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Evolutionary Aspects of Aggression: The Importance of Sexual Selection

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ABSTRACT

Aggressive behaviors in animals, for example, threat, attack, and defense, are commonly related to competition over resources, competition over mating opportunities, or fights for survival. In this chapter, we focus on aggressive competition over mating opportunities, since this competition explains much of the distribution of weaponry and large body size, but also because this type of competition sheds light on the sex skew in the use of violence in mammals, including humans. Darwin (1871) termed this type of natural selection, where differences in reproductive success are caused by competition over mates, sexual selection. Not all species have a pronounced competition over mates, however. Instead, this aspect of sociality is ultimately determined by ecological factors.

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In species where competition over mates is rampant, this has evolutionary effects on weaponry and body size such that males commonly bear more vicious weapons and are larger than females. A review of sexual selection in mammals reveals how common aggressive competition over mating opportunities is in this group. Nearly half of all mammal species exhibit male-biased sexual size dimorphism, a pattern that is clearly linked to sexual selection. Sexual selection is also common in primates, where it has left clear historical imprints in body mass differences, in weaponry differences (canines), and also in brain structure differences. However, when comparing humans to our closest living primate relatives, it is clear that the degree of male sexual competition has decreased in the hominid lineage. Nevertheless, our species displays dimorphism, polygyny, and sex-specific use of violence typical of a sexually selected mammal. Understanding the biological background of aggressive behaviors is fundamental to understanding human aggression.

I. INTRODUCTION

Why does aggression exist in nature? Darwin (1859, 1871) pointed out that the ultimate explanation for *any* trait has to be found in the effect that it has on survival and reproduction. From an evolutionary standpoint, individuals should thus mainly be expected to fight over resources, for survival and for mating opportunities, because these are what mainly affect how many genes that individual contributes to the gene pool of the coming generation. Another prediction is that the amount of aggression displayed in the encounters should increase with increasing value of the fought-over resource. Aggressive behaviors are associated with costs, and individuals are simply expected to take higher risks, that is, pay potentially higher costs, with increasing potential gains. In this chapter, we focus on aggression over mating opportunities—sexual selection—in mammals in general and in primates in particular. We focus on sexual selection because evidence suggests that it is the primary reason why animals fight with conspecifics and because it is the most likely explanation of some aspects of human aggression, such as why males tend to be more aggressive than females.

An important point about evolutionary explanations is the philosophical distinction between proximate and ultimate explanations. Take sex, for example. Do humans have sex because it feels good or in order to have children? Most sexual intercourse in current society probably has very little to do with actual procreation; on the contrary, there are many birth control methods available to make it possible to have sex without this resulting in a pregnancy. Despite the fact that protected sex happens “because” it feels good, the evolutionary explanation of sexual intercourse is “because” of procreation. This is where the crucial distinction between proximate and ultimate explanations comes into play. A proximate explanation is the explanation that is closest to the event that is to be explained. The higher, ultimate explanation is instead the deeper reason for why something happened.

In biology, the division in ultimate and proximate explanations has been extended to what is usually termed "Tinbergen's four questions" (Tinbergen, 1963); the four potential explanations of any behavior: (1) survival value or adaptive function, (2) phylogenetic history, (3) individual development, and (4) causal mechanisms such as hormonal mediation of behavior. The first two of Tinbergen's questions are ultimate whereas the latter two are proximate. To fully shed light on a biological phenomenon all four types of questions are needed and the answers complement each other. However, in this chapter, we focus entirely on ultimate, evolutionary answers to the question of why aggression exists and takes the form it does.

II. SEXUAL SELECTION

Natural selection is all about who gets to reproduce and who does not (Darwin, 1859). A central aspect of getting to reproduce is to survive until the opportunity to reproduce arises and to gain access to resources enabling you to do so, but another important aspect concerns direct competition in connection with the reproductive act itself. Darwin termed this second aspect "sexual selection": differences in reproductive success caused by competition over mates (Darwin, 1871).

Why did Darwin give a specific name to one part of natural selection: why not just stick to the umbrella term "natural selection"? Darwin had noted that there often seems to be a conflict of interest between traits that increase survival and traits that increase reproduction; many traits that give an advantage in reproduction have negative consequences for survival. A male peacock's large tail feathers are a prime example of such a trait. How can such a long colorful tail evolve when it makes the bearer simultaneously more visible and less adept at escaping predators? When thinking about this problem before having formulated the theory of sexual selection, Darwin wrote in a letter to his friend, the botanist Asa Gray, the famous line: "The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" (Darwin, 1860).

To clarify this second aspect of natural selection—selection that has to do with competition over mates—Darwin wrote a follow-up to "On the Origin of Species" (1859), "The Descent of Man and Selection in Relation to Sex" (1871). In this book, Darwin points out that there are two potential kinds of competition over mates, two forms of sexual selection. Either individuals of one sex (usually males) can fight with each other over mating opportunities (*intra*sexual selection) or, alternatively, individuals of one sex (usually females) can choose individuals of the other sex on the basis of some trait (*inter*sexual selection).

This second form of sexual selection is the explanation of the peacock's tail: peahens simply find it attractive and prefer to mate with the peacocks with the most elaborate tail. Further, the tail provides information on the genetic quality of the male—it is an honest signal (Petrie, 1994).

It is noteworthy that it was the idea of intersexual selection that caused the most furious debate in Darwin's time, foremost because it was judged utterly questionable that female aesthetical judgment could be the ultimate explanation for so many conspicuous characters in nature. However, partner choice is a more peaceful process than direct competition within a sex. Thus, because it induces so much aggression in nature, we focus in this chapter mainly on *intra*sexual selection; physical competition over mating opportunities. It should be pointed out that the two forms of sexual selection sometimes occur simultaneously, for instance, in lekking species where females choose as mating partners the winning males from physical competition (Andersson, 1994).

Sexual selection arises when one sex limits the reproductive success of the other. Most often it is females who are the limiting resource for the reproductive success of males due to a fundamental asymmetry between males and females in their defining characteristic, their gametes. Males are designated by their smaller, mobile gametes, called sperm cells. Females are designated by their larger, nutrition-carrying gametes, called eggs. Males can make more gametes than females, simply because sperm are energetically cheaper to make than eggs; thus, there is a fundamental reproductive difference between males and females. This initial asymmetry has consequences. Making sperm is cheap and easy, so this is not what limits the reproductive possibilities of males. Making eggs, on the other hand, is much costlier. Thus, sexual selection commonly—but not exclusively—affects males, because given an equal sex ratio, male reproductive success is limited by access to matings with females. Conversely, female reproductive success is limited by the number of eggs she can produce (Andersson, 1994). This sex specificity is so common that the reverse pattern, termed sex role reversal, is subject to intense interest from evolutionary biologists when it occurs (e.g., Ralls, 1976; Vincent *et al.*, 1992).

An important experimental verification of this theoretical insight was made by the geneticist Bateman (1948), who experimented on fruit flies. Bateman noted a pattern demonstrating that the number of offspring a male fruit fly can have is directly correlated with his number of matings. The same does not hold true for females, who have roughly the same number of offspring no matter how many times they mate (as long as it is at least once). This pattern is termed Bateman's principle. Later studies, however, have documented that a number of exceptions to Bateman's principle exist in nature (Birkhead, 2001). Individuals are not only sperm and eggs; there are a number of additional factors that need to be incorporated to understand what is going on in different species. In mammals, especially, one needs to incorporate two unique adaptations. While the energy investments in the mammal zygotes differ only marginally in relation to the body mass of most mammals, the cost to mammal females greatly exceeds that to males due to effects of pregnancy and lactation. This energy investment inequality has existed since the origin of the class Mammalia, 125 million years ago.

There are some exceptions to the general mammalian pattern, however. For instance, some mammal babies are so expensive to bring up to maturation that both sexes have to partake in the upbringing for it to be possible. In these species, where males and females work together to guard and rear the young, intrasexual competition occurs just prior to pair formation. In these species, the two sexes are usually morphologically alike. In other mammal species, however, competition between males over mating opportunities is fierce. In some species this affects the entire social life of the species, in that males physically exclude other males from the group. The result is a social system akin to a harem structure, with immature males roaming outside the social gathering or forming bachelor groups.

The importance of sexual selection in understanding aggression in mammals is most clearly illustrated by the presence and absence of weaponry. For example, male ungulates are commonly equipped with horns while females are not. Horns would be a good weapon to fend off predators, especially when you need to defend your young, or to fight off conspecific competitors. But most young are cared for by single mothers; the fathers—who have the weapons—are absent. Ungulate horns are commonly ready just in time for rutting season and are then shed (e.g., deer). Instead of predator defense, male ungulates mainly use their horns to fight each other (Caro *et al.*, 2003; Stankowich and Caro, 2009). A similar case can be made for the large, sharp canines of primates (Thorén *et al.*, 2006), and large body size in male mammals in general (Lindenfors *et al.*, 2007a). Such sex-skewed distribution of size and weaponry, in combination with observations of fierce aggression, is what enables us to assert that most serious conflict and aggression in mammals is over mating opportunities.

Sexual selection acting primarily on one sex may have indirect but pronounced consequences for the relationship between the sexes. Thus, direct conflicts between males sometimes result in conflicts of interest between males and females. Early thoughts on this issue (Parker, 1979, Trivers, 1972; Williams, 1966) have received much empirical support (Arnqvist and Rowe, 2005), and it now almost seems the norm rather than an exception that there exists such a conflict and that this becomes more severe under strong intrasexual competition. This can lead to the interesting phenomena of sexually antagonistic coevolution where males and females become involved in an arms race, as traits in one sex entice the evolution of resistance in the other (Holland and Rice, 1998; Gavrilets *et al.*, 2001; and others). On the other hand, intrasexual competition can lead to one sex dominating the other. With regard to aggression and physical prowess, the common situation in mammals, including primates (Hrdy, 1981), is that males are physically dominant over females.

III. MATING SYSTEMS

Not all animals have clear sexual differences (Fairbairn *et al.*, 2007). In birds, for example, many species of gulls and penguins are so alike that it is impossible to determine the sex except by closer inspections of the genitals. At the other extreme are mallards, where the sexes are so different that Linnaeus classified them as two different species (Andersson, 1994). In mammals, we find the same variation even within a given mammalian order. Thus, within Pinnipedia we have, on the one hand, elephant seals where males may weigh up to five times as much as females and on the other hand, species such as Baikal seals where females are of similar weight as males (Lindenfors *et al.*, 2002). These differences in dimorphism are due to differences in the degree of sexual selection. But why are there differences in the degree of sexual selection between species to start with?

Fundamentally, this question is about factors affecting male and female social group size. These issues are commonly addressed by focusing on the ecological variables that determine the spatiotemporal distribution of females, based on the expectation that resources and predation account for variation in female reproductive success. By comparison, access to females is generally assumed to be the major factor influencing male reproductive success (Emlen and Oring, 1977; Trivers, 1972; Wilson, 1975). After risks and resources have determined the spatiotemporal distribution of females, the distribution of females is in turn expected to influence the degree of male intrasexual competition (Emlen and Oring, 1977). For instance, a group of concurrently fertile females opens the field for male competition and monopolization. The general framework is therefore that social evolution is driven by females.

The theoretical expectation that social evolution is ultimately driven by female distribution is empirically supported by comparative studies on primates, a group for which there is a significant correlation between evolution of male and female sociality (e.g., Altmann, 1990; Mitani *et al.*, 1996; Nunn, 1999). Further, a phylogenetic investigation has shown that the evolution of female group size precedes the evolution of male group size, that is, that evolutionary changes in male group size lag changes in female group size (Lindenfors *et al.*, 2004).

Ecological factors determine whether it is possible for a male to monopolize several mating opportunities. For example, elephant seal females give birth on beaches. With a limited number of suitable beaches available in the elephant seal range, females tend to crowd together when giving birth. Elephant seals mate soon after they have given birth, so at the time of mating females are gathered tightly on limited stretches of beach. Males can exclude other males from a stretch of beach and thereby secure matings with a large number of females. Successful males in this competition gain all matings, while the losers get none. Fighting among elephant seals over mating opportunities is thus a fierce and bloody affair, a scenario which has resulted in extreme size dimorphism. In other pinniped species, females give birth in isolated caves on the polar ice pack; thus, no opportunity exists to monopolize matings. Without evolutionary pressure for male fighting ability, the sexes are more equal in size (Lindenfors *et al.*, 2002).

In conclusion, the ultimate cause for differences in mating systems can be traced back to ecological circumstances. The differences in mating systems in turn trigger differences in aggressive competition for mating opportunities which is what drives the evolution of sex differences in size and weaponry. These morphological sex differences are clear indicators of the severity of male–male aggression.

IV. WHEN TO FIGHT AND WHEN TO FLEE

Given that fighting is most often about mating opportunities, how are they predicted to pan out in terms of ferocity, number of behaviors involved, length of time, and so on? There are two things that determine the ferocity of fighting: the value of the object being fought over and the risks involved. The problem can be reduced to a cost-benefit analysis. A male can not give up at first instance to maximize his chances of survival, because that would result in total nonreproduction. Neither can he go “all-in” in just any aggressive encounter if there exists only a minute chance of success. Instead, males in competitive situations have to weigh the probabilities of success, injury, and survival against each other, while considering other factors such as energy expenditures and probabilities of success in future interactions with other competitors. It is important to note that animals make calculations and decisions about how to act, but such processes do not necessarily require the consciousness about the process usually ascribed to human decision-making. Rather, animals are believed to use cues with regard to the environment, as well as their own and the opponent’s current status, and to use this information in an unconscious way when making decisions.

One consequence this accounting has had over evolutionary history is that competitive interactions often take the form of a “sequential assessment game”. Simply put, this prescribes that each competitor should attempt to assess his opponent’s strength using as little energy as possible. Escalation should only be initiated by the competitor that feels he has the upper hand, or by either opponent if they cannot determine who is superior (Enquist and Leimar, 1983). Thus, a meeting between two deer males often starts out with a stage of roaring, which acts as a forcedly honest signal of body size. If this does not settle who is the larger/stronger, it is followed by “parallel walking,” where each competitor tries to judge the size and strength of the other by walking back and forth in parallel. Only if it is still unclear who is the larger or stronger will the

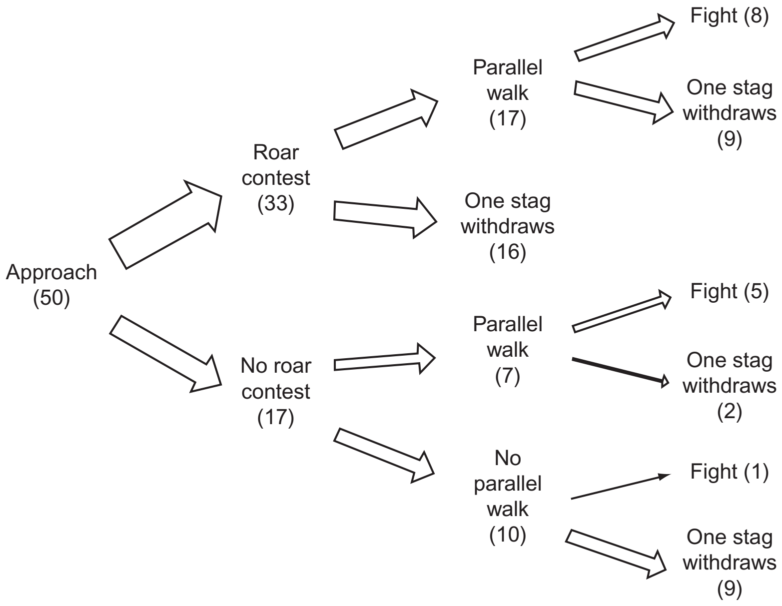

Figure 2.1. Sequential assessment in red deer (from Clutton-Brock and Albon, 1979).

competition escalate to actual fighting (Clutton-Brock and Albon, 1979; Fig. 2.1). Thanks to this "game," really fierce fights only happen between opponents of equal size—inferior competitors flee quickly to fight another day (and another opponent).

There is a common interest among fighters in trying to expend as little energy as possible while simultaneously minimizing the possibility of injury. For example, wolves and other canids ritualistically greet each other several times each day and display dominance or submission on a regular basis—they do not determine their relationship at every encounter. Some cichlid fish have a system akin to that of red deer, with different stages of escalation (Brick, 1999). Male lions fight savagely only if they stand a good chance of winning a pride of females. Research shows that they determine the quality of their rivals on cues from each other's manes (West and Packer, 2002). Lekking birds such as black grouse have distinctive courtship rituals where they make calls and visual displays, an odd mix of strength comparison and showing off, where females can pick winners according to some criterion, sometimes just by copying other females' choices (Andersson, 1994; Dugatkin and Godin, 1993; Wade and Pruett-Jones, 1990). Seldom do fights turn into vicious fighting, and when they do it is usually because either the contestants are judged by each other to be of equal strength, or because the benefit of winning—the value of the contested item—is much larger than the cost of losing. If the choice is reproduction or death, fights become deadly. This is why fights among elephant seals are so fierce and bloody. The chance to mate occurs only once per year and most males never even get close. For the successful males it is another story—in a study of Southern elephant seals, harem holders accounted for 89.6% of the recorded paternities (Fabiani *et al.*, 2004; Fig. 2.2).

The sequential assessment game is a variant of a game theoretical setup termed the "hawk-dove game" (see also Chapter 3). In this game, there are two possible strategies: always fight ("hawk") and always yield ("dove"), where it is assumed that the two competitors have equal fighting ability. An Evolutionarily

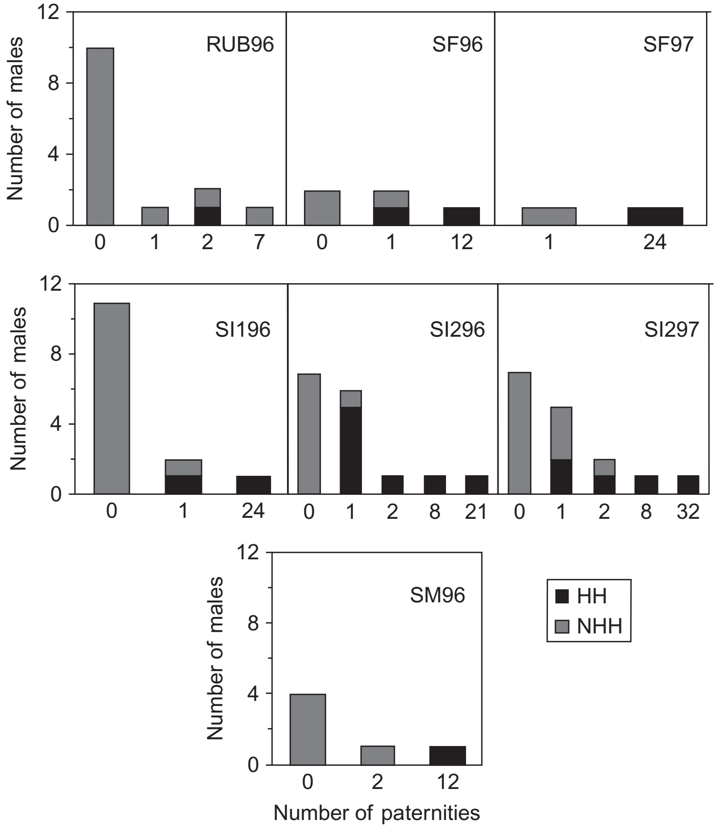

Figure 2.2. Number of paternities achieved by the harem holder (HH) and the other males (NHM) associated with each harem in seven different populations of Southern elephant seals (from Fabiani *et al.*, 2004).

Stable Strategy is a strategy which, if adopted by a population of players, cannot be invaded by any alternative strategy. It has been shown that the ESS is a mix of hawks and doves with proportions determined by the cost of fighting in relation to the benefit of winning (Maynard Smith, 1982). This game provides theoretical information that in a population of nonfighters it is profitable to be a fighter, and vice versa. If one extends the game to include a strategy called "assessor" that determines whether it will act as a "hawk" or a "dove" based on some criterion—for example, depending on priority at the resource—one can arrive at the sequential assessment game. The assessment strategy is also an ESS (Maynard Smith, 1982).

The prediction from these game theoretical models is that populations where individuals compete over resources or matings should consist of individuals utilizing different strategies depending on situation, where important factors are the current size and physical state of self and opponents and the value of resources (for instance, the number of females in the group being fought over). In this context, it should be noted that some animal populations have evolved alternatives to fighting strategies, usually known as sneaker strategies. Such males are usually much smaller than fighting males and can covertly sneak matings from females while the fighters are occupied with physical combat (Gross, 1996).

V. CASE STUDIES: SEXUAL DIMORPHISM

As mentioned above, animal groups differ in both the way and the degree to which they are exposed to sexual selection, and this will have great effects on the evolution of sex differences (Fairbairn *et al.*, 2007). Although mammals as a group are characterized by a high degree of intrasexual selection (as compared with, for instance, birds, where intersexual selection seems to be more common), there is variation in the strength of sexual selection both within and among mammalian orders. An example of this variation is the pinnipeds (seals, sea lions, and walruses) where there exists a clear relationship between harem size and sexual size dimorphism (Lindenfors *et al.*, 2002; Fig. 2.3).

In this section, we bring up some studies that have compared different mammalian groups with respect to the consequences of sexual selection on behavioral and morphological evolution. There are 4629 extant or recently extinct mammalian species, as listed by Wilson and Reeder (1993). In a survey of 1370 of these, Lindenfors *et al.* (2007a) showed that sexual selection is a prevalent selective force in mammals. With a cutoff point at a 10% size difference in either direction to "count" as sexual dimorphism, mammals were, on average, male-biased size dimorphic (average male/female mass ratio = 1.184; paired t-test $p \ll 0.001$; Table 2.1) with males being larger than females in 45% of

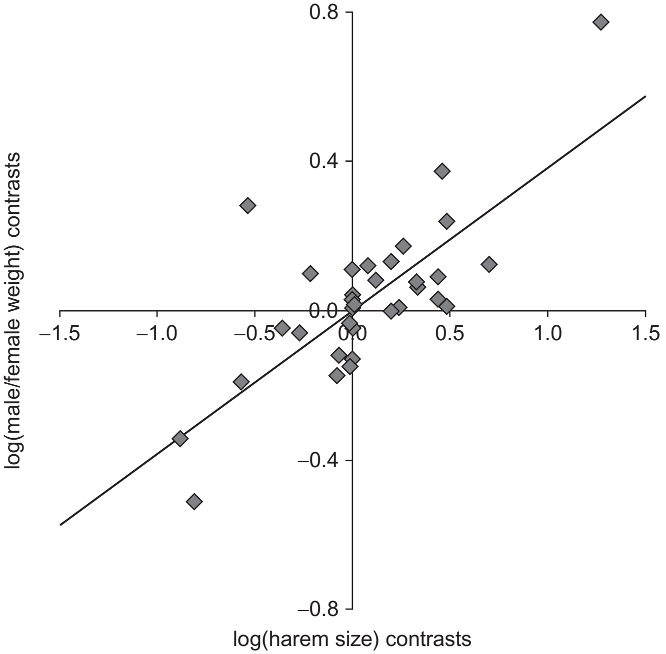

Figure 2.3. Regression line through the origin on harem size and body weight dimorphism. The data points are from a phylogenetic independent contrasts analysis. There is a significant relationship between harem size and sexual size dimorphism ($b = 0.376$, $p = 0.000$, $R^2 = 0.577$, $n = 36$) (from Lindenfors *et al.*, 2002).

extant species (Table 2.1). Systematists recognize 26 monophyletic mammalian orders (Wilson and Reeder (1993)). When investigating each order separately, the majority of orders also turned out to be significantly male-biased dimorphic (average male/female mass ratio > 1.0 and $p < 0.05$). Some orders exhibited no significant size dimorphism, and only one (Lagomorpha; hares, rabbits, and pikas) was significantly female-biased dimorphic on average (average male/female mass ratio < 1.0, $p < 0.05$; Table 2.1).

The mating system in a species describes the number of females a male can monopolize and thus affects the potential strength of sexual selection males are exposed to in that species. Using a phylogenetic tree for all mammals (Bininda-Emonds *et al.*, 2007) together with information about mating system and sexual size dimorphism, Lindenfors *et al.* (2007a) tested whether sexual selection could explain the variation in sexual size dimorphism among mammals. Mating system was used as a three-state unordered categorical variable, an independent variable used to test for differences in dimorphism between

Table 2.1. Summary of the Patterns of Dimorphism Found in Mammals

Order	Number of recognized species	Number of species with body mass data	Average dimorphism	Sexual size dimorphism
	Mammalia			
All mammals	4629	1370	1.184	$p \ll 0.001$
	Subclass Prototheria			
Monotremata (Monotremes)	3	2	1.273	–
	Subclass Metatheria			
Didelphimorphia (American marsupials)	63	13	1.323	$p = 0.002$
Paucituberculata (Shrew oppossums)	5	2	1.840	–
Microbiotheria (Monito del monte)	1	1	1.044	–
Dasyuromorphia (Dasyuroids)	63	24	1.465	$p \ll 0.001$
Peramelemorphia (Bandicoots and bilbies)	21	9	1.496	$p = 0.015$
Notoryctemorphia (Marsupial moles)	2	0	–	–
Diprotodontia (Kangaroos, etc.)	117	63	1.306	$p \ll 0.001$
	Subclass Eutheria			
Insectivora (Insectivores)	428	59	1.048	$p = 0.081$
Macroscelidea (Elephant shrews)	15	5	0.964	$p = 0.142$
Scandentia (Tree shrews)	19	1	–	–
Dermoptera (Colugos)	2	0	–	–
Chiroptera (Bats)	925	354	0.999	$p = 0.091$
Primates (Primates)	233	198	1.247	$p \ll 0.001$
Xenarthra (sloths, armadillos, and anteaters)	29	4	0.914	$p = 0.216$
Pholidota (Pangolins)	7	3	1.767	$p = 0.001$
Lagomorpha (Rabbits and pikas)	80	21	0.930	$p = 0.012$
Rodentia (Rodents)	2015	295	1.092	$p \ll 0.001$
Cetacea (Whales, dolphins, and porpoises)	78	10	1.414	$p = 0.082$
Carnivora (Carnivores)	271	180	1.476	$p \ll 0.001$
Tubulidentata (Aardwark)	1	0	–	–
Proboscidea (Elephants)	2	2	1.900	–
Hyracoidea (Hyraxes)	6	1	1.111	–
Sirenia (Dugongs and manatees)	5	0	–	–
Perissodactyla (Horses, rhinos, and tapirs)	18	8	1.164	$p = 0.156$
Artiodactyla (Antelopes, camels, pigs, etc.)	220	115	1.340	$p \ll 0.001$

Dimorphism is given as male mass/female mass. Mammals and the majority of mammalian orders are on average male-biased dimorphic (average dimorphism > 1.0 and $p < 0.05$), even if there exist a few orders with no significant dimorphism ($p > 0.05$) or female-biased dimorphism (Lagomorpha: average dimorphism < 1.0 and $p < 0.05$). p-Values represent the significance of paired t-tests where male body mass was paired with female body mass. Dashes indicate orders with too few data points for statistical analysis ($n < 3$ for tests of the presence of dimorphism, from Lindenfors *et al.*, 2007a).

"more" and "less" sexually selected (polygynous) sister taxa. These tests revealed that a higher degree of sexual selection was associated with a higher degree of male-biased dimorphism. More polygynous taxa not only had larger males but also larger females than their less polygynous sister taxa. These results indicate that sexual selection is a significant explanatory factor of both sexual dimorphism as such, and of the general size increase in many mammalian lineages.

In primates, the mammal order humans belong to, the pattern is similar. Again using mating system as a three-state unordered categorical variable, testing for differences in dimorphism between "more" and "less" sexually selected sister taxa, a higher degree of sexual selection was associated with a higher degree of male-biased dimorphism. Again, more polygynous taxa also had larger males and females than their less polygynous sister taxa (Lindenfors, 2002; Lindenfors and Tullberg, 1998). Here, however, a novel method investigating temporal order of events revealed not only a correlation but also a causal link between sexual selection and sexual size dimorphism where changes in mating systems occurred before changes in the degree of sexual selection (Lindenfors and Tullberg, 1998). Using similar methods, sexual selection has also been shown to be an important determinant of sexual dimorphism in canine size in primates (Thorén *et al*., 2006), although primate canines are also of importance in predator defense (Harvey *et al*., 1978). Thus, both body size and canine size bear witness to an evolutionary history of male–male aggression in primates.

This selection history has its grounds in a sexual difference in behavior. While males compete more over matings than females, female reproduction is instead limited by resource allocation (Emlen and Oring, 1977). These differing demands should be expected to produce variation in the relative sizes of various brain structures, just as they are expected to produce differences in other morphological structures. However, data on brain structures in primates are not available for males and females separately. Instead, investigating *species* differences in brain structures and comparing them on basis of differences in the species-typical degree of sexual selection, research has shown that the degree of male intrasexual selection is positively correlated with several structures involved in autonomic functions and sensory-motor skills, and in pathways relating to aggression and aggression control (Lindenfors *et al*., 2007b).

The sizes of the mesencephalon, diencephalon (containing the hypothalamus), and amygdala, all involved in governing aggressive behaviors, are positively correlated with the degree of sexual selection, whereas the size of the septum, which has a role in facilitating aggression control, is negatively correlated with the degree of sexual selection. These correlations indicate that sexual selection affects physical combat skills. Moreover, male group size was positively correlated with the relative volume of the diencephalon and negatively correlated with relative septum size, further strengthening the conclusion that aggression is an evolutionarily important component of male–male interactions (Lindenfors *et al.*, 2007b). Thus, primate brain organization also reflects a history of male–male aggression.

VI. HUMANS AND THE MAMMALIAN PATTERN

So where do humans fit into this picture? Humans are one of the sexually size-dimorphic species in the primate order in Table 2.1. But compared to our closest relatives (chimpanzees, bonobos, gorillas, and orangutans) humans have the lowest degree of size dimorphism (Lindenfors, 2002), indicating a decreasing degree of sexual selection over human evolution. Nevertheless, in all measurements of length that have ever been carried out in human populations, males have been taller than females. The average dimorphism in humans from these surveys is 1.07 (Gustafsson and Lindenfors, 2004). Does this mean that we exhibit a tendency toward the polygyny that accompanies such size dimorphism?

According to the Ethnographic Atlas Codebook (Gray, 1999), a database of cultural characteristics for 1231 comparable cultures from around the world, polygyny is common in 48% of human societies. In another 37% polygyny is allowed, and in only 15% is monogamy the norm. Only four reported societies are considered polyandrous. From these data and the degree of human size dimorphism, one may draw the conclusion that humans are at least more polygynous than monogamous (see also Low, 2000), and also that Western cultures fall within the monogamous 15% of the world. Interestingly, intergroup differences in size dimorphism are not correlated with differences in the degree of polygyny (Gustafsson and Lindenfors, 2004), a clear indication that cultural evolution proceeds faster than biological evolution.

There are more indications that humans have an evolutionary history of sex differences as an explanatory factor in human aggression. For example, men commit most of the world's violent acts that are reported to the police. Men are consequently overrepresented in the world's prisons. Women typically make up only 10–15% of the prison population (Harrendorf *et al.*, 2010). Further, soldiering is most often an all-male vocation (personal observation). Humans are, however, the products of both biological and cultural inheritance (Boyd and Richerson, 2005). Here, we have presented only the biological side of the story, but we agree with Archer (2009) that sexual selection probably is the best explanation for the magnitude and nature of human sex differences in aggression. Humans fit into the mammalian scheme of things very well.

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References

Altmann, J. (1990). Primate males go where the females are. *Anim. Behav.* **39,** 193–195.

Andersson, M. (1994). Sexual Selection. Princeton University Press, New Jersey.

Archer, J. (2009). Does sexual selection explain human sex differences in aggression? *Behav. Brain Sci.* **32,** 249–311.

Arnqvist, G., and Rowe, L. (2005). Sexual Conflict. Princeton University Press, Princeton.

Bateman, A. J. (1948). Intra-sexual selection in Drosophila. *Heredity* **2,** 349–368.

Bininda-Emonds, O. R. P., *et al.* (2007). The delayed rise of present-day mammals. *Nature* **446,** 507–512.

Birkhead, T. (2001). Promiscuity: An Evolutionary History of Sperm Competition. Harvard University Press, Cambridge.

Boyd, R., and Richerson, P. J. (2005). The Origin and Evolution of Cultures. Oxford University Press, Oxford.

Brick, O. (1999). A test of the sequential assessment game: The effect of increased cost of sampling. *Behav. Ecol.* **10,** 726–732.

Caro, T. M., Graham, C. M., Stoner, C. J., and Flores, M. M. (2003). Correlates of horn and antler shape in bovids and cervids. *Behav. Ecol. Sociobiol.* **55,** 32–41.

Clutton-Brock, T. H., and Albon, S. D. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour* **69,** 146–170.

Darwin, C. (1859). The Origin of Species by Means of Natural Selection. Penguin, London.

Darwin, C. (1860). Darwin Correspondence Project. Letter 2743—Darwin, C. R. to Gray, Asa, 3 Apr (1860).

Darwin, C. (1871). The Descent of Man and Selection in Relation to Sex. Murray, London.

Dugatkin, L. A., and Godin, J.-G. J. (1993). Female mate copying in the guppy (*Poecilia reticulata*): Age-dependent effects. *Behav. Ecol.* **4,** 289–292.

Emlen, S. T., and Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197,** 215–223.

Enquist, M., and Leimar, O. (1983). Evolution of fighting behavior: Decision rules and assessment of relative strength. *J. Theor. Biol.* **102,** 387–410.

Fabiani, A., Galimberti, F., Sanvito, S., and Hoelzel, A. R. (2004). Extreme polygyny among southern elephant seals on Sea Lion Island, Falkland Islands. *Behav. Ecol.* **15,** 961–969.

Fairbairn, D. J., Blanckenhorn, W. U., and Székely, T. (eds.) (2007). *In* "Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism". Oxford University Press, Oxford.

Gavrilets, S., Arnqvist, G., and Friberg, U. (2001). The evolution of female mate choice by sexual conflict. *Proc. R. Soc. Lond. B* **268,** 531–539.

Gray, J. P. (1999). A corrected ethnographic atlas. *World Cultures* **10,** 24–85.

Gross, M. R. (1996). Alternative reproductive strategies and tactics: Diversity within sexes. *Trends Ecol. Evol.* **11,** 92–97.

Gustafsson, A., and Lindenfors, P. (2004). Human size evolution: No allometric relationship between male and female stature. *J. Hum. Evol.* **47,** 253–266.

Harrendorf, S., Heiskanen, M., and Malby, S. (2010). International Statistics on Crime and Justice. United Nations Office on Drugs and Crime (UNODC), Helsinki, Finland.

Harvey, P. H., Kavanagh, M., and Clutton-Brock, T. H. (1978). Sexual dimorphism in primate teeth. *J. Zool.* **186,** 475–485.

Holland, B., and Rice, W. R. (1998). Chase-away sexual selection: Antagonistic seduction versus resistance. *Evolution* **52,** 1–7.

Hrdy, S. B. (1981). The Woman that Never Evolved. Harvard University Press, Cambridge.

Lindenfors, P. (2002). Sexually antagonistic selection on primate size. *J. Evol. Biol.* **15,** 595–607.

Lindenfors, P., and Tullberg, B. S. (1998). Phylogenetic analyses of primate size evolution: The consequences of sexual selection. *Biol. J. Linn. Soc.* **64,** 413–447.

Lindenfors, P., Tullberg, B., and Biuw, M. (2002). Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behav. Ecol. Sociobiol.* **52,** 188–193.

Lindenfors, P., Fröberg, L., and Nunn, C. L. (2004). Females drive primate social evolution. *Proc. R. Soc. Lond. B* **271,** S101–S103.

Lindenfors, P., Gittleman, J. L., and Jones, K. E. (2007a). Sexual size dimorphism in mammals. *In* "Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism" (D. J. Fairbairn, W. U. Blanckenhorn, and T. Szekely, eds.), pp. 19–26. Oxford University Press, Oxford.

Lindenfors, P., Nunn, C. L., and Barton, R. A. (2007b). Primate brain architecture and selection in relation to sex. *BMC Biol.* **5,** 20.

Low, B. S. (2000). Why Sex Matters. Princeton University Press, Princeton.

Maynard Smith, J. (1982). Evolution and the Theory of Games. Cambridge University Press, Cambridge.

Mitani, J. C., Gros-Louis, J., and Manson, J. H. (1996). Number of males in primate groups: Comparative tests of competing hypotheses. *Am. J. Primatol.* **38,** 315–332.

Nunn, C. L. (1999). The number of males in primate social groups: A comparative test of the socioecological model. *Behav. Ecol. Sociobiol.* **46,** 1–13.

Parker, G. A. (1979). Sexual selection and sexual conflict. *In* "Sexual Selection and Reproductive Competition in Insects" (M. S. Blum and N. A. Blum, eds.), pp. 123–166. Academic Press, New York.

Petrie, M. (1994). Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* **371,** 598–599.

Ralls, K. (1976). Mammals in which females are larger than males. *Q. Rev. Biol.* **51,** 245–276.

Stankowich, T., and Caro, T. (2009). Evolution of weaponry in female bovids. *Proc. R. Soc. Lond. B* **276,** 4329–4334.

Thorén, S., Lindenfors, P., and Kappeler, P. M. (2006). Phylogenetic analyses of dimorphism in primates: Evidence for stronger selection on canine size than on body size. *Am. J. Phys. Anthropol.* **130,** 50–59.

Tinbergen, N. (1963). On aims and methods in ethology. *Z. Tierpsychol.* **20,** 410–433.

Trivers, R. L. (1972). Parental investment and sexual selection. *In* "Sexual Selection and the Descent of Man 1871–1971" (B. Campbell, ed.), pp. 136–179. Aldine, Chicago, IL.

Vincent, A., Ahnesjö, I., Berglund, A., and Rosenqvist, G. (1992). Pipefishes and seahorses: Are they all sex role reversed? *Trends Ecol. Evol.* **7,** 237–241.

Wade, M. J., and Pruett-Jones, S. G. (1990). Female copying increases the variance in male mating success. *Proc. Natl. Acad. Sci. USA* **87,** 5749–5753.

West, P. M., and Packer, C. (2002). Sexual selection, temperature, and the lion's mane. *Science* **297,** 1339–1343.

Williams, G. C. (1966). Adaptation and Natural Selection. Princeton University Press, Princeton.

Wilson, E. O. (1975). Sociobiology, the New Synthesis. Belknap, Cambridge, MA.

Wilson, D. E., and Reeder, D. M. (eds.) (1993). *In* "Mammal Species of the World: A Taxonomic and Geographic Reference". 2 nd edn. Smithsonian Institution Press, Washington and London.