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The human operational sex ratio: Effects of marriage, concealed ovulation, and menopause on mate competition

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ABSTRACT

Among mammals, male–male competition for sexual access to females frequently involves fighting. Larger body size gives males an advantage in fighting, which explains why males tend to be larger than females in many species, including anthropoid primates. Mitani et al. derived a formula to measure the operational sex ratio (OSR) to reflect the degree of male–male competition using the number of reproductively available males to females who are cycling and capable of conceiving. The OSR should predict the degree of sexual dimorphism in body mass—at least if male–male competition involves much fighting or threatening. Here, we use hunter-gatherer demographic data and the Mitani et al. formula to calculate the human OSR. We show that humans have a much lower degree of body mass sexual dimorphism than is predicted by our OSR. We suggest this is because human competition rarely involves fighting. In human hunter-gatherer societies, differences in the ages of marriage have an impact on competition in that the age of males at first marriage is younger when there is a lower percentage of married men with two or more wives, and older when there is a higher percentage of married men with two or more wives. We discuss the implications of this for females, along with the effects of two key life history traits that influence the OSR, concealed ovulation and menopause. While menopause decreases the number of reproductively available females to males and thus increases male–male competition, concealed ovulation decreases male–male competition. Finally, we discuss the importance of mostly monogamous mate bonds in human evolution.

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Introduction

Sexual selection theory involves two basic mechanisms originally proposed by Darwin (1871): intrasexual selection (e.g., male–male competition) and intersexual selection (e.g., female mate choice). Sexual selection theory has since developed to reveal a wide variety of mechanisms such as cryptic female choice, haplodiploidy, and sequential hermaphroditism to name but a few (Cronin, 1991; Charnov, 1993; Andersson, 1994; Kokko et al., 2002; Lindfors, 2002; Carnahan and Jensen-Seaman, 2008). How sexual selection operates in humans is a popular but contentious topic (Anderson et al., 1999; Penton-Voak et al., 1999; Puts, 2010; Harris, 2011). Intersexual selection in humans has been investigated extensively through the study of mate preferences. On the other hand, there has been much less systematic analysis of intrasexual selection in humans, particularly documenting frequencies of

dyadic agonistic conflict. Since humans are primates it is useful to compare our mating patterns to those seen in other primates, especially apes and monkeys (anthropoids). Here we focus on intrasexual competition in humans in comparison with other anthropoids using a formula developed to measure the strength of sexual selection across species.

Male–male competition in primates can take various forms including but not limited to: fighting and mate-guarding, sperm competition, displaying ornaments, scramble competition, or helping to provision offspring and/or mates (Petrie et al., 1991; Andersson, 1994; Birkhead, 2000; Weir et al., 2011). Dyadic agonistic competition involves the resolution of conflicts through physical violence or threats of violence. This would certainly apply to a male gorilla ousting a previous silver back. Sperm competition, in which each adult male may copulate with an estrus female, is typical of chimpanzees (*Pan troglodytes*; Wroblewski et al., 2009). There can also be scramble competition, in which female dispersal favors males who disperse in search of mates rather than mate guard, as in Bornean orangutans (*Pongo pygmaeus*; Harrison and Chivers, 2007). Among several species of South American

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monkeys, males compete by helping provision their long-term mates and offspring (Garber and Leigh, 1997).

Male–male agonistic competition appears to be the dominant mechanism operating in anthropoids, and it is associated with sexual dimorphism in body mass and canine tooth size (Clutton-Brock et al., 1977; Dixon, 1998; Plavcan, 2001; Kappeler and van Schaik, 2004). Mate choice by females, male coercion of females, and female counterstrategies also operate (Heistermann et al., 2001; Harrison and Chivers, 2007). The degree to which body size plays a role in the outcome of contests and access to mates will determine how sexual selection should be associated with size dimorphism. When male–male competition for access to mates involves fighting (or mate-guarding) we should expect males to be considerably larger than females (Clutton-Brock, 1985; Mitani et al., 1996; Kappeler and van Schaik, 2004).

Early attempts to measure the relationship between sexual selection and sexual dimorphism in anthropoid primates assumed that the adult sex ratio was proportional to the strength of sexual selection, reasoning that competition should be proportional to the number of females per male available. These early attempts failed to make a convincing case that more competition resulted in greater sexual dimorphism in body mass when monogamous species were removed and phylogenetic relatedness taken into account (Clutton-Brock et al., 1977; Alexander et al., 1979). The number of adult males to adult females fails to capture the actual number of potential mating opportunities for each male because some adult females are pregnant or nursing and not cycling. By counting only those females that are capable (or appear to be capable) of conceiving at any given time, a more accurate measure of the operational sex ratio (OSR) can be obtained (Kvarnemo and Ahnesjö, 1996).

Using the number of reproductively available males to reproductively available females, the degree to which males were larger than females was found to be greater in anthropoid primate species with a higher OSR (Mitani et al., 1996). When females gestate and nurse for several years (have a long inter-birth interval) there should be more competition among males for those few females that are ready to mate. In addition, when females conceive within a few estrous cycles and there is a brief estrous period there will be fewer mating opportunities and more male–male competition. Mitani et al.'s OSR formula was tested on anthropoid primates, but their sample did not include humans. To the best of our knowledge this is the first attempt to calculate the human OSR using the Mitani et al. formula to see if it predicts our degree of sexual dimorphism in body mass.

We have three main aims: 1) to analyze how well the OSR might predict human body size dimorphism, or age ranges of those in the mating pool, 2) to measure the effects of two rare and important human life-history traits, menopause and concealed ovulation, on the OSR and their broader consequences, and 3) to investigate how long-term monogamous or polygynous mate bonds alter the nature of human mate competition.

Calculating the OSR

The formula Mitani et al. (1996) derived to calculate OSR, or the number of reproductively available males to reproductively available females for non-seasonal breeders, is:

$$\frac{m * B * 365}{f * \sum_{i=1}^n c}$$

where m is the number of males in the reproductive mate pool, B is the duration of birth intervals in years, 365 equals the days per year, f is the number of females in the reproductive mate pool, n the

number of estrous cycles females experience before conception, and c is the duration of estrus in days.

Here we investigate the human OSR using life history and demographic data. Because we want to explore the traits that were selected for in the past, we use hunter-gatherers who have natural fertility and little or no access to medicine, and who live on a diet of wild foods that must be acquired at considerable energetic costs. Generally, for individuals within different foraging societies, we do not know exactly how many days are spent in estrus by each female, or the number of cycles to conception, and length of birth intervals. Instead, we use data on the mean forager values for the duration of the birth interval (B), duration of estrus (c), and the number of estrous cycles females experience before conception (n) in place of individual-level values summed, as in the Mitani formula. We use our Hadza demographic data to know how many males (m) and females (f) are reproductively active. Our formula is therefore:

$$\frac{m * B * 365}{f * c * n}$$

Our simplified formula produces almost the exact same values for species in Table 1 of Mitani et al. (1996; see our Table 1).

To calculate the OSR we must first decide what ages to use in the formula for m (the number of adult males) and f (the number of adult females). In many species, this is not such a problem because individuals can be observed copulating, but in humans since we cannot observe who is copulating it is not so straightforward. Fortunately, this dilemma results in two different possible ways of considering the human reproductive span, which turn out to be especially useful for our goal here: a) when individuals are capable of reproducing (the physiological span) and, b) when individuals are engaged in mating as indexed by marital ages (the behavioral span). In the case of humans, we notice that some individuals who are capable of reproducing are not doing so, for example, many young males who have reached spermatarche. Then there are the females who have reached the age of menopause, something we would not have to deal with in other primate species. Using both the physiological and behavioral spans helps to illuminate how competition works to shape physiological markers as well as how it constrains some who could technically reproduce but have less competitive ability to do so.

We calculate the OSR using ages that appear to best capture adults that are reproductively active, the tertiary sex ratio (Box 1).

Table 1
OSR of human hunter-gatherers vs. some primates from Mitani et al. (1996)

Species	OSR	Social group mating system
Gelada (<i>Theropithecus gelada</i>)	Mitani et al. = 12.46 Our calculation = 12.34	MM, MF with mate bonds
Savanna baboon (<i>Papio anubis</i>)	Mitani et al. = 7.01 Our calculation = 7.02	MM, MF, no mate bonds
Orangutan (<i>Pongo pygmaeus</i>)	Mitani et al. = 55.02 Our calculation = 55.22	Mostly solitary
Gorilla (<i>Gorilla gorilla</i>)	Mitani et al. = 83.75 Our calculation = 83.79	Promiscuity
Chimpanzee (<i>Pan troglodytes</i>)	Mitani et al. = 4.54 Our calculation = 4.46	UM, MF polygynous bonds
Human (<i>Homo sapiens</i>)		
Behavioral OSR:		
$\frac{178 * 3.25 * 365}{178 * 23 * 6} = 24,564$	8.6, Behavioral OSR	MM, MF mostly monogamous bonds
Physiological OSR		
$\frac{242 * 3.25 * 365}{178 * 23 * 6} = 287,073$	11.7, Physiological OSR	

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