variance in reproductive success among males. As Jones et al. (2001) noted, this conjecture was based on the assumption that monogamy is the prevailing mating system (since the authors were often studying birds); under monogamy, reproductive success is generally equal for all males and thus there is no variation in reproductive success. Given an equal sex ratio, any deviations from monogamy owing to some monogamous males engaging in EGFs will result in variation among male reproductive success. This point is rarely considered when looking at the mild levels of dimorphism among ostensibly monogamous primates—deviations from monogamy via EGFs by males can increase the opportunity for intrasexual selection to occur.

Two points emerge from this discussion: 1) extra-group reproduction has the potential to greatly diminish the opportunity for

intrasexual selection. In the simple case outlined above, it is possible to have a multi-male/multi-female mating system, but given the effects of EGFs, the morphological “signal” of sexual dimorphism will be reduced; and 2) If monogamy is the prevailing mating system and some males obtain EGFs within this system, this will increase the opportunity for intrasexual selection, and one possible result is more sexual dimorphism than expected given the pair-bonded mating system (this latter point assumes that the traits used to obtain EGFs are things like body mass and canine size). In both of these cases, EGFs disrupt the “expected” relationship between mating system and levels of sexual dimorphism. Thus, one potential explanation for reduced dimorphism in multi-male groups is extra-group reproduction. This explanation relates to a broader point made by previous researchers that the mating system and social organization of a species is not always a good proxy for the strength of intrasexual selection (e.g., Plavcan, 2001). However, the focus on reproduction both within and among social groups (i.e., the population-wide pattern of reproduction) serves to re-emphasize that the population is the proper level of analysis regarding microevolutionary change, despite the fact that the social group is often the unit of analysis in most behavioral studies of wild primates.

Conclusions

To be sure, there are plenty of “what-ifs” in this commentary (e.g., what if females don't mate with extra-group males? What if some males experience stabilizing selection and some experience directional selection? What if the pattern of EGF differs from that outlined here?). These “what-ifs” need to be determined empirically and will vary from species to species; that said, I hope it is clear that additional factors should sometimes be considered when inferring mating systems on the basis of morphology alone. Further, although I have not focused on the role of females in this commentary, it is reasonable to ask: what role does female choice play in the above scenarios? The simplest answer is that, on the whole, the underlying process—female choice or male-male competition—does not necessarily matter. That is, if intermediate-sized males vanquish their sexual rivals during fierce competition (i.e., intrasexual selection) or they are proactively sought by females in the absence of male-male competition (i.e., intersexual selection), no sexual dimorphism will result because directional selection does not increase the mean body mass in males relative to females. In the context of extra-group reproduction, the degree to which the opportunity for directional sexual selection is tempered will depend on the covariation between mating success among males within their resident group and outside their resident group. The reasons why females choose particular within-group or extra-group males is an area of active investigation; however, it is worth noting that females will choose mates that maximize *net* fitness, hence extra-group males might be chosen for mates if they provide indirect benefits (i.e., good genes), even if this means the females incur reduced survivorship or fecundity in their pursuit of these males (Kokko et al., 2003). The relationship between male-male competition and female choice is reviewed in Wong and Candolin (2005).

Investigating the ecological and social factors that produce a particular mating system remains a major focus of primate socioecology. However, far from being an exercise restricted to extant primates, mating systems have the power to shape evolutionary trajectories in primates lineages and thus alter the course of primate evolution; as such, it is important to consider every possible socioecological mechanism that can influence our ability to reliably assess sexual dimorphism in fossil primates as well. Both stabilizing selection as well as EGFs (acting in concert or separately) can create patterns of morphology that—if fossilized and later

recovered for analysis—can lead to a mischaracterization of the ancestral mating system.

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