When Violence Pays: A Cost-Benefit Analysis of Aggressive Behavior in Animals and Humans

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Abstract

An optimization analysis of human behavior from a comparative perspective can improve our understanding of the adaptiveness of human nature. Intra-specific competition for resources provides the main selective pressure for the evolution of violent aggression toward conspecifics, and variation in the fitness benefits and costs of aggression can account for inter-specific and inter-individual differences in aggressiveness. When aggression reflects competition for resources, its benefits vary in relation to the characteristics of the resources (their intrinsic value, abundance, spatial distribution, and controllability) while its costs vary in relation to the characteristics of organisms and how they fight (which, in turn, affects the extent to which aggression entails risk of physical injury or death, energetic depletion, exposure to predation, psychological and physiological stress, or damage to social relationships). Humans are a highly aggressive species in comparison to other animals, probably as a result of an unusually high benefit-to-cost ratio for intra-specific aggression. This conclusion is supported by frequent and widespread occurrence of male-male coalitionary killing and by male-female sexual coercion. Sex differences in violent aggression in humans and other species probably evolved by sexual selection and reflect different optimal competitive strategies for males and females.

Understanding the evolution of human nature: the importance of comparative research

The earliest systematic attempts to investigate human behavior from an evolutionary perspective focused on demonstrating the existence of human universals, i.e., patterns of behavior, emotional expression, and thought that could be observed in all human cultures and therefore were hypothesized to be genetically determined, hardwired in our brains, and presumably the result of evolution by natural selection. Examples of this approach include

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the documentation of cross-cultural similarities in facial expressions of emotions (Eibl-Eibesfeldt, 1972) and the study of sex differences in mate preferences across cultures (Buss, 1989). At the same time, parallels were increasingly being made between human behavior and the behavior of other animals, particularly other primates (Morris, 1967). These two approaches were aimed at establishing the existence of human nature and thus legitimizing studies of human behavior grounded in evolutionary biology and animal behavioral ecology.

Subsequent research in evolutionary psychology shifted its focus to empirical testing of hypotheses derived chiefly from the theories of sexual selection, life history and parental investment (Barrett, Dunbar, and Lycett, 2002; Buss, 2005; Dunbar and Barrett, 2007). There was also a parallel shift in interest from "normative" aspects of human nature to inter-individual variation (e.g., Belsky, Steinberg, and Draper, 1991; Gangestad and Simpson, 2000).

Although many evolutionary psychologists focus their attention exclusively on human mind and behavior, the comparative study of adaptations in other organisms has made an important historical contribution to evolutionary psychology through the development of evolutionary theories and hypotheses, which are now being tested with human psychological and behavioral data (Daly and Wilson, 1999; Smith, Borgerhoff Mulder, and Hill, 2000, 2001). Studies of nonhuman animals continue to be a source of ideas, inspiration, and guidance for evolutionary psychologists, and in some cases human studies are specifically designed to assess whether the findings from animal research can be extrapolated to humans. For these reasons, it is important to be familiar with the historical findings of comparative research that led to the development of evolutionary theories (beginning with Darwin's own studies of many different living organisms) as well as to keep up with advances in comparative research.

It may be argued that evolutionary psychologists should not only know about comparative research but also actively engage in it. Although much evolutionary psychology research has moved away from the investigation of "normative" behaviors, many aspects of human nature are not yet well characterized, some old questions about human nature have not yet been answered, and many new questions can be raised. The issue of whether human nature exists has been effectively investigated with cross-cultural studies and could be further addressed with the investigation of genetic or neurobiological substrates of psychological and behavioral traits that are common across all human cultures. More importantly, the question of how human nature evolved is far from being settled and this question can be addressed only with a comparative approach.

There are two main approaches to comparative research on the evolution of human nature: phylogenetic analyses and functional "optimization" analyses. Comparative phylogenetic analyses aim to document the phylogenetic history of a trait and to test hypotheses about the trait's functional significance across taxa (Nunn, 2011). These analyses cannot be applied effectively to traits that have a recent evolutionary history and have evolved within the *Homo* lineage, such as language. Many human psychological and behavioral traits, however, particularly those associated with cooperation, competition, mating, or parenting, are also present in other species (Kappeler and Silk, 2009). In some cases, the presence of similar traits in different species is the product of inheritance from a common ancestor (i.e., the traits are homologous). Homologous traits are more likely to occur in closely-related than in distantly-related species. Traits that have an ancient phylogenetic history and are observed in many different organisms are unlikely to be neutral or deleterious; rather, they likely represent adaptations that are so valuable as to be highly conserved (Roney and Maestripieri, 2002). Thus, phylogenetic "mapping" of human psychological and behavioral traits can be

an important contribution toward understanding the evolution of many adaptive aspects of human nature.

A comparative approach can also be used to investigate traits that are similar in different species due to the process of convergent evolution. When different species confront similar problems in their environment, they often come up with similar optimal solutions to these problems. An optimal strategy to solve a problem is one that results in maximal benefits at a minimal cost (Clutton-Brock and Harvey, 1984). Analyzing the fitness benefits and costs of psychological and behavioral traits, along with knowledge of the relevant environmental selective pressures and constraints, allows evolutionary psychologists to obtain evidence that these traits are adaptations. Cost-benefit analyses of human adaptive traits, when conducted from a comparative perspective, can shed light on the evolution of these adaptations and on the evolution of human nature more generally.

Let us take aggressiveness as an example of an aspect of human nature for which there are still many unanswered questions (Buss and Dentley, 2006; Buss and Shackelford, 1997; Liddle, Shackelford, and Weeks-Shackelford, 2012). Two such questions are: why is it that humans seem to have a high potential for violent aggression toward their conspecifics? And why is it that this potential for violent aggression seems to be much higher in men than in women? In this article we will attempt to answer these questions by taking a comparative approach and examining aggression in humans and other animals from a functional perspective, i.e., examining the fitness benefits and costs of this behavior. In our discussion of intra-specific aggression, we assume that the general potential for aggression of a species and the average levels of aggression of males and females are the product of natural selection and not of aberrant environmental circumstances (for example, dramatic alterations of the habitat of wild animal populations induced by human activity), cultural forces, or selection on other traits that are associated with aggression.

What makes an animal species more or less aggressive

From a functional perspective, aggression can be viewed as an expression of competition (Darwin, 1859, 1871). Competition for resources between individuals of the same species is widespread in nature, and to some extent, inter-specific variation in aggressiveness reflects species differences in the overall intensity of competition. There are different ways in which organisms can compete for resources, however, and competitive strategies do not necessarily involve aggression. From an optimization perspective, organisms in any given species will use a particular competitive strategy only when its benefits outweigh the costs. If different competitive strategies are available, organisms will tend to use the strategy with the highest benefit/cost ratio.

In animal species that are relatively less aggressive, the benefits of aggressive competition are probably lower than its costs. It is also possible that less aggressive species can pursue alternative competitive strategies with higher benefit/cost ratios than competitive aggression. Finally, regardless of benefits and costs, there may be physical, social, ecological, or behavioral constraints that make it difficult or impossible for aggression to be expressed in these species (e.g., in sessile marine invertebrates, highly solitary animals, or small nocturnal animals under heavy predation pressure). The opposite is true for highly aggressive species. Here the benefits of aggression are presumably higher than its costs, making aggression the preferred competitive strategy. In addition, there may be few or no constraints on the expression of aggressive behavior.

To understand inter-specific variation in the benefit/cost ratios for aggression, it may be useful to examine separately variation in the benefits and in the costs. Whenever aggression reflects competition for resources, the benefit of aggression is obtaining those resources.

Variation in the potential benefits of aggression generally depends on the characteristics of the resources. Aggression can entail many different types of costs including risk of injury or death, physiological or psychological stress, energy expenditure, increased risk of attracting predators, and damage to social relationships, as well as time-allocation trade-offs with other survival- or reproduction-related activities such as feeding or mating. Variation in the potential costs of aggression generally depends on the characteristics of the organisms and the kind of aggressive behavior they use. In a nutshell, the benefits of aggression depend on what animals fight about, while the costs depend on how they fight.

Inter-specific variation in the benefits of aggression

The benefits of aggression vary in relation to the characteristics of the resource being contested: its value, abundance, spatial distribution, and the extent to which it can be effectively monopolized by individuals or groups. As examples, we will briefly discuss how the characteristics of resources such as food, mates, or space influence the probability that competition will be aggressive.

Competition for food

When organisms compete for food that has high nutritional value, is generally scarce, and is distributed in small patches that can be effectively monopolized, the potential benefits of aggressive competition are high (Isbell, 1991; Koenig and Borries, 2009; Wrangham, 1980). The most clear example of a food type that is patchily distributed, is difficult to obtain, and can be monopolized effectively is meat. Intense aggressive ("contest") competition over meat is typical of social carnivores such as lions or hyenas (Kruuk, 1972; Schaller, 1972).

At the other extreme is low-quality food that is widely distributed and cannot be monopolized, such as grass or leaves. Herbivorous and folivorous organisms still compete with their conspecifics over food but competition is indirect ("scramble"), which means that individuals try to consume as much as possible of the resource without attacking or displacing others from it (Isbell, 1991; van Schaik, 1989). Note that the prediction here refers to the quality of the food rather than to the specific type of food. Thus, if some folivores show selectivity and feed only on high-quality leaves that are less common in their environment and therefore worth fighting for, aggressive contest competition is expected to occur, as has been shown for between-group feeding competition in black-and-white colobus monkeys (Harris, 2006; Snaith and Chapman, 2007).

In-between the two extremes of species that feed on meat and grass or leaves are the species that feed on fruit. Fruit is a highly nutritious food that is usually distributed in discrete patches that can be monopolized by one individual or, more often, by a group. The benefits of aggressive competition for access to fruit are high, so that frugivores are generally more aggressive than folivores or herbivores, and in some cases as aggressive as carnivores (for nonhuman primates, see Van Schaik, 1989).

Competition for mates

In most species of vertebrates, fertile males are an abundant, "low-value" resource that cannot and need not be monopolized by females. As a result, if females were to use aggression to compete with other females over access to males, or to sexually coerce males to have exclusive access to them, the benefits of such aggression would be low. In contrast, fertile females are a relatively scarce, high-value resource. In many mammals, most adult females are either pregnant or lactating most of the time; when they are neither pregnant nor lactating, they are fertile only a few days every month. The distribution of females in space and time generally affects whether or not they can be effectively monopolized by males for reproductive purposes (Clutton-Brock, 1989; Emlen and Oring, 1977). This, in turn,

determines the potential benefits of male-male aggressive competition. When fertile females forage alone and are widely dispersed in space (usually due to ecological needs or constraints), many of them cannot be effectively monopolized by a single male or a group of males; social and sexual monogamy tends to evolve, which in some cases is accompanied by high male parental investment (e.g. Clutton-Brock, 1991). In this situation the benefits of male aggression are low. Accordingly, in socially or sexually monogamous species, there is little male-male aggressive competition for mates, at least after the initial establishment of pairs, and little male-female sexual coercion. These low levels of male-male aggressive competition and the low potential for sexually coercive tactics are reflected in the lower sexual dimorphism in body size among monogamous species both in mammals and in birds (Clutton-Brock and Harvey, 1977; Dunn, Whittingham, and Pitcher, 2001; Pérez-Barbería, Gordon, and Pagel, 2002; Plavcan, 2004).

In contrast, when females are clumped in space because they live and forage in groups, groups of females can be monopolized either by a single male (one-male groups with a harem mating system) or by multiple males (multi-male multi-female groups with a promiscuous mating system). Such species typically have higher levels of sexual dimorphism than monogamous species. This is indicative of intense intra-sexual selection and also suggests potential for sexual coercion of females. In such polygynous and promiscuously mating species, the benefits of male-male aggressive competition (Fabiani, Galimberti, Sanvito, and Hoelzel, 2004) and male-female sexual coercion can be high (Muller, Emery Thompson, Kahlenberg, and Wrangham, 2011).

Competition for space

Competition for space (e.g., territories) is a special case of competition because instead of competing directly for food or mates, animals may compete for the space in which they are found. Aggressive competition also occurs over nesting sites (Semel and Sherman, 2001), shelter (Holbrook and Schmitt, 2002) and access to drinking water (Wrangham, 1981). Territorial aggression can be intense when the benefits are high. This is illustrated by the territorial behavior of chimpanzees, which have been reported to seek out and kill rival males one at a time, progressively expanding their own territory into what had previously been their neighbors' land (Goodall, Bandora, Bermann, Busse, Matama, Mpongo, Pierce, Risset, 1979; Mitani, Watts, and Amsler, 2010). Males benefit from expanding their own home range in two ways. First, range-expansion increases the number of fruit trees to which their community has access. Chimpanzees are ripe-fruit specialists and the quality of the females' diet determines important parameters of their reproductive function and success (Emery Thompson and Wrangham, 2008). Expanding the range of the community and thereby increasing both the quantity and the quality of foods available to females leads to higher reproduction rates (Williams, Oehlert, Carlis, and Pusey, 2004). Moreover, by eliminating the males of neighboring communities, the resident males may also gain additional mating opportunities: neighboring females are likely to join the territorially aggressive community and thus provide new sexual opportunities for the winning males (Emery Thompson, Newton-Fisher, and Reynolds, 2006; Nishida, Hiraiwa-Hasegawa, Hasegawa, and Takahata, 1985). Such events, in turn, set in motion another cycle of violence: any new female chimpanzees arriving into a community will be subject to aggressive harassment from the resident females (Kahlenberg, Emery Thompson, Muller, and Wrangham, 2007), behavior that is related to female-female competition over good foraging areas within the community's territory (Kahlenberg, Emery Thompson, and Wrangham, 2008).

Many primate, and also human, inter-group interactions are related to competition over food or mates and aggression plays a key role in all of them (Crofoot and Wrangham, 2009). However, to explain the variation in the intensity of such aggressive interactions (e.g., why

in some species but not others individuals seek out and kill their rivals as opposed to just repelling them temporarily from their territory) we also need to consider the costs of aggression.

Inter-specific variation in the costs of aggression

Physical costs: injury or death

Fighting between conspecifics entails risk of injury or even death due to irreparable damage to vulnerable body parts, massive bleeding from open wounds, or bacterial infections of wounds. Such costs of aggression are potentially higher in animal species equipped with weapons such as horns or antlers, or large and sharp canine teeth or claws, and lower in species that do not possess these or other natural weapons.

Most horn-like weapons among ungulates probably evolved through sexual selection for fighting ability (Geist, 1966). Even though in some species antler development may signal male fertility to potential mates (Malo, Roldan, Garde, Soler, and Gomendio, 2005), they are primarily used in male-male contests and only secondarily as a defense against predators (Clutton-Brock, 1982). Intense fighting in species with antlers and horns is usually restricted to the breeding season when the potential benefits of risky aggression are high. This leads to a concomitant increase in the rate of injuries and deaths among male competitors during such periods (Clutton-Brock, Albon, Gibson, and Guinness, 1979; Geist, 1974; Wilkinson and Shank, 1976).

Individuals in species that do not have antlers or horns can still kill each other given the opportunity. Deaths from intra-specific aggression typically result from infection of bite wounds and overall exhaustion from fighting (Baker and McCann, 1989; Knott, 1999; Knott and Laman, 1998; Palombit, 1993) rather than from direct blows and punctures of vital organs. Among wild baboons, wounding is more common among males and occurs more frequently during periods when individuals of either sex compete most intensely for dominance (MacCormick MacNulty, Bosacker, Lehman, Bailey, Collins, and Packer, 2012). In rhesus macaques, adult male mortality is significantly higher during the mating season than during the birth season, presumably as a result of increased male-male fighting during periods of time in which many females are fertile (Hoffman, Ruiz-Lambides, Davila, Maldonado, Gerald, and Maestripieri, 2008).

Lethal killing is relatively rare in animals, in part because many organisms have evolved mechanisms to reduce the risk of serious injury or death associated with fighting. Some of these mechanisms include ritualized fighting, in which two opponents barely touch each other or direct their attacks to non-vulnerable body parts, dominance, in which contests are settled by an exchange of signals rather than fighting, and coalition formation, in which two or more individuals can simultaneously attack a target and incur little or no risk of injury (see below).

Physiological and psychological costs

Even in the absence of physical injury, fighting can entail significant physiological and psychological costs. Chronically elevated testosterone associated with aggressive competition may suppress the immune system and thus have deleterious consequences for health and fitness (Folstad and Karter, 1992; Muehlenbein and Bribiescas, 2005; but see: Fuxjager, Foufopoulos, Diaz-Uriarte, and Marler, 2011; Nunn, Lindenfors, Pursall, and Rolff, 2009; Roberts, Buchanan, and Evans, 2004). High testosterone levels have also been implicated in higher susceptibility to oxidative stress (Alonso-Alvarez, Bertrand, Faivre, Chastel, and Sorci, 2007), another factor that can affect survivorship and fitness.

Frequent fighting can also be associated with chronically elevated cortisol levels (Sapolsky, 2004). In species that form dominance hierarchies, cortisol can be elevated in high-ranking individuals (who must use aggression to maintain their status and repel challenges from lower-ranking individuals) or in low-ranking individuals (who receive frequent attacks), or both, depending on the species (Abbott, Keverne, Bercovitch, Shively, Mendoza, Saltzman, Snowdon, Ziegler, Banjevic, Garland, and Sapolsky, 2003; Creel, 2001; Creel and Sands, 2003). Regardless of the species-typical relationship between dominance and glucocorticoid production, however, chronically elevated cortisol can result in damage to body organs and tissues including the brain (Sapolsky, 2004). Finally, aggression and fighting, via their effect on dominance rank, can result in psychological alterations such as chronic anxiety or depression (e.g., Shively, Register, Friedman, Morgan, Thompson, and Lanier, 2005), which can negatively impact survival or reproduction.

Energetic costs

Aggressive behavior can affect the energy budget of an individual via two pathways: by increasing energy expenditure and by reducing energy intake. Aggressive contests tend to be physically taxing and, depending on the relative competitive ability of the contestants, prolonged. African elephant bulls may fight up to six hours when competitors are similarly matched in size and motivation (Poole, 1989). Aggressive interactions increase oxygen consumption (Hack, 1997) and animal contests are therefore constrained by the physiological costs of fighting (Briffa and Sneddon, 2007). Aggression also tends to constrain feeding behavior. Escalated rates of aggression among males that mate-guard fertile females are frequently associated with significant reduction in foraging in lizards (Ancona, Drummond, and Zalvidar-Rae, 2010). A similar cost of aggressive behavior exists among chimpanzee males, as a male's daily rate of aggression is negatively associated with his feeding time (Georgiev, 2012). Combining the increases in energy expenditure with the decreases of energy intake, many males suffer significant reductions in their energy reserves during periods of intense male-male aggressive competition (Clutton-Brock, Guiness, and Albon, 1982; Galimberti, Sanvito, Braschi, and Boitani, 2007; Georgiev, 2012; Higham, Heistermann, and Maestripieri, 2011; Low, 2006; Marler, Walsberg, White, and Moore, 1995; Pelletier, Hogg, and Festa-Bianchet, 2006; Rovero, Hughes, Whiteley, and Chelazzi, 2000). Additional evidence for the significant energetic costs of aggression also comes from studies demonstrating increases in aggressive behavior during periods of high food availability (Georgiev, 2012; Golabek, Ridley, and Radford, 2012; Powers and McKee, 1994; Southwick, 1967)—i.e., when energy surplus allows diverting more resources to agonistic competition. The energetic costs of aggression are therefore expected to vary between species in relation to (1) type of aggressive behavior (i.e., more or less exertive; longer or shorter confrontations); (2) ability of individuals to store energy (e.g., in the form of fat) that can be used during periods of aggressive competition; and (3) ecological circumstances, particularly with regards to variation in food abundance.

Increased risk of predation

Aggressive behavior can affect an individual's risk of being killed by a predator in three different ways. First, aggressive interactions interfere with vigilance behaviors; second, aggressive challenges may make individuals temporarily less risk-sensitive in their choices of habitat and behavior (i.e., becoming more exposed); and third, aggressive interactions may attract the attention of predators due to their conspicuous nature. For example, fighting reduces vigilance and increases the risk of predation in fish, birds and lizards (Diaz-Uriarte, 1999; Jakobsson, Brick, and Kullberg, 1995). In species that avoid detection by hiding, such as small solitary nocturnal animals, the noise associated with fighting can increase the risk of attracting predators. In gregarious species that avoid predators by escaping quickly when the predator has been spotted, fighting may interfere with the ability to escape effectively.

Thus, overall, species that are less vulnerable to predation (e.g., those living in predator-free environments, those with larger body size, those that live in social groups, and in particular those that employ a cooperative system to monitor threats from predators), all other things being equal, are expected to be more aggressive than species that are more susceptible to predation.

Damage to social relationships

In group-living species in which individuals depend on cooperation with conspecifics for defense of resources from other groups, or in which cooperation is needed for friendships and alliances, fighting can damage social relationships with friends and allies, including relatives. Social bonds have important fitness benefits (Silk, Alberts, and Altmann, 2003) and thus alienating friends can be disadvantageous. The importance of social relationships is supported by evidence that, among primates, individuals sharing a 'valuable relationship' tend to reconcile their conflicts more often than other, less-strongly affiliated, individuals (Aureli, Cords, and van Schaik, 2002; de Waal, 2000; Palagi, Antonacci, and Norscia, 2008; Watts, 2006). Aggression would thus be expected to be more intense and its escalation more frequent in species where little social affiliation, bonding and cooperation exist among group members. Similarly, in species where males are not able to dominate females, behaving aggressively toward a female may damage a male's chances of mating and thus male-female aggression would be selected against (Hare, Wobber, and Wrangham, 2012).

Sex differences in aggression across different animal species

In many species of vertebrates there are important differences in the resources males and females compete for as well as in the strategies they use to obtain these resources. Because of sex differences in parental investment, females compete primarily over access to food while males compete primarily over access to mates (Trivers, 1972). For example, wild adult female chimpanzees in Kanyawara, Kibale National Park (Uganda) fight most often over plant food, while males are most commonly aggressive in the context of sexual competition (Muller, 2002). Males are almost 14 times more aggressive than females, with the female rate of aggression probably being an overestimate (Muller, 2002).

Inter-specific variation in sex differences in aggressiveness can result from differences in the benefits or the costs (or both) of aggression to males and females. Because of the greater benefits of male-male aggressive competition (see above), sexual selection has favored larger body size among males in many mammals (in >45% of species males are 10% larger than females; Lindenfors, Gittleman, and Jones, 2007). Although recent comparative work challenges the notion that the male-bias in body size dimorphism is consistently associated with male social dominance over females (Hemelrijk, Wantia, and Isler, 2008), a moderate to high degree of dimorphism seems to be a prerequisite for the evolution of one particular form of aggression: sexual coercion. Sexually coercive behavior occurs mostly in species in which males are both larger than and socially dominant to females, i.e., when the costs of male-female aggression are low for males (Clutton-Brock and Parker, 1995; Emery Thompson and Alvarado, 2012; Muller and Wrangham, 2009; Smuts and Smuts, 1993). Conversely, because the benefits of sexual coercion by females rarely outweigh its costs, this is not a reproductive strategy that has been documented among female animals, even in species in which females are socially dominant over males.

Although females in many species engage in intense competitive aggression for resources (Clutton-Brock, 2009; Rosvall, 2011; Stockley and Bro-Jorgensen, 2011; Tobias, Montgomerie, and Lyon, 2012), a situation of complete sex-role reversal, in which females compete for mates more intensely than males, is rare in animals and occurs mostly among birds and fish (Eens and Pinxten, 2000). In these cases females have a higher potential

reproductive rate and a higher benefit/cost ratio for aggression than males (Clutton-Brock and Vincent, 1991). In spotted hyenas, females are larger than males and dominate them in social interactions. Compared to males, they exhibit both higher overall rates of aggression and higher rates of inter-sexual aggression (Szykman et al., 2003; Van Meter, 2009). Female aggression in spotted hyenas is adaptive in the context of intense feeding competition and has also been explained as an extreme form of maternal investment due to the exceptionally long time that the specialized bone-crushing feeding apparatus takes to develop in this species and thus the need of maternal aggressive support during feeding (Watts, Tanner, Lundrigan, and Holekamp, 2009).

Like spotted hyenas, females in many lemur species tend to be dominant over males and, at least in some cases, this dominance is achieved through or associated with higher rates of female aggression (Kappeler, 1990; Meredith, 2012). Female dominance in lemurs may be associated with a high benefit/cost ratio for aggression relative to males: females may gain more from competitive aggression over food than males because of low food availability in Madagascar and the constraints it poses on female reproduction (Dunham, 2008); in addition, the costs of female aggression may be lower in lemurs than in other primates because most lemurs are sexually monomorphic.

In polygynous or promiscuous mammalian species, the need to aggressively defend offspring from infanticidal conspecifics may also select for high female aggressiveness (Maestripieri, 1992); given that the certainty of parenthood in these species is higher for females than for males, the benefits of offspring defense are higher in females than in males and under certain conditions may outweigh the risks associated with aggressing against larger males.

Inter-specific variation in sex differences in the costs of aggression can be the result of sex differences in body size, strength, and weaponry. In species in which males are larger, stronger, and have more weapons than females, the costs of inter-sex aggression are higher for females than for males due to an increased risk of injury or death (Maestripieri and Carroll, 1999). Differences between males and females can also occur in the energetic, psychological or social costs of aggression. In mammals, the energetic and psychological costs of aggression could be high for females because aggression-related energy expenditure and stress can interfere with fertility, pregnancy, or motherhood and lactation (Campbell, 1999). The social costs of aggression are expected to be higher in the sex that shows higher levels of bonding and alliance formation. In mammals, dispersal is more common in males, and philopatry is common in females. In all mammalian species in which females are philopatric and form strong bonds with female relatives (Wrangham, 1980), the social costs of aggression may be higher in females than in males.

In some socially and sexually monogamous species, the benefit/cost ratios of aggression may be similar for males and females because they are similar in body size, strength and weaponry, in ecological characteristics and dietary needs, and in social styles and mating strategies, including confidence of parenthood. In other species, males and females may be equally aggressive because competition for resources is mediated by competition for social status, and such competition is equally intense for males and females. For example, in rhesus macaques and many other cercopithecine monkeys, both males and females have rigid dominance hierarchies that regulate access to resources. Aggressive competition for high status is highly beneficial to males in terms of higher access to fertile females during the mating season and to females in terms of greater access to food and better protection of the offspring during the birth season (Maestripieri, 2007). Since sexual dimorphism in body size, physical strength, and weaponry is limited in rhesus macaques, the physical costs of aggression are probably similar for males and females. Overall, the benefit/cost ratio of

aggression is high for both male and female rhesus macaques, and in this species, there are no observable differences in male and female aggressiveness.

Benefits and costs of violent aggression in humans

Human beings clearly have the ability to live peacefully in close proximity to millions of other people, as it happens in many cities around the world. Yet, violent crimes have been reported in every human society, and wars and genocide have occurred repeatedly throughout human history (Pinker, 2011). Human beings seem to have a high potential for violent aggression and since virtually all wars have been fought by men and most murders and other violent crimes are committed by men, this aggressive potential seems to be much higher in men than in women. Women, however, are not necessarily peaceful; they also engage in many forms of aggression—physical, verbal, and psychological. Relative to other animals, humans should probably be categorized as one of the most aggressive species, and one in which there is a relatively large sex difference in aggression. To explain the characteristics of human aggression from a comparative perspective, we will first examine the benefits and costs of aggression for the species as a whole, and then for males and females separately.

As with other animals, the benefits of aggression in humans depend on the characteristics of the resources being fought over. From an evolutionary perspective, it is likely that competition for food, mates, and territories played a key role in shaping our aggressive nature. Modern humans are omnivorous and there are large geographic, cultural, and individual differences in the extent to which our diet includes meat, fish, dairy products, or vegetables. For much of human evolutionary history, however, our diet was probably more similar to that of chimpanzees than to that of herbivorous or folivorous animals. Meat, fruit, and other highly caloric foods have probably always been a central component of the human diet. The benefits of aggressive competition over valuable food that can be effectively monopolized by individuals or groups was probably high throughout the early history of *Homo sapiens* and that of our most recent hominid and nonhuman primate ancestors. Insofar as valuable food was localized in areas that could be effectively defended, aggressive competition for space was also highly beneficial. Human beings are a highly territorial species, both at the individual and at the group level. Trespassing into another individual's territory can elicit highly aggressive responses, particularly by men. At the group level, territorial disputes between countries or ethnic groups have precipitated many wars, not to mention the colonization of other continents and the extermination of local people (Diamond, 1997).

Aggressive competition for access to mates is much more beneficial for human males than for females, as will be discussed below. Whether aggressive competition is over food, territories, mates, or the social status that enhances the access to these valuable resources, it is safe to conclude that ours is a species in which inter-individual competition can be very intense and in which aggressive competitive strategies can be highly beneficial, especially for males.

Relative to some other mammals, humans are not particularly large and strong, or equipped with dangerous weapons such as large and sharp canine teeth or claws, or horns or antlers. Before humans started using objects and tools as weapons, physical combat depended on hits inflicted with hands or feet, and scratches or bites. The risk of injury or death from this type of fighting is relatively low, when compared with the potential costs of fighting in larger and more dangerous animals such as elephants or rhinos, lions or tigers, bears or crocodiles, deer or goats. Therefore, the physical costs of aggression in humans are relatively low compared to some other species. An additional factor that reduces the cost of

aggression in humans is the ability of men to form coalitions (Wrangham, 1999). Similar to the pattern typical of inter-group coalitionary aggression in male chimpanzees, hunter-gatherer men kill rivals from neighboring groups when opportunities for low-cost aggression ('safe killing') are present, i.e., when the attacking group has a numerical advantage and the victims are unprepared to retaliate (Wrangham and Glowacki, 2012).

The energetic costs of aggression are probably lower for humans than for other, larger-bodied animals. However, muscle mass is energetically expensive to build and maintain; an adult man's muscle tissue can consume up to one-fifth of his energy (Muehlenbein and Bribiescas, 2005). Sexual dimorphism in body composition—especially in the upper body, where it is most useful in aggressive contexts—suggests that the costs of fighting in human populations are not insignificant (Sell, Tooby, and Cosmides, 2009); human females cannot afford to develop such costly weaponry given the energetic demands of pregnancy and lactation. That human males allocate so much energy to musculature development despite the fact that it is a substantial caloric investment further evinces the benefits of being aggressive.

The psychological and hormonal costs of aggression in humans are probably comparable to those in other social species, or possibly higher given that humans have greater ability for thinking about the self and greater ability to feel empathy for others' pain. However, these stress-related costs of aggression are expected to be significant mainly with regard to aggression between family members, or friends and allies. These costs may be much lower if aggression is directed toward enemies from other groups.

Finally, the social costs of human aggression are expected to be high when fighting occurs between relatives, friends and allies, or members of one's group, and low when aggression is directed toward unrelated individuals belonging to other groups. Although violent aggression is quite common between related individuals or unrelated but highly familiar individuals, such rates of aggression are actually low controlling for the amount of time that these individuals spend together. Human beings have opportunities to interact with many unrelated individuals from other groups to a much greater extent than other animals. If damage to valuable social relationships is considered one of the main social costs of aggression, then aggression toward individuals in other groups has low social costs because relationships with them are nonexistent. Similarly, large-scale aggression toward other groups, such as in wars, has low social costs.

The invention and elaboration of projectile weapons, from hand-held spears to remotely controlled drones, and the consequent ability to hit, injure, and kill other individuals from a distance has brought about a significant reduction of all the costs of aggression. Killing someone from a distance by launching a spear or firing a gun has virtually eliminated the risk of physical injury for the aggressor. The energy expenditure involved in the use of various types of weapons is minimal as well. Finally, the psychological, physiological, and social costs of aggression through projectile weapons are also low, because this type of aggression allows one to attack individuals (or groups) that are not seen or known, with whom there are no social relationships of any kind, and without being exposed to the direct consequences of the violence.

With some exceptions, competition through violent aggression generally has a high benefit/cost ratio for humans. Consider, for example, the situation of the European colonial armies that first encountered the local populations in America, Africa, Asia, or Australia. The benefits of using violent aggression against the indigenous populations were enormous: taking away their land, their possessions, and even their people to use as slaves. The costs of the colonists' aggression were minimal: armed with rifles, they could quickly kill large

numbers of indigenous individuals at little or no physical risk to themselves. Moreover, the indigenous populations looked different and spoke a different language; it must have been quite easy for the colonists to find a psychological, political, historical, or religious justification for their violence, without suffering any consequences. These unusually high benefit/cost ratios for violent aggression against people from other countries are rare or nonexistent in animals, which may explain why large-scale aggression toward conspecifics is absent in animals, with the possible exception of chimpanzees and some species of ants and termites that stage wars against other colonies, destroying or taking away their resources and enslaving the workers.

When the benefit/cost ratio of violent aggression is lowered, for example, by punishing aggressive individuals or imposing sanctions on belligerent countries, humans do become less aggressive. A historical trend for a general reduction in human violent aggression (Pinker, 2011) suggests that human behavior is sensitive to current selective pressures and any changes in the environment that might affect its adaptive value. The benefits and costs of human violent aggression may vary and be differentially weighted not only over historical time but also in relation to geographic location, culture, education, intelligence, religion, availability of resources, and many other factors. To give just one example of this variation, consider two human populations such as the Moriori of the Chatham Islands and the Maori of New Zealand (Diamond, 1997). Although both populations had descended from the same group of Polynesian farmers, the Maori had developed a culture of violence and war while the Moriori had developed a culture of peaceful resolution. This disparity was likely due to a complex combination of environmental and technological factors that calibrated the costs and benefits of violence differently for each population. The Maori lived in a climate stable enough to permit agriculture, which allowed for the development of more advanced weaponry and for increased population growth, leading to the emergence of tribes and coalitions. A culture of violent aggression would have been advantageous for the Maori, as a system of agriculture would have increased the benefit of fighting over monopolizable food and territory, while the use of weapons and the formation of coalitions would have minimized costs. In contrast, the harsh environmental conditions on the Chatham Islands impeded technological advancement and population growth and forced the Moriori to revert back to the hunter-gatherer lifestyle. The Moriori could not effectively monopolize food resources, had very simple weaponry, and remained a small population with few or no subgroups. Violent aggression may have been more costly than beneficial for the Moriori, and so a culture of peaceful resolution to conflict emerged on the Chatham Islands. Not surprisingly, when these populations came into contact in 1835, the aggressive Maori exterminated the peaceful Moriori (Diamond, 1997).

Sex differences in human aggression

Sexual selection theory provides the most convincing evolutionary explanation for the marked difference in aggressiveness between men and women (Archer, 2009; Lindenfors and Tullberg, 2011; Puts, 2010). The benefits of both intra- and inter-sexual aggression are higher for men than women and they are all related to reproductive effort (competition for mates and sexual coercion). Among our ancestors, males who were successful in aggressively keeping their competitors away from fertile females, who could monopolize these females during their fertile periods and mate exclusively with them, and who could overcome any female reticence to mate through aggressive coercion presumably gained a great deal in terms of reproductive success. In contrast, the advantage gained by females who aggressively competed against other females to mate with superior males may have been relatively small, given that many females managed to reproduce regardless of their competitive ability, superior males may have been difficult to find, and monopolizing mating with these superior males would have little benefit. For these reasons, attempting to

aggressively coerce and monopolize superior males was probably ineffective and did not bring females significant reproductive benefits.

Risk of injury or death, and energetic, stress-related, and social costs of intra-sexual aggression may be generally equal in males and females. Being pregnant or having to breastfeed a child, however, poses a significant energetic constraint on a human female's ability to engage in violent aggressive behavior—and indeed even on her ability to build the muscle necessary to win confrontations. Although relative to other primates humans are not highly sexually dimorphic (Plavcan, 2012), differences in male and female stature, musculature development and strength are not insignificant. Thus, sexual selection pressures favoring the increase in body size and aggressiveness in males presumably increased the costs of female aggression. Human females likely developed alternative, non-physical competitive strategies such as verbal social/relational aggression toward other women and social manipulation tactics involving sex and investment with men.

Conclusions

The use of aggression in the context of intra-specific competition for resources can be viewed as an optimization problem and investigated with the fitness cost/benefit analyses typically used in behavioral ecology. Aggressive competitive strategies evolve when the benefits of aggression outweigh its costs and when its benefit/cost ratio is higher than that of alternative, non-aggressive strategies. The benefits and costs of aggressive competition depend on organisms' physical characteristics, their diet, their mating system and reproduction, and their anti-predator and social strategies as well as on their environment.

Humans—males more than females—have a propensity to compete for resources with others, especially non-group members, via violent aggression, when compared to other animal species. This characteristic of human nature likely evolved because ancestral humans could fight with rivals or rival bands at relatively low cost (low risk of lethal injury, or extreme energetic depletion or social stigmatization) but with significant benefit (access to valuable resources such as meat and fertile females). Sexual dimorphism in body size, muscle mass, and physical strength also favors male sexual coercion of females. Lower physical aggressiveness in human females is likely accounted for by lower benefits and higher costs of aggression, in addition to constraints imposed by reproduction.

A high potential for aggression appears to be a relatively stable characteristic of human nature that is best understood from a comparative perspective, by examining animal species that are subjected to similar selective pressures and/or are phylogenetically close to us. Predicting, however, the extent to which violent aggression is actually exhibited in human social interactions at the individual or the group level requires a consideration of historical, geographic, and cultural factors because these factors can impact the benefits and costs of aggression as much as other biological or environmental variables.

References

Abbott D, Keverne E, Bercovitch F, Shively C, Mendoza S, Saltzman W, Snowdon C, Ziegler T, Banjevic M, Garland T, Sapolsky R. Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. Hormones and Behavior. 2003; 43:67–82. [PubMed: 12614636]

Alonso-Alvarez C, Bertrand S, Faivre B, Chastel O, Sorci G. Testosterone and oxidative stress: The oxidation handicap hypothesis. Proceedings of the Royal Society of London B. 2007; 274:819–825.

Ancona S, Drummond H, Zalvidar-Rae J. Male whiptail lizards adjust energetically costly mate guarding to male-male competition and female reproductive value. Animal Behaviour. 2010; 79:75–82.

Archer J. Does sexual selection explain human sex differences in aggression? Behavioral and Brain Sciences. 2009; 32:249–311. [PubMed: 19691899]

Aureli F, Cords M, van Schaik CP. Conflict resolution following aggression in gregarious animals: A predictive framework. Animal Behaviour. 2002; 64:325–343.

Baker JR, McCann TS. Pathology and bacteriology of adult male antarctic fur seals, *Arctocephalus gazella*, dying at Bird Island, South Georgia. British Veterinary Journal. 1989; 145:263–275. [PubMed: 2736383]

Barrett, L.; Dunbar, R.; Lycett, J. Human evolutionary psychology. Basingstoke and New York: Palgrave; 2002.

Belsky J, Steinberg L, Draper P. Childhood experience, interpersonal development, and reproductive strategy: An evolutionary theory of socialization. Child Development. 1991; 62:647–670. [PubMed: 1935336]

Briffa M, Sneddon LU. Physiological constraints on contest behaviour. Functional Ecology. 2007; 21:627–637.

Buss DM. Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. Behavioral and Brain Sciences. 1989; 12:1–49.

Buss, DM., editor. The handbook of evolutionary psychology. Hoboken, NJ: John Wiley and Sons, Inc; 2005.

Buss, DM.; Dentley, JD. The evolution of aggression. In: Schaller, M.; Simpson, JA.; Kenrick, DT., editors. Evolution and social psychology. Madison, CT: Psychosocial Press; 2006. p. 263-285.

Buss DM, Shackelford TK. Human aggression in evolutionary psychological perspective. Clinical Psychology Review. 1997; 17:605–619. [PubMed: 9336687]

Campbell A. Staying alive: evolution, culture, and women's intrasexual aggression. Behavioral and Brain Sciences. 1999; 22:203–252. [PubMed: 11301523]

Clutton-Brock TH. The functions of antlers. Behaviour. 1982; 79:108–124.

Clutton-Brock TH. Review lecture: Mammalian mating systems. Proceedings of the Royal Society of London B. 1989; 236:339–372.

Clutton-Brock, TH. The evolution of parental care. Princeton, NJ: Princeton University Press; 1991.

Clutton-Brock TH. Sexual selection in females. Animal Behaviour. 2009; 77:3–11.

Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE. The logical stag: Adaptive aspects of fighting in red deer (*Cervus elaphus*l.). Animal Behaviour. 1979; 27:211–225.

Clutton-Brock, TH.; Guiness, FE.; Albon, SD. Red deer: Behavior and ecology of two sexes. Chicago: University of Chicago Press; 1982.

Clutton-Brock TH, Harvey PH. Primate ecology and social organization. Journal of Zoology. 1977; 183:1–39.

Clutton-Brock, TH.; Harvey, PH. Comparative approaches to investigating adaptation. In: Krebs, JR.; Davies, NB., editors. Behavioral ecology: An evolutionary approach. 2. Sunderland, MA: Sinauer Associates; 1984.

Clutton-Brock TH, Parker GA. Sexual coercion in animal societies. Animal Behaviour. 1995; 49:1345–1365.

Clutton-Brock TH, Vincent ACJ. Sexual selection and the potential reproductive rates of males and females. Nature. 1991; 351:58–60. [PubMed: 2027382]

Creel S. Social dominance and stress hormones. Trends in Ecology and Evolution. 2001; 16:491–497.

Creel, S.; Sands, J. Is social stress a consequence of subordination or a cost of dominance? In: de Waal, F.; Tyack, P., editors. Animal social complexity. Cambridge, MA: Harvard University Press; 2003. p. 153-169.

Crofoot, MC.; Wrangham, RW. Intergroup aggression in primates and humans: The case for a unified theory. In: Kappeler, PM.; Silk, JB., editors. Mind the gap: Tracing the origins of human universals. Berlin and Heidelberg: Springer-Verlag; 2009.

Daly M, Wilson MI. Human evolutionary psychology and animal behaviour. Animal Behaviour. 1999; 57:509–519. [PubMed: 10196040]

Darwin, C. On the origin of species. London: John Murray; 1859.

Darwin, C. The descent of man and selection in relation to sex. London: John Murray; 1871.

de Waal FBM. Primates - a natural heritage of conflict resolution. Science. 2000; 289:586–590. [PubMed: 10915614]

Diamond, J. Guns, germs, and steel: The fates of human societies. New York, NY: W. W. Norton and Company; 1997.

Diaz-Uriarte R. Anti-predator behaviour changes following an aggressive encounter in the lizard *tropidurus hispidus*. Proceedings of the Royal Society of London B. 1999; 266:2457–2464.

Dunbar, RIM.; Barrett, L., editors. Oxford handbook of evolutionary psychology. Oxford: Oxford University Press; 2007.

Dunham AE. Battle of the sexes: Cost asymmetry explains female dominance in lemurs. Animal Behaviour. 2008; 76:1435–1439.

Dunn PO, Whittingham LA, Pitcher TE. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. Evolution. 2001; 55:161–175. [PubMed: 11263736]

Eens M, Pinxten R. Sex-role reversal in vertebrates: Behavioural and endocrinological accounts. Behavioural Processes. 2000; 51:135–147. [PubMed: 11074317]

Eibl-Eibesfeldt, I. Love and hate: The natural history of behavior patterns. New York, NY: Holt, Rinehart and Winston; 1972.

Emery Thompson, M.; Alvarado, LC. Sexual conflict and sexual coercion in comparative evolutionary perspective. In: Shackelford, TK.; Goetz, AT., editors. The oxford handbook of sexual conflict in humans. Oxford: Oxford University Press; 2012.

Emery Thompson M, Newton-Fisher N, Reynolds V. Probable community transfer of parous adult female chimpanzees in the budongo forest, uganda. International Journal of Primatology. 2006; 27:1601–1617.

Emery Thompson M, Wrangham RW. Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. American Journal of Physical Anthropology. 2008; 135:171–181. [PubMed: 18046778]

Emlen ST, Oring LW. Ecology, sexual selection and the evolution of mating systems. Science. 1977; 197:215–223. [PubMed: 327542]

Fabiani A, Galimberti F, Sanvito S, Hoelzel AR. Extreme polygyny among southern elephant seals on sea lion island, falkland islands. Behavioral Ecology. 2004; 15:961–969.

Folstad I, Karter AJ. Parasites, bright males, and the immunocompetence handicap. The American Naturalist. 1992; 139:603–622.

Fuxjager MJ, Foufopoulos J, Diaz-Uriarte R, Marler CA. Functionally opposing effects of testosterone on two different types of parasite: Implications for the immunocompetence handicap hypothesis. Functional Ecology. 2011; 25:132–138.

Galimberti F, Sanvito S, Braschi C, Boitani L. The cost of success: Reproductive effort in male southern elephant seals (*Mirounga leonina*). Behavioral Ecology and Sociobiology. 2007; 62:159–171.

Gangestad SW, Simpson JA. The evolution of human mating: Trade-offs and strategic pluralism. Behavioral and Brain Sciences. 2000; 23:573–644. [PubMed: 11301543]

Geist V. The evolution of horn-like organs. Behaviour. 1966; 27:175–214.

Geist V. On fighting strategies in animal combat. Nature. 1974; 250:354. [PubMed: 4852701]

Georgiev, AV. PhD dissertation. Harvard University; Cambridge, MA: 2012. Energetic costs of reproductive effort in male chimpanzees.

Golabek KA, Ridley AR, Radford AN. Food availability affects strength of seasonal territorial behaviour in a cooperatively breeding bird. Animal Behaviour. 2012; 83:613–619.

Goodall, J.; Bandora, A.; Bermann, E.; Busse, C.; Matama, H.; Mpongo, E.; Pierce, A.; Riss, D. Intercommunity interactions in the chimpanzee population of gombe national park. In: Hamburg, DA.; McCown, ER., editors. The great apes. Menlo Park, CA: Benjamin/Cummings; 1979.

Hack MA. The energetic costs of fighting in the house cricket, *Acheta domesticus*l. Behavioral Ecology. 1997; 8:28–36.

Hare B, Wobber V, Wrangham RW. The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. Animal Behaviour. 2012; 83:573–585.

Harris T. Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behavioral Ecology and Sociobiology. 2006; 61:317–329.

Hemelrijk CK, Wantia J, Isler K. Female dominance over males in primates: Self-organisation and sexual dimorphism. Plos One. 2008; 3:e2678.10.1371/journal.pone0002678 [PubMed: 18628830]

Higham JP, Heistermann M, Maestripieri D. The energetics of male-male endurance rivalry in free-ranging rhesus macaques, *Macaca mulatta*. Animal Behaviour. 2011; 81:1001–1007.

Hoffman CL, Ruiz-Lambides V, Davila E, Maldonado E, Gerald MS, Maestripieri D. Sex differences in survival costs of reproduction in a promiscuous primate. Behavioral Ecology and Sociobiology. 2008; 62:1711–1718. [PubMed: 23645968]

Holbrook SJ, Schmitt RJ. Competition for shelter space causes density-dependent predation mortality in damselfishes. Ecology. 2002; 83:2855–2868.

Isbell LA. Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. Behavioral Ecology. 1991; 2:143–155.

Jakobsson S, Brick O, Kullberg C. Escalated fighting behaviour incurs increased predation risk. Animal Behaviour. 1995; 49:235–239.

Kahlenberg S, Emery Thompson M, Muller M, Wrangham R. Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. Animal Behaviour. 2007; 76:1497–1509.

Kahlenberg SM, Emery Thompson M, Wrangham RW. Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. International Journal of Primatology. 2008; 29:931–947.

Kappeler PM. Female dominance in *Lemur catta*: More than just female feeding priority? Folia Primatologica. 1990; 55:92–95.

Kappeler, PM.; Silk, JB., editors. Mind the gap: Tracing the origins of human universals. Berlin and Heidelberg: Springer-Verlag; 2009.

Knott, C. PhD dissertation. Harvard University; Cambridge, MA: 1999. Reproductive, physiological and behavioral responses of orangutans in borneo to fluctuations in food availability.

Knott CD, Laman T. Orangutans in the wild. National Geographic. 1998; 194:30–57.

Koenig A, Borries C. The lost dream of ecological determinism: Time to say goodbye? … or a white queen's proposal? Evolutionary Anthropology. 2009; 18:166–174.

Kruuk, H. The spotted hyena: A study of predation and social behavior. Chicago: University of Chicago Press; 1972.

Liddle JR, Shackelford TK, Weekes-Shackelford VA. Why can't we all just get along? Evolutionary perspectives on violence, homicide, and war. Review of General Psychology. 2012; 16:24–36.

Lindenfors, P.; Gittleman, JL.; Jones, KE. Sexual size dimorphism in mammals. In: Fairbairn, DJ.; Blanckenhorn, WU.; ST, editors. Sex, size and gender roles: Evolutionary studies of sexual size dimorphism. Oxford: Oxford University Press; 2007.

Lindenfors P, Tullberg BS. Evolutionary aspects of aggression: the importance of sexual selection. Advances in Genetics. 2011; 75:7–21. [PubMed: 22078475]

Low M. The energetic cost of mate guarding is correlated with territorial intrusions in the new zealand stitchbird. Behavioral Ecology. 2006; 17:270–276.

MacCormick HA, MacNulty DR, Bosacker AL, Lehman C, Bailey A, Anthony Collins D, Packer C. Male and female aggression: Lessons from sex, rank, age, and injury in olive baboons. Behavioral Ecology. 2012; 23:684–691.

Maestripieri D. Functional aspects of maternal aggression in mammals. Canadian Journal of Zoology. 1992; 70:1069–1077.

Maestripieri, D. Macachiavellian intelligence: How rhesus macaques and humans have conquered the world. Chicago: University of Chicago Press; 2007.

Maestripieri D, Carroll KA. Costs and benefits of female aggressiveness in humans and other mammals. Behavioral and Brain Sciences. 1999; 22:231–232.

Malo AF, Roldan ERS, Garde J, Soler AJ, Gomendio M. Antlers honestly advertise sperm production and quality. Proceedings of the Royal Society of London B. 2005; 272:149–157.

Marler CA, Walsberg G, White ML, Moore M. Increased energy expenditure due to increased territorial defense in male lizzards after phenotypic manipulation. Behavioral Ecology and Sociobiology. 1995; 37:225–231.

Meredith, SL. PhD dissertation. Arizona State University; Phoenix, AZ: 2012. The development of adult sex-typed social behavior in Lemur catta.

Mitani JC, Watts DP, Amsler SJ. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. Current Biology. 2010; 20:R507–R508. [PubMed: 20620900]

Morris, D. The naked ape : A zoologist's study of the human animal. London: Cape; 1967.

Muehlenbein MP, Bribiescas RG. Testosterone-mediated immune functions and male life histories. American Journal of Human Biology. 2005; 17:527–558. [PubMed: 16136532]

Muller, MN. Agonistic relations among kanyawara chimpanzees. In: Boesch, C.; Hohmann, G.; Marchant, L., editors. Behavioural diversity in chimpanzees and bonobos. Cambridge: Cambridge University Press; 2002. p. 112-124.

Muller MN, Thompson ME, Kahlenberg SM, Wrangham RW. Sexual coercion by male chimpanzees shows that female choice may be more apparent than real. Behavioral Ecology and Sociobiology. 2011; 65:921–933.

Muller, MN.; Wrangham, RW., editors. Sexual coercion in primates and humans: An evolutionary perspective on male aggression against females. Cambridge, MA: Harvard University Press; 2009.

Nishida T, Hiraiwa-Hasegawa M, Hasegawa T, Takahata Y. Group extinction and female transfer in wild chimpanzees in the mahale national park, tanzania. Zeitschrift für Tierpsychologie. 1985; 67:284–301.

Nunn, CL. The comparative approach in evolutionary anthropology and biology. Chicago: University of Chicago Press; 2011.

Nunn CL, Lindenfors P, Pursall ER, Rolff J. On sexual dimorphism in immune function. Philosophical Transactions of the Royal Society of London B. 2009; 364:61–69.

Palagi E, Antonacci D, Norscia I. Peacemaking on treetops: First evidence of reconciliation from a wild prosimian (*Propithecus verreauxi*). Animal Behaviour. 2008; 76:737–747.

Palombit RA. Lethal territorial aggression in a white-handed gibbon. American Journal of Primatology. 1993; 31:311–318.

Pelletier F, Hogg J, Festa-Bianchet M. Male mating effort in a polygynous ungulate. Behavioral Ecology and Sociobiology. 2006; 60:645–654.

Pérez-Barbería FJ, Gordon IJ, Pagel M. The origins of sexual dimoprhism in body size in ungulates. Evolution. 2002; 56:1276–1285. [PubMed: 12144026]

Pinker, S. The better angels of our nature. New York: Viking; 2011.

Plavcan JM. Sexual size dimorphism, canine dimorphism, and male-male competition in primates. Where do humans fit in? Human Nature. 2012; 23:45–67. [PubMed: 22388772]

Plavcan, JM. Sexual selection, measures of sexual selection, and sexual dimorphism in primates. In: Kappeler, PM.; van Schaik, CP., editors. Sexual selection in primates: New and comparative perspectives. Cambridge: Cambridge University Press; 2004.

Poole JH. Announcing intent - the aggressive state of musth in african elephants. Animal Behaviour. 1989; 37:140–152.

Powers DR, McKee T. The effect of food availability on time and energy expenditures of territorial and non-territorial hummingbirds. Condor. 1994; 96:1064–1075.

Puts DA. Beauty and the beast: Mechanisms of sexual selection in humans. Evolution and Human Behavior. 2010; 31:157–175.

Roberts ML, Buchanan KL, Evans MR. Testing the immunocompetence handicap hypothesis: A review of the evidence. Animal Behaviour. 2004; 68:227–239.

Roney JR, Maestripieri D. The importance of comparative and phylogenetic analyses in the study of adaptation. Behavioral and Brain Sciences. 2002; 25:525–525.

Rosvall KA. Intrasexual competition in females: Evidence for sexual selection? Behavioral Ecology. 2011; 22:1131–1140. [PubMed: 22479137]

Rovero F, Hughes RN, Whiteley NM, Chelazzi G. Estimating the energetic cost of fighting in shore crabs by noninvasive monitoring of heartbeat rate. Animal Behaviour. 2000; 59:705–713. [PubMed: 10792926]

Sapolsky RM. Social status and health in humans and other animals. Annual Review of Anthropology. 2004; 33:393–418.

Schaller, G. The serengeti lion. Chicago: University of Chicago Press; 1972.

Sell A, Tooby J, Cosmides L. Formidability and the logic of human anger. Proceedings of the National Academy of Sciences of the United States of America. 2009; 106:15073–15078. [PubMed: 19666613]

Semel B, Sherman PW. Intraspecific parasitism and nest-site competition in wood ducks. Animal Behaviour. 2001; 61:787–803.

Shively CA, Register TC, Friedman DP, Morgan TM, Thompson J, Lanier T. Social stress-associated depression in adult female cynomolgus monkeys (*Macaca fascicularis*). Biological Psychology. 2005; 69:67–84. [PubMed: 15740826]

Silk J, Alberts S, Altmann J. Social bonds of female baboons enhance infant survival. Science. 2003; 302:1231–1234. [PubMed: 14615543]

Smith EA, Borgerhoff Mulder M, Hill K. Evolutionary analyses of human behaviour: A commentary on Daly and Wilson. Animal Behaviour. 2000; 60:F21–F26.

Smith EA, Borgerhoff Mulder M, Hill K. Controversies in the evolutionary social sciences: A guide for the perplexed. Trends in Ecology and Evolution. 2001; 16:128–135. [PubMed: 11179576]

Smuts BB, Smuts RW. Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. Advances in the Study of Behavior. 1993; 22:1–63.

Snaith TV, Chapman CA. Primate group size and interpreting socioecological models: Do folivores really play by different rules? Evolutionary Anthropology. 2007; 16:94–106.

Southwick CH. An experimental study of intragroup agonistic behavior in rhesus monkeys (*Macaca mulatta*). Behaviour. 1967; 28:182–209. [PubMed: 4959568]

Stockley P, Bro-Jorgensen J. Female competition and its evolutionary consequences in mammals. Biological Reviews. 2011; 86:341–366. [PubMed: 20636474]

Szykman M, Engh AL, Van Horn RC, Boydston EE, Scribner KT, Holekamp KE. Rare male aggression directed toward females in a female-dominated society: Baiting behavior in the spotted hyena. Aggressive Behavior. 2003; 29:457–474.

Tobias JA, Montgomerie R, Lyon BE. The evolution of female ornaments and weaponry: Social selection, sexual selection and ecological competition. Philosophical Transactions of the Royal Society of London B. 2012; 367:2274–2293.

Trivers, RL. Parental investment and sexual selection. In: Campbell, B., editor. Sexual selection and the descent of man. Chicago: Aldine; 1972. p. 136-179.

Van Meter, PE. PhD Dissertation. Michigan State University; East Lansing, MI: 2009. Hormones, stress and aggression in the spotted hyeana (Crocuta crocuta).

van Schaik, CP. The ecology of social relationships amongst females primates. In: Standen, V.; Foley, R., editors. Comparative socioecology. Oxford: Blackwell Scientific Publications; 1989. p. 195-218.

Watts D. Conflict resolution in chimpanzees and the valuable-relationships hypothesis. International Journal of Primatology. 2006; 27:1337–1364.

Watts HE, Tanner JB, Lundrigan BL, Holekamp KE. Post-weaning maternal effects and the evolution of female dominance in the spotted hyena. Proceedings of the Royal Society of London B. 2009; 276:2291–2298.

Wilkinson PF, Shank CS. Rutting-fight mortality among musk oxen on banks island, northwest territories, canada. Animal Behaviour. 1976; 24:756–758.

Williams JM, Oehlert G, Carlis JV, Pusey AE. Why do male chimpanzees defend a group range? Animal Behaviour. 2004; 68:523–532.

Wrangham RW. An ecological model of female-bonded primate groups. Behaviour. 1980; 75:262–300.

Wrangham RW. Drinking competition in vervet monkeys. Animal Behaviour. 1981; 29:904–910.

Wrangham RW. Evolution of coalitionary killing. Yearbook of Physical Anthropology. 1999; 42:1–30.

Wrangham RW, Glowacki L. Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers. Human Nature. 2012; 23:5–29. [PubMed: 22388773]