
Evolution, Biology, and Aggression

D.B. Krupp, Lakehead University

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Summary

There are numerous complementary approaches to the biology of aggression, ranging from genetic to cognitive research. Arguably, the most successful of them have been guided by hypotheses derived from evolutionary theory. In contrast to the view that human aggression is symptomatic of psychological impairment, social disorganization, or both, evolution-minded hypotheses typically begin from the premise that aggression has been designed by natural selection to serve one or more adaptive *functions*, and that the mechanisms involved can be sensitive to cues of reproductive consequences in the social environment. Specifically, anatomical, physiological, and psychological adaptations for aggression are expected to evolve when they help individuals secure resources and matings for themselves and for their genealogical kin. From a theoretical perspective, contexts of predation, sexual competition, and sexual conflict are especially likely to foment aggression. A considerable body of research on aggression in nonhuman animals reinforces the adaptationist position, and central findings of this viewpoint—such as differential risk of violence according to sex and kinship—are closely mirrored in humans. Although many features of human aggression are likely the result of adaptations designed to yield these very features, others are more plausibly understood as byproducts of adaptations designed for different purposes. In either case, evolutionary approaches can help to identify the mechanisms underlying aggression and thereby provide ways to reduce its impact.

Keywords: natural selection, social evolution, violence, homicide, warfare, kinship, relatedness, animal behavior

Subjects: Social Psychology

Introduction

The biology of aggression has, for some time, been divided by two opposing positions. One, consumed by the obvious physical, emotional, and societal toll of aggression, assumes that it is a manifestation of individual or social disorder. The other, cognizant of its equally obvious signs of adaptive design, such as its ubiquity in nature, the widespread existence of

specialized weaponry, and the benefits it brings to aggressors and their relatives, assumes instead that it is a manifestation of evolved function. Perhaps unsurprisingly, the frontier of this division is a single species: *Homo sapiens*.

Human aggression is commonly seen as a symptom of individual impairment, though its causes may nevertheless arise at higher levels of social organization, such as communities or even whole civilizations. Conceivably, this is because the damage that aggression inflicts is often severe. And, just as often, it is unnecessary and repugnant. To the impartial observer, there is no good reason why one man's casual insult should lead to his death at the hands of another when an apology—or simply walking away—would have sufficed. Yet, aggression in other animals is commonly understood as the norm: it is a strategic response to the pernicious and pervasive influence of competition and conflict between agents in the wild, each bearing a distinct and incompatible agenda.¹ The same observer is not so easily puzzled by a flock of seagulls squabbling over scraps of food or by a pair of male elephant seals battling for a harem of females. It is no accident that Tennyson proclaimed Nature “red in tooth and claw.”

Evolutionary theory represents an important bridge connecting human and nonhuman aggression. While recognizing that aggression can result from maladaptive sources of variation, evolution-minded hypotheses extend to humans the same theoretical arguments that explain the origins of aggression in other animals. Like them, humans are in persistent conflict over the state of objects, individuals, or outcomes that depend on the actions of differing parties (Queller & Strassmann, 2018). Aggression is an altogether common result: it is the product of generations of natural selection on the anatomy, physiology, and psychology of species, designing adaptations that maximize reproductive success, particularly in the contexts of predation, sexual competition, and sexual conflict. Consequently, human aggression is expected to be organized, complex, and purposeful. Even when it is not adaptive—as is often the case—it will still be the product of systems that were “purpose-built” to serve evolutionary interests.

Evolutionary Theory and Aggression

Aggression encompasses a vast array of behaviors, particularly in humans. This can include anything from rumormongering to murder (Groves & Anderson, 2019). In the context of evolved function, what unites them is the imposition of a cost on the reproductive success, or fitness, of others. Moreover, it does not much matter whether the cost is actualized by damage or by mere threat: when deterred by an antagonist, a missed opportunity to increase one's fitness is a cost nonetheless.

Of course, for aggression to evolve by natural selection, it must benefit *someone*. Depending on the circumstances, that “someone” may be the aggressor or it may be the aggressor's genealogical kin—individuals who are relatively likely to possess copies of the aggressor's genes and who may also profit from the aggression. By representing the genetic consequences formally with mathematical models (Smaldino, 2017), evolutionary theorists can identify the circumstances in which individuals are expected to gain or lose from acting aggressively.

Because differential reproduction is the wellspring of natural selection, a great deal of aggression is expected to emerge in reproductive contexts—particularly in sexually reproducing species, where diverging fitness interests play out between members of the same sex (sexual competition) and between members of the two sexes (sexual conflict).² This is because the benefits to one party will often come at a cost to the other. For example, an egg that is fertilized by one male is an egg that cannot be fertilized by another, and an egg that is fertilized by an undesirable male is an egg that cannot be fertilized by a desirable one. The former dilemma brings males into competition with one another, whereas the latter brings males into conflict with females.

The intensity of sexual competition and conflict depends on many species-specific physiological and ecological details, but their effects can be captured by two complementary and interrelated measures of sexual selection (Kokko et al., 2012): (1) the average individual's chances of successfully mating, known as the operational sex ratio (Emlen & Oring, 1977); and (2) the size of the reproductive benefit of mating, known as the Bateman gradient (Bateman, 1948; Trivers, 1972). The extent to which one sex invests in aggression, or any other trait, for mating will often depend on both the operational sex ratio and the Bateman gradient. However, it will also trade off against other possible sources of fitness, such as investing more in parental effort (Kokko et al., 2012). Thus, sexual competition and conflict may not necessarily lead to aggression, though they do increase its likelihood.

Social Evolution Theory and Inclusive Fitness

Contemporary arguments for the evolution of aggression emerge from social evolution theory, a framework that synthesizes and builds on earlier theoretical contributions from Hamilton (1964, 1970), Maynard Smith (1982), and Price (1970), among others (for reviews, see Bourke, 2011; Frank, 1998; Marshall, 2015). Indeed, the concept of an evolutionarily stable strategy, a fundamental tool of evolutionary game theory, was coined in an attempt to explain aggression between same-species competitors: Maynard Smith and Price (1973) demonstrated that selection will tend to favor limited conflicts, in which adversaries exercise a degree of restraint, over total conflicts, in which they battle to the death.

Social evolution theory can be applied in many different ways, including at the level of social groups. From a causal standpoint, however, most cases of animal aggression—human or otherwise—are best conceived of as taking place at the individual level, for reasons discussed in Okasha (2016) and Krupp (2016). The progenitor of social evolution theory is the inclusive fitness approach, which follows the change in the frequency of an allele (a gene variant) at the individual level, through its influence on the development of physical and behavioral traits that affect the fitness of its bearers (Hamilton, 1964). Thus, a focal allele will increase in the population when it improves the fitness of individuals expressing it as well as the fitness of others who are more likely than chance to share identical copies of it—namely, genealogical kin. It is this latter effect of the allele on the fitness of others that distinguishes social evolution from classical Darwinian evolution.

Inclusive fitness distinguishes two parties at the center of an interaction: the “actor,” who performs an action, and the “recipient,” who feels the effects of this action firsthand. However, it also accounts for the secondary effects of the action on the actor's and recipient's competitors. This is because populations cannot grow indefinitely, and so gains to one party

must be offset by losses to another (Krupp, 2013). If, for example, the effect increases the actor's fitness, then it also decreases the fitness of the actor's competitors downstream. Similarly, if the effect decreases the recipient's fitness, then it also increases the fitness of the recipient's competitors downstream. Thus, the primary interaction between actor and recipient is distinct from, but intimately linked to, secondary competition in the population.

In structured populations, this competition can range from strictly "global" to strictly "local" (West et al., 2006). Under strictly global competition, interaction partners have equal odds of competing with anyone in the wider population, including each other. Thus, in large populations, the actor can affect the recipient's fitness without either party imposing significant downstream consequences on the other: the actor's fitness is measured against the entire population. Conversely, under strictly local competition, interaction partners are exclusively one another's competitors. Thus, the actor's effect on the recipient entails significant downstream effects on itself: the actor's fitness is measured relative only to the recipient's fitness, and no one else's.

Hamilton's Rule

Inclusive fitness is often formalized by Hamilton's rule, which gives the condition for a trait, such as an act of aggression, to be favored by selection. Hamilton's rule states that a trait will evolve when

$$Rb - c > 0,$$

where c is the net, lifetime cost of the behavior to the actor, b is the net, lifetime benefit of the behavior to the recipient, and R is the genetic relatedness between the actor and recipient. Genetic relatedness was originally measured by r , the probability that the actor and recipient share copies of the focal allele identical by descent, which therefore ranges from 0 to 1. However, this characterization is only a special case (in which competition is global) of a broader concept. Relatedness is better understood as a measure of genetic similarity, relative to the genotypes of the actor's and recipient's average competitors,

$$R = \frac{r - \bar{r}_y}{1 - \bar{r}_x},$$

where \bar{r}_x and \bar{r}_y are, respectively, the probability that a random competitor of the actor and a random competitor of the recipient bear copies of the focal allele identical by descent (Queller, 1994). In this way, R folds together genetic information with information about interaction and competition: if we define "chance" as the frequency of the focal allele among the actor's and recipient's competitors (\bar{r}_x and \bar{r}_y), then "positive" relatedness ($R > 0$) means that the actor and recipient are more likely than chance to bear copies of the focal allele and "negative" relatedness ($R < 0$) means that the actor and recipient are less likely than chance to bear copies of it (Gardner & West, 2004).

Classifying behavior in terms of the net lifetime fitness costs and benefits of an action, the inclusive fitness approach explains the four categories of social behavior: mutual benefit, selfishness, altruism, and spite (Table 1; Krupp, 2013; Patel et al., 2020; West et al., 2007). However, it was first developed to explain the evolution of altruism, which entails, by definition, a fitness cost to the actor and a fitness benefit to the recipient (Hamilton, 1964). An unfortunate quirk of this history is that the two fitness measures run in opposite directions from one another: a fitness increase is represented by $c < 0$ for the actor but by $b > 0$ for the recipient; conversely, a fitness decrease is represented by $c > 0$ but by $b < 0$ for the recipient. Thus, it is important to be mindful of the meanings of the b and c terms.

Table 1. Categories of Social Behavior

		Total Effect on Recipient's Fitness	
		Increase ($b > 0$)	Decrease ($b < 0$)
Total effect on actor's fitness	Increase ($c < 0$)	Mutual benefit	Selfishness
	Decrease ($c > 0$)	Altruism	Spite

Models of the Evolution of Aggression

Social evolution theory holds a few broad implications for the evolution of aggression in humans and other animals. Specifically, because aggression entails a cost to the recipient, it evolves for selfish or spiteful reasons alone (right column of Table 1). Moreover, kinship between actor and recipient can temper aggression under certain conditions, and its absence can inflame aggression under others. The resulting dynamics can be stunningly complex (e.g., Ratnieks et al., 2005), so it can help to illustrate the basic forces by applying Hamilton's rule to a few toy models—numerical examples, really. In each model, individuals in an infinitely large population interact with a partner, paying a cost c (which could be positive or negative) to hurt their social partners by an amount $b < 0$. Based on their payoffs, they then compete either globally or locally with others to reproduce clonal offspring.

Model 1. First, suppose that individuals both interact and compete with random partners drawn from the population at large. That is, interactions are between nonkin and competition is global. This means that $r = \bar{r}_x = \bar{r}_y = 0$ because, in an infinitely large population, random pairs are highly unlikely to bear copies of the same allele identical by descent. Substituting these values into Hamilton's rule gives $\frac{0-0}{1-0}b - c > 0$, which, after simplification and rearrangement, solves to $c < 0$. Thus, in these circumstances, aggression evolves when the actor gains any benefit from it; the cost to the recipient is irrelevant.

Model 2. Second, suppose that individuals typically interact with their kin, with $r = 0.75$, but competition remains global, giving $\bar{r}_x = \bar{r}_y = 0$. Substituting these values into Hamilton's rule gives $\frac{0.75-0.75}{1-0.75}b - c > 0$, which, after simplification and rearrangement, solves to $c/b > 0.75$. Since aggression entails $b < 0$, it must benefit the actor if it is to evolve, and this benefit must be more than three-quarters of the cost to the recipient. In contrast to Model 1, then, aggression is constrained by its effects on the recipients because they are usually kin.

Model 3. Third, suppose that individuals typically both interact and compete locally with their kin, with $r = \bar{r}_x = \bar{r}_y = 0.75$. Substituting these values into Hamilton's rule gives $\frac{0.75-0.75}{1-0.75}b - c > 0$, which, after simplification and rearrangement, solves to $c < 0$. Thus, just as in Model 1, aggression evolves simply when the actor benefits from it. This result may seem surprising since the actor and recipient are likely to be siblings, just as in Model 2. However, in Model 3, the actor's and recipient's *competitors* are also their siblings; hence, the benefits of refraining from harming one sibling are exactly canceled by the costs of that sibling competing with other siblings downstream (Taylor, 1992).

Model 4. Finally, suppose that individuals again tend to compete locally with their kin, with $\bar{r}_x = \bar{r}_y = 0.75$. However, they also have the ability to recognize kin (Krupp & Taylor, 2015), and only aggress when they interact with nonkin, giving $r = 0$. Substituting these values into Hamilton's rule gives $\frac{0-0.75}{1-0.75}b - c > 0$, which, after simplification and rearrangement, solves to $c/b > -3$. Thus, in this example, aggression against nonkin evolves even when the actor pays a cost up to three times *larger* than the cost paid by the recipient. This is because these costs benefit the actor's siblings, who are the recipient's competitors downstream (Krupp & Taylor, 2015).

While these examples lack the specificity of a good model, they suffice to show how the evolution of aggression depends on its effects on actors and their kin in complex ways. Aggression evolves when it selfishly benefits the actor (Models 1–4), but may be curtailed when the actor and recipient are positively related, as they will be when they are kin and competition is global (Model 2). However, this suppressing effect of kinship may instead be countered when actor and recipient, or other kin, are also local competitors (Model 3). Finally, aggression may be spiteful when the actor and recipient are negatively related, as they will tend to be when they are not kin but are both competing against the actor's kin (Model 4); indeed, the actor can pay surprisingly large costs in some cases, as Model 4 shows. Each of these results mirrors an example of aggression in the real world.

The Adaptive Design of Aggression

A theoretical model can show how aggression evolves in principle, but the abstractness that gives the model its power must be converted into concrete, testable hypotheses about the design features of aggression in living organisms if it is to bear empirical fruit. Many such hypotheses begin with the question of evolved function—the apparent goal of the aggressive trait—and the answers lead to hypotheses about form—the mechanisms involved and their developmental (and phylogenetic) origins. The virtue of this method is efficiency: a good functional hypothesis narrows the range of mechanistic and developmental hypotheses from the “possible” to the “plausible” (Daly, 2015; Sherry, 2005).

Interspecific Aggression

Aggression can benefit an individual in a number of ways. The most obvious of these—and, certainly, the easiest to explain—plays out between species. Perhaps because the rationale is so clearly functional, interspecific aggression is often characterized as something other than aggression. Nevertheless, it fits most intuitive definitions of aggressive behavior and can be an instructive entry point for an adaptationist analysis of behavior.

Interspecific aggression commonly emerges when different species compete for the same resources, including food and territory (Grether et al., 2009). This is easily witnessed at backyard birdfeeders, where certain species (e.g., grackles, rock pigeons, and house sparrows) “bully” others away from the seed. However, since it is rarely in an animal's reproductive interests to serve itself up as a meal,³ interspecific aggression, in the form of predation, is also required for many species to survive. Predictably, then, predators come equipped with a wide range of physical and behavioral tools for capturing, killing, and consuming prey. For instance, the sabertooth cats had impressively large canines, but their shapes varied, and so too did their methods of killing prey: scimitar-toothed species likely used their teeth to hold prey, much like lions do, whereas dirk-toothed species used their forelimbs to tackle their prey and then their teeth to stab and shear them (Figueirido et al., 2018). Mantis shrimp also use their forelimbs, often with extraordinary speed and power, to spear or smash their prey (deVries et al., 2012). Or consider venom, which has evolved independently in snakes, scorpions, octopuses, centipedes, spiders, and jellyfish, among other lineages, primarily for the purpose of immobilizing or killing prey (Casewell et al., 2013). Moreover, since venom can be terrifically expensive to produce, numerous species have further evolved to use it selectively or to “meter” its use (Morgenstern & King, 2013).

In response to predation pressure, prey species will go to great lengths to avoid being eaten (Langerhans, 2007). Desert night lizards conceal themselves all day long in the shelter of fallen trees, plants, and rocks (Zweifel & Lowe, 1966). Hiding in plain sight, some fishes and shrimps are translucent (Carvalho et al., 2006), and leafy sea dragons masquerade as seaweed (Cott, 1940). In the presence of predation cues, water fleas dive deeper into the dark of the water column (Cousyn et al., 2001) and produce eggs that delay their development, potentially for decades or more (Ślusarczyk, 1999). When given a choice, hermit crabs wear larger and stronger shells, which are harder for predators to crush (Borjesson & Szelistowski, 1989). Skunks spray a malodorous musk from their hindquarters (with “astonishing” accuracy, according to Cuyler, 1924), Texas horned lizards squirt blood laced with chemical deterrents (Sherbrooke & Middendorf, 2004), and young snails sacrifice their feet to evade capture by snakes (Hoso, 2012).

While impressive, these self-interested antipredator adaptations are limited by the individual’s need to survive the defense itself. In eusocial insects, however, sterile workers and soldiers benefit not from their own survival so much as from the survival of their reproductively viable relatives, and antipredator adaptations can be spectacularly destructive as a result. For instance, honeybees have evolved sting autotomy, whereby their stinging apparatus becomes severed from their body by design. The sting has barbs that hook into the skin of mammalian predators threatening the colony, and the apparatus tears off easily, so the bee sacrifices itself even as it pumps venom into the assailant (Hermann, 1971; Shorter & Rueppell, 2012). More dramatically still, certain ant and termite species have evolved autothysis, in which individuals turn their bodies into explosive chemical weapons of sorts. When faced with arthropod attackers, they rupture their own bodies to spray sticky compounds that immobilize or dispatch the predators, killing themselves in the process (Shorter & Rueppell, 2012).

Intraspecific Aggression

A good deal of the conflict that arises between members of the same species manifests as aggression and violence. While some of the aggression between conspecifics is lethal, most of it is not. In either case, the circumstances surrounding conflict can reveal the psychological design of aggression. For instance, individuals often fight over territory and other “privatized” resources, especially when those resources are valuable, defensible, and rare (Strassmann & Queller, 2014). “Owners” may allow only a select few individuals, such as their offspring or mates, to access a resource, and they may protect it by concealing it, fortifying it, or by using physical force to defend it. Moreover, many species recognize entitlements of ownership: they fight harder as residents, to keep the resource, than as intruders, to steal it away (reviewed in Kokko et al., 2006). Similarly, individuals may evaluate the odds of winning prior to fighting, or during the fight itself, based on information they have gathered about themselves and their competitors (Arnott & Elwood, 2009). Finally, while intraspecific aggression is not limited to sexual contexts, it is liable to arise under chronic competition for mates and conflict over mating.

Sexual Competition

Intraspecific aggression frequently occurs in contests between members of the same sex competing over access to mates or over resources that may attract them (Andersson, 1994). Typically, sexual selection is stronger in males than in females (Janicke et al., 2016; Janicke & Morrow, 2018). As a result, males are usually the more pugnacious sex, and have evolved physical attributes to help them fight (Miller, 2013). This includes growing larger bodies, as evidenced by the seven-fold size difference between males and females of the enormous southern elephant seal (3,510 kg and 503 kg, respectively) and the 12-fold size difference between males and females of the tiny cichlid fish *Lamprologus callipterus* (33.21 g and 2.74 g, respectively; Bininda-Emonds & Gittleman, 2000; Schütz & Taborsky, 2000; reviewed in Fairbairn, 2007). But males also routinely develop armaments, which are used to intimidate or combat other males. As testament to this, some of the most dazzling weapons in nature exist for the purpose of fending off sexual rivals. Fiddler crab claws, Irish elk antlers, and narwhal tusks are among the most notorious examples of sexually selected armaments, but there are countless other species sporting horns, spines, mandibles, claspers, pincers, swords, and saws. Weapons used in male-male contests are highly variable both within and across species, and they tend to evolve when individuals compete over valuable, defendable resources, such as burrows where females congregate (Emlen, 2008a, 2014; see also Rico-Guevara & Hurme, 2019). They can also be highly specialized and remarkably coordinated with behavior: males of different rhinoceros beetle species bear distinct weapons that are adapted to their own species' fighting styles (e.g., twisting, squeezing, lifting, or pushing; McCullough et al., 2014).

Nevertheless, males are not always larger or more aggressive than females. Indeed, females tend to be larger than males in most animal species outside of the mammal and bird classes (Fairbairn, 2007) and, even within these classes, there are exceptions, such as spotted hyenas and jacanas (Emlen & Wrege, 2004; Swanson et al., 2013). Likewise, although females rarely bear sexually selected armaments (jacanas again being a notable exception; Berglund, 2013; Rico-Guevara & Hurme, 2019), they can evolve to be more aggressive in intrasexual contexts than males. Examples include black-chinned tilapia (Balshine-Earn & McAndrew, 1995), northern tidewater gobies (Swenson, 1997), moorhens (Petrie, 1983), and midwife toads (Verrell & Brown, 1993). Such "sex-role reversed" species, and sex role variability more generally, provide a clue to the selection pressures that shaped intrasexual aggression: the Bateman gradient and the operational sex ratio (Kokko et al., 2012). For example, the Bateman gradient predicts sexual dimorphism in body size among four species of seed beetles, two of which are sex-role reversed (Fritzsche & Arnqvist, 2013), and experimental manipulation of the operational sex ratio over multiple generations affects the extent of behavioral sex-role reversal in one of these latter species (Fritzsche et al., 2016).

Sexual Conflict

Finally, intraspecific aggression also emerges when males and females come into conflict over reproduction. Male and female reproductive interests are rarely identical, and sexually antagonistic coevolution will often result, with one sex evolving traits to help them reproduce and the other sex evolving traits to minimize the costs of these effects. For instance, males of many insect species have evolved claspers to hold on to a female during mating, preventing her from ending the reproductive bout earlier. In at least some of these species, females have responded by evolving spines around their genitalia to make copulation more difficult

(Arnqvist & Rowe, 2005). Likewise, males of various seed beetle species have also evolved spiny projections on their genitals, which function to increase the chances of fertilization by puncturing the female reproductive tract (Hotzy et al., 2012), harming females in the process (Rönn et al., 2007). In turn, females have evolved behavioral counteradaptations, such as kicking the males to terminate copulation sooner (Crudgington & Siva-Jothy, 2000), alongside physiological counteradaptations, such as reinforcing the reproductive tract with connective tissue (Rönn et al., 2007). Among bed bugs, males forgo the reproductive tract completely, using their genitals to pierce the female's abdominal wall; unsurprisingly, this also harms females, decreasing their lifespans—and their fitness—as a result (Stutt & Siva-Jothy, 2001).

In many species, males treat females as their property, “guarding” them from other males and limiting their reproductive options. They also engage in sexual coercion and violence (Arnqvist & Rowe, 2005; Lalumière et al., 2005; Wilson & Daly, 1992). Male bottlenose dolphins in groups of two or three will “herd” a female by threatening or attacking her, often while she attempts to escape (Connor et al., 1996). Male chacma baboons intimidate fertile females by attacking them during their estrus cycles and guarding them during ovulation (Baniel et al., 2017). And males of numerous species of waterfowl attempt to force females—whether they are their mates or not—to copulate with them (McKinney & Evarts, 1998).

Last, a male will sometimes kill a female's offspring (infanticide) or destroy her eggs (oocide), neither his own, to increase his opportunities to reproduce with her. If given the opportunity, male *Stegodyphus lineatus* spiders will remove a female's egg sac from her web and throw it to the ground, where it cannot be recovered. Females will aggressively chase males off the web if the males attempt this behavior, but if they are unsuccessful, they will remate with the oocidal males (Schneider & Lubin, 1996, 1997). Similarly, male lions that have taken over a pride will kill the young of the previous male to hasten the mother's sexual receptivity (Packer & Pusey, 1983). Males of several different primate species do this, too, after a male who has sired recent young disappears or becomes indisposed, and females tend to counter infanticidal aggression with aggression of their own, though this strategy is not always effective (van Schaik, 2000).

Alternative Tactics and Polymorphisms

One of the most striking examples of the adaptive design of aggression is the existence of alternative individual “types” or “morphs” that pursue different tactics or strategies. Such polymorphism can be in the service of other colony members, as is the case for workers and soldiers of eusocial species. Consider, for instance, the polyembryonic parasitoid wasp *Copidosoma floridanum*: unlike their reproductive counterparts, soldiers are sterile, develop early, have long bodies and fighting mandibles, and attack nonrelatives (Giron et al., 2004).

However, polymorphisms may also be the expression of alternative tactics or strategies between same-sex rivals to secure reproductive opportunities (reviewed in Oliveira et al., 2008). For example, as a consequence of genetic differences at a single locus, males of the isopod *Paracerceis sculpta* develop into one of three morphs: alphas are large, armed with hornlike uropods, and guard sponges where females congregate to breed, fighting with other alphas to control the sponge; betas are smaller and similar to females in both appearance and behavior, deceiving alphas into giving them access to the sponge and to the females therein; and gammas are smaller still and fast, zipping by alphas to access the sponge (Shuster &

Sassaman, 1997). Likewise, as a consequence of differences in nutritional resources, males of several dung beetle species develop into one of two morphs (reviewed in Emlen, 2008b). Well-fed males grow large, develop long horns, and install themselves inside the entrance of a tunnel where, once again, females congregate to breed. These males use their horns to fight other males attempting to access the tunnel. Conversely, poorly fed males grow small and do not develop horns. Rather than attempt to breach a tunnel through combat, they either sneak by the guarding male or dig their own tunnel and connect it to the main one after they have bypassed the guard.

The existence of alternative tactics among males can also impose costs on females, increasing sexual conflict. This will occur whenever alternative tactics among males decrease female fitness (Alonzo, 2008). For example, in the plainfin midshipman, females are attracted to larger male morphs that court and guard nests, releasing their eggs to be fertilized by these males (Brantley & Bass, 1994). However, smaller males may already be hiding in these nests and surreptitiously fertilize a portion of the eggs instead, thus violating the female's preferences. In more severe cases, the alternative tactics entail aggression via coercion or forced copulation. For instance, female orangutans greatly prefer to mate with territorial male morphs, whereas nomadic morphs are far more likely than their territorial counterparts to attempt forced copulation (Mitani, 1985; reviewed in Setchell, 2008).

Aggression and Kinship

Many of the cases discussed so far illustrate the results of Model 1; that is, when individuals compete globally with nonkin, aggression evolves simply to the extent that it benefits the actor. Thus, predators kill prey, conspecifics assail each other over resources, same-sex rivals fight over mates, and males coerce females into mating with them. As Models 2, 3, and 4 show, however, genealogical kinship and local competition can complicate this picture. The regulation of aggression by kinship and competition can arise as a consequence of dispersal patterns: whether relatives are born, live, and reproduce near each other, or instead migrate elsewhere at one of these stages, may determine an individual's optimal level of aggression toward neighbors. But it can also arise as a consequence of psychological mechanisms designed to estimate kinship and the extent of local competition. Kin recognition systems are common, making use of a range of information, including spatiotemporal context (e.g., interactions inside versus outside the natal colony) and physical and behavioral characteristics correlated with kinship (e.g., odor, coloration, sound; Hepper, 1991; Krupp et al., 2011; Waldman, 1987). Likewise, effects of the availability of resources and mates on behavior illustrate that animals are able to evaluate the intensity of competition, and perhaps also the extent to which competition is local versus global (e.g., Krupp & Cook, 2018).

When individuals compete globally with kin, they can be expected to temper their response, as found in Model 2. Such nepotistic restraint has been documented many times. For instance, social insects such as sweat bees and neotropical termites aggress specifically against unrelated intruders (Adams, 1991; Buckle & Greenberg, 1981), adult pike, guppies, and black mollies preferentially cannibalize unrelated juveniles (Bry & Gillet, 1980; Loekle et al., 1982), and ground squirrels are both less aggressive toward close relatives and more likely to attack and kill unrelated young (Holmes & Sherman, 1982; Sherman, 1981). Vervet monkeys are even disproportionately more likely to threaten the *relatives* of individuals they have

previously fought with (Cheney & Seyfarth, 1986). And, perhaps most remarkably, Argentine ants and guppies tailor their aggression toward relatives as a function of the genetic diversity of their surrounding environments (Daniel, 2020; Tsutsui et al., 2003), as predicted by theoretical models that allow relatedness estimates to be informed by the distribution of kinship cues in the population (Krupp & Taylor, 2013, 2015).

As competition becomes increasingly local, however, kinship may not be enough to mitigate the effects of self-interest, as found in Model 3. Black-tailed prairie dogs, for instance, are more aggressive toward nonkin than kin, but increase their aggression toward kin as competition between them increases (Hoogland, 1986). Communal-nesting female acorn woodpeckers destroy their sisters' eggs before laying their own in their shared nest (Mumme et al., 1983). And male fig wasps of species that spend their entire lives in the same fig adjust their fighting not according to kinship, but to the number of females available in the fruit (West et al., 2001). Indeed, siblicide is a recurring feature of ecologies that breed local competition and occurs in various species of birds, insects, gastropods, and mammals, among others (Mock & Parker, 1998). For example, honeybee queens are outfitted with stingers, which they use just to kill rival sister-queens—their only competitors for reproductive primacy—in tournamentlike fashion (Gilley, 2001). Unlike workers, queens do not die from using their stingers: although their stingers are larger, their barbs are not as defined as those of workers (Shing & Erickson, 1982).

Finally, spiteful aggression can evolve under local competition among nonkin, as found in Model 4. This problem has not received as much empirical attention as selfish aggression, but there are a few well-documented cases of spite in bacteria, including the production of toxic compounds (bacteriocins) that selectively harm nonrelatives (Hawlana, Bashey, & Lively, 2010; Hawlana, Bashey, Mendes-Soares, & Lively, 2010; Inglis et al., 2009), and a few more among animals. Star tunicates fuse with their clones to form a colonywide vasculature, but when they come into contact with unrelated individuals they produce a cytotoxic reaction that destroys the tissues surrounding the contact site (Scofield & Nagashima, 1983). Moreover, the polyembryonic parasitoid wasp *C. floridanum* mentioned previously produces sterile female soldiers who spare their clonal sisters but attack the larvae of unrelated females developing inside the same host (see the section on “Alternative Tactics and Polymorphism”; Gardner et al., 2007; Giron et al., 2004). Interestingly, they also attack their brothers who, because they are not their sisters' clones, have their own interests and may also be negatively related. Thus, spite can evolve even among genealogical (but not clonal) kin.

Collective Violence

Aggression can also play out among organized collectives. For instance, by marking the entrance of a honeybee colony with a pheromone, Asian giant hornet scouts can recruit a handful of their nestmates to slaughter upwards of 30,000 honeybees with terrible efficiency, feeding on them thereafter (Matsuura & Yamane, 1990; Ono et al., 1995). Japanese honeybees, however, can defend themselves with their own form of collective violence, in which they lure the hornet scout into the nest and pounce on it in great numbers: approximately 500 honeybees swarm the hornet, cooking it to death with their body heat (Ono et al., 1995).

Ants also provide many interesting examples (Keller & Gordon, 2009). When presented with cues of rival colonies nearby, *Pheidole pallidula* colonies increase their production of soldiers in anticipation of colony defense (Passera et al., 1996). In the springtime, when they are hungriest, wood ants go to war with other colonies, often recruiting thousands of workers to the battlefield (Mabelis, 1984). And the aptly named army ants make a regular habit of being on the attack, hunting for prey in groups, with different morphological castes serving distinct functions (e.g., Powell & Franks, 2005).

Hornets, honeybees, and ants are bound together by shared interests in genealogical kinship. But collective violence can also be reinforced by self-interest. Unlike any other nonhuman primate, chimpanzees form raiding parties, making incursions into the territories of other communities nearby (Manson & Wrangham, 1991). These raiding parties consist of coalitions of unrelated males drawn from the same community (Goldberg & Wrangham, 1997; Langergraber et al., 2007). These groups significantly outnumber their victims, who are typically single adult males or infants (Wilson et al., 2014). Thus, the expected costs of raids are low, and the killers and their communities appear to benefit over the long term through decreased competition (Wrangham & Glowacki, 2012).

The Adaptive Design of Human Aggression

It is clear that aggression pervades the animal kingdom, often taking complex forms and serving a vast array of functions that enhance survival and reproduction. Against the backdrop of dangerous bodily weapons such as venom, stings, claws, and tusks, however, humans do not seem particularly well-suited to a life of violence. And, relative to many other species, we are not. We are considerably less sexually dimorphic than most primates in size and in our canines (widely used as weapons among primates; Plavcan, 2012; Wrangham, 1993), and the frequency with which we aggress against one another is a mere fraction of the frequencies with which bonobos and chimpanzees, our closest relatives, do (Wrangham, 2018). Yet, humans are hardly meek and mild. With considerable consistency, we hunt, assault, coerce, and kill. The question, then, is whether these behaviors reflect adaptive design in our species as they do in others.

Interspecific Aggression in Humans

One of the ways that humans have distinguished themselves from other primates is by devoting a large portion of their diet to vertebrate meat. Hunter-gatherers consume anywhere from 7 to 140 times more meat than chimpanzees do, amounting to between 26% and 79% of their diets (Kaplan et al., 2000). Nearly all of this meat is the result of hunting game, both large and small, and it is possible that our remarkable capacity for endurance running, as well as the development of tools, arose for this very purpose (Barrett, 2016; Carrier, 1984). Of course, with the advent of agriculture, some individuals have come to eschew meat altogether, and most meat-eaters today do not have to kill their own food.

Intraspecific Aggression in Humans

Sexual Competition in Humans

Most human societies have practiced polygyny either simultaneously, whereby a man maintains a mateship with multiple women concurrently, or serially, whereby a man begins a new mateship after the termination of the previous one (Ember et al., 2007; Fortunato, 2015). By implication, some men will have multiple mates and others will have none. This leads to greater variance in male than female reproductive success in most populations studied (Betzig, 2012; Brown et al., 2009), implying more competition among men. Consequently, we might expect differences between the sexes in anatomy, physiology, cognition, and behaviors associated with aggression.

In keeping with this, men are slightly taller and somewhat heavier, and have substantially more lean muscle and bone mass, on average, than women (Plavcan, 2012; Wells, 2007). These differences are detectable at birth, but increase markedly throughout adrenarche and puberty (Wells, 2007). There is also preliminary evidence that men's hands, arms, and skulls have been designed to deliver—and withstand—blows from buttressed fists (Carrier & Morgan, 2014; Horns et al., 2015; Morgan & Carrier, 2013; Morris et al., 2020). Coupled with the sex differences in muscle and bone mass, this suggests that intrasexual competition has led to the evolution of increased male aggression in humans, but the case requires further examination (Plavcan, 2012).

One of the first dedicated efforts to apply evolutionary theory to human behavior was a decades-long study of homicide, begun in the 1980s, by Martin Daly and Margo Wilson. They noted that, as with other species, intraspecific killing—or, at least, that which occurs within rather than between communities—is unlikely to be adaptive in humans, and is instead better understood as the maladaptive tail of a distribution of aggressive actions (Daly & Wilson, 1988).⁴ However, because of its severity, homicide is the consequence of powerful emotions that may nevertheless reflect the adaptive design of human aggression. Beyond this, it is more likely to be reported and less ambiguous to interpret than other forms of aggression. Consequently, homicide is a useful index of aggressive cognition and behavior. Murder is an extraordinarily risky gambit: victims can fight back, and if they are hurt or killed, the perpetrator (or his kin) may become the target of reprisal. Most instances of violence stop well short of death, even when there is a clear victor who could permanently dispatch his opponent. Indeed, much human aggression is regulated and ritualized. For instance, Yanomamö men engage in duels involving chest pounding, side slapping, and clubbing that allow the combatants to settle the majority of disputes without resorting to killing (Chagnon, 2012).

So, although most instances of homicide are unlikely to be adaptive, patterns of homicide are still predictable from evolutionary theory. Men everywhere are vastly more likely than women to commit homicide, particularly in intrasexual contexts: the overwhelming majority of same-sex homicides are committed by men (Daly & Wilson, 1988, 1990). Moreover, young men are far and away the most likely group to commit violence, arguably because they face more reproductive competition than any other age-sex class (Daly & Wilson, 1988; Wilson & Daly, 1985). Further, conflict over women—ranging from sexual jealousy to infidelity to outright abduction—is a common source of violence (Chagnon, 2012; Daly & Wilson, 1988; Flinn, 1988;

Walker & Bailey, 2013). And, where possible, men who are able to accrue large amounts of resources and power tend to use them to acquire more wives and consorts and to punish other men, often with extraordinary cruelty (Betzig, 1986).

Despite these regularities, homicide rates vary quite a bit over place and time (Daly & Wilson, 1988; Gómez et al., 2016) and this variation is largely due to differences in the tendencies of young men to kill one another. Conflict is expected to increase with inequality in resources (e.g., Daly, 2016; de Courson & Nettle, 2021; Krupp & Cook, 2018), and aggression is expected to rise with it. Accordingly, measures of income inequality explain a substantial share of the variance in homicide rates at the city, region, and country levels (Daly, 2016; Daly & Wilson, 2010; Ouimet, 2012; Wilson & Daly, 1997). Indeed, current research may actually underestimate the effect of inequality on violence, because: (1) homicide is thought to be a response to inequality between local competitors, but income inequality is typically measured at considerably more global scales; and (2) this effect is amplified by the degree of local competition, which is rarely measured at all (Krupp & Cook, 2018).

The large sex difference in homicide rates and the variability therein are important, but they can obscure patterns of competition and aggression among women. Although women typically face less variance in reproductive success than do men, there is some such variance nonetheless, so women are also in competition with one another. As expected, women routinely come into conflict with other women over men, status, and resources, and young women are particularly prone to act aggressively as a result (Campbell, 1995, 2013). However, women's aggression peaks sooner than men's aggression, arguably because they enter into sexual competition earlier, as indicated by the advanced onset of puberty (Campbell, 1995). The relative difference between men and women in the intensity of intrasexual competition likely explains why women's aggression rarely escalates to the same extremes, in terms of both frequency and severity, as men's aggression does (Daly & Wilson, 1988). However, the difference may also be explained in part by sex-specific trade-offs in aggression: maternal contributions are more important than paternal contributions to offspring survival, and so it may pay women more than men to direct investment into parental effort rather than into sexual competition (see Campbell, 1999; Kokko et al., 2012). Thus, we expect, and observe, that women do engage in aggression, but typically less of it—specifically, less of the violent sort (Archer, 2004; Card et al., 2008).

Sexual Conflict in Humans

Human mateships are cooperative alliances, all the more so because we are a biparental species, mutually investing in shared offspring. Nevertheless, mateships have considerable scope for conflict because the reproductive interests of the parties involved are not identical (Wilson & Daly, 1992). For example, it may be in the interests of a woman to increase the extent of investment from mates in her and her offspring by mating with multiple men (Scelza, 2013), but it may be in the interests of any given mate that he sires all of her offspring. Conversely, it may be in the interests of a man to increase offspring number by mating with multiple women, but it may be in the interests of any given mate that he invests only in her offspring. Moreover, since human reproduction proceeds by internal fertilization, there is an asymmetrical risk of cuckoldry—that a man may unknowingly invest in offspring that are not his own.

Marriage, in one form or another, is a universal means of resolving some of this conflict: the parties enter into a socially recognized relationship with mutual obligations and entitlements that reinforce their shared interests (Wilson & Daly, 1992). Yet, marital relations remain a significant source of violence, and the effects are highly sex-biased. As with males of numerous other species, men tend to treat their wives as reproductive “property,” a cross-cultural phenomenon that has been codified in legal systems of independent origin (Daly et al., 1982). For instance, adultery laws have historically criminalized infidelity when it involved a married woman and a man outside of the union but not when it involved a married man and a woman outside of the union. Indeed, violent men are often incensed by circumstances that evoke sexual jealousy (Daly et al., 1982; Daly & Wilson, 1988; Wilson & Daly, 1992; see also Edlund & Sagarin, 2017, for a detailed examination of laboratory research on sex differences in jealousy).

As a consequence of this sexual proprietariness, men may use aggression to exert control over women. They “guard” potential and actual mates from other men, fighting not only with these men but also with the women themselves, especially if those women are fecund and if the relationship is not exclusive (Flinn, 1988). Moreover, men who are especially likely to use nonviolent tactics to limit their wives’ autonomy are also especially likely to assault their wives, and they are increasingly likely to use violence if their wives have separated from them (Wilson et al., 1995). And young women, who have the greatest expected future reproductive output of any age class, are at greatest risk of assault by their husbands (Wilson et al., 1995).

These effects are mirrored by homicide data. Men are considerably more likely to kill their partners if they are in a cohabiting union than if they are in a registered marriage (Daly & Wilson, 1988; Shackelford, 2001a, 2001b; Wilson et al., 1993), though the homicide rates of the former group dropped quite a bit in the early 2000s, converging with those of the latter group (James & Daly, 2012). More striking is the effect of the dissolution of the relationship: men are far more likely to kill partners who have separated from them than those who continue to co-reside with them (Daly & Wilson, 1988; Wilson & Daly, 1993; Wilson et al., 1993, 1995). And, once again, young women are more likely to be killed by their husbands than are women at later ages (Daly & Wilson, 1988; Wilson et al., 1993, 1995). Predictably, men routinely cite the wife’s infidelity (real or imagined) as motivation for their actions, whereas women who kill their partners routinely cite self-defense or defense of their children as motivation (Daly et al., 1982; Daly & Wilson, 1988).

Finally, drawing parallels from a growing literature on nonhuman animals (see the section on “Sexual Conflict”), some have hypothesized that human male psychology has undergone selection for sexual violence, while others have instead suggested that it is a byproduct of other adaptations and is not, in itself, adaptive (e.g., Thornhill & Palmer, 2000). This issue remains highly controversial, in no small part because hypotheses about the adaptiveness of sexual violence are often seen—erroneously—as excusing it (see Travis, 2003, for an array of critical arguments). Unfortunately, both sides of the controversy have failed to address relevant empirical facts in their arguments: that sexual coercion, including forced sex, is widespread in the animal kingdom and throughout human societies; that rapists tend to have an early and varied sexual history and engage in high mating effort; that an appreciable subset of rapists are sexually aroused by depictions of sexual violence whereas most men are not; that rapists do not typically suffer neurodevelopmental problems; that young, unmarried women are highly overrepresented as victims; and that rape is most likely to occur when the expected or perceived costs are low (Lalumière, 2006; Lalumière et al., 2005). While some of

these findings might conform to a particular hypothesis that sexual violence is an adaptation in humans, all fit with the alternative hypothesis that it is not an adaptation but rather is mainly a byproduct of investment in mating effort and antisocial behavior more generally (Lalumière et al., 2005; Palmer, 1991; Symons, 1979).

Alternative Tactics and Polymorphisms in Humans

There is growing evidence of alternative reproductive tactics and behavioral polymorphisms in human aggression. A promising case in the contexts of both sexual competition and sexual conflict is psychopathy, which has been proposed to be an alternative tactic of social and sexual exploitation (Harpending & Sobus, 1987; Harris et al., 2001; Mealey, 1995). Psychopaths are typically risk takers, with low empathy and a versatile criminal history (reviewed in Hare et al., 2012). They are estimated to make up approximately 1% of the general population and 15% of the prison population, and are responsible for a vastly disproportionate amount of violent crime. Men are much more likely than women to meet the diagnostic criteria for psychopathy.

Psychopathy has historically been considered a mental disorder, but there is little evidence that psychopaths bear any of the hallmarks of developmental disruption characteristic of other serious disorders: they are of average intelligence and, relative to nonpsychopathic offenders, have suffered fewer obstetrical problems and show degrees of bilateral symmetry like those of the general population (Harris et al., 2001; Lalumière et al., 2001). Further, psychopaths are less likely to harm their genealogical kin, are more likely to engage in precocious and coercive sexuality, and have as many children, or more, as controls (Harris, Hilton et al., 2007; Harris, Rice et al., 2007; Hilton et al., 2015; Krupp, Sewall, et al., 2012; Lalumière et al., 2001; Vachon et al., 2012). Finally, psychopathy is highly heritable (Dhanani et al., 2018), which suggests that, if adaptive, it may be maintained through negative frequency-dependent selection: that is, it is favored when rare, but performs less well as it becomes common (Mealey, 1995). Of course, more research is needed, particularly in identifying the genetic architecture of psychopathy and in describing the psychological features that form the basis of the putative tactic.

Aggression and Kinship in Humans

As noted in the section “Models of the Evolution of Aggression,” human aggression and violence are clearly patterned in ways expected by social evolution theory. For instance, the vast majority of homicides concern genetically unrelated men competing somewhat globally, as predicted by Model 1.

When both kin and nonkin come into conflict, genetic relatedness is protective, as predicted by Model 2. Within households—which controls for “opportunity” to commit homicide—people are many times more likely to kill their spouses and in-laws than they are to kill their genealogical kin (Daly & Wilson, 1982, 1988). Likewise, relative to genetic offspring, stepchildren are at greatly increased risk of being abused or killed in every culture studied (Daly & Wilson, 1985, 1988, 2001; Lightcap et al., 1982). Again, such homicides are not adaptive in humans: it remains rare for people to kill their spouses, in-laws, or stepchildren;

there is little to gain from it and there is quite a lot to lose. Rather, differential homicide risks reflect a psychology that values genealogical relationships over others, making bonds between kin less conditional than bonds between nonkin (Daly & Wilson, 1980, 1988).

On occasion, local competition arises between kin. This can be especially pernicious in societies in which offspring inherit valuable resources from their parents, because this can put children in competition with their parents (who still hold the resources) and put siblings in competition with each other. In keeping with Model 3, then, killings of parents and siblings typically occur under such locally competitive circumstances (Daly & Wilson, 1988; Daly, Wilson, Salmon et al., 2001; Daly, Wilson, & Vasdev, 2001).

Finally, with respect to Model 4, it is uncertain whether any human ecology satisfies the conditions for the evolution of spite. However, we do appear capable of distinguishing positive from negative relatives, and the widespread existence of ethnocentric behavior is certainly suggestive of a spiteful psychology leading to aggression and violence (Krupp, DeBruine et al., 2012; Krupp & Taylor, 2015). Further research in this area would be valuable.

Collective Violence in Humans

A fair proportion of homicides involve collaboration between two or more perpetrators. In these cases, offenders are more closely related to one another, on average, than either is to the victim, as would be expected from social evolution theory (Daly & Wilson, 1988). Collaborative killing often takes the form of “blood revenge,” a common motive for homicide in which groups avenge the death of a kinsman by eliminating the killer or the killer’s kin. Although this can perpetuate cycles of violent feuding, a swift and decisive response by the victim’s kin may serve to deter retaliation against them, whereas a failure to respond may lead to further exploitation (Chagnon, 1988; Daly & Wilson, 1988). Even if blood revenge is not adaptive per se, it appears to be the product of adaptations for violence: the perpetrators are usually male, risks are often kept low by dint of planned ambushes by groups of related raiders, and benefits can include deterrence and dominance over competing groups.

By extension, warfare may be a more extreme means of using collective violence to realize the benefits of intergroup dominance. Although chimpanzees engage in premeditated violence against outgroup members, humans practice this sort of violence on a far more variable scale (Glowacki et al., 2020). We can do battle in small, loosely organized, voluntary raiding parties and in massive, hierarchically structured, conscripted armies. We have invented a terrifyingly effective arsenal, ranging from arrows capable of killing one at a time to bombs capable of killing millions at once. And, despite this, we are also able to build lasting cooperative relationships with outgroup members, averting the prospect of war for long periods (Glowacki et al., 2020; Hames, 2019; Lopez, 2016).

The reasons for variation in the extent of warfare are unclear (Durrant, 2011; Glowacki et al., 2020). Although hotly debated, the available evidence suggests that human societies were more violent in the past and that a sizable fraction of this violence was due to intergroup conflict (Bowles, 2009; Glowacki et al., 2020; Gómez et al., 2016; Keeley, 1996; Lopez, 2016; Pinker, 2011; Walker & Bailey, 2013). That the vast majority of participants in war are male suggests the possibility of sexual competition (Micheletti et al., 2018), and there is indeed evidence that successful warriors have greater fitness (Chagnon, 1988; Glowacki & Wrangham, 2013, 2015). There may also be benefits of war that are shared among the victors’

wider social groups (Zefferman & Mathew, 2015), such as increased territory size, which may lead to indirect fitness benefits via effects on warriors' genealogical kin. Once more, however, more research is needed to understand how evolutionary processes have shaped the psychology of war: whether humans bear any adaptations for warfare or are simply exercising adaptations designed for other purposes remains a contentious issue.

Conclusions

In much of the social sciences, aggression and violence are routinely characterized as expressions of maladaptation or dysfunction occurring at the level of individuals, communities, or civilizations. That the behavior is harmful implies that something must be *broken*. But an evolutionary perspective that places humans within the wider context of the natural world shows that harm can be *functional*—that it can be the product of successive generations of natural selection designed to increase the fitness of the actor and their kin by securing reproductive and material resources at the expense of others. Such is the story of predation, sexual competition, sexual conflict, and collective violence. There is no inherent contradiction here: violence can be morally wrong and, at the same time, a product of biological adaptation.

By seeking to answer questions about evolved function, we can more easily identify the mechanistic details of aggression and thereby learn to contain it. Knowing the effects of genealogical kinship on child abuse and infanticide may help to inform child protection agencies on how best to keep children safe in their care (Daly & Perry, 2011; Perry et al., 2014). Knowing the effects of inequality on homicide may help shape housing, education, and tax policy to slash the rates of violence, particularly among young men (Daly, 2016; Krupp & Cook, 2018). Knowing the effects of opportunism and mating effort on sexual assault may help institutions to mitigate the risks of coercion (Lalumière et al., 2005). And knowing the effects of revenge motives and individual and group benefits on warfare may help state and nonstate actors to search for alternative routes to achieving their goals without resorting to bloodshed (Glowacki et al., 2020; Lopez, 2016).

Of course, the success of the adaptationist approach depends on more than mere functionalist logic. To move the study of aggression forward, meticulous theory and painstaking empirical research must be coupled with serious efforts to integrate the ecological, genetic, endocrine, neural, and cognitive particulars. Faced with a replication crisis that has roiled many disciplines, including psychology (Open Science Collaboration, 2015), genetics (Duncan et al., 2019), and neuroscience (Botvinik-Nezer et al., 2020; Poldrack et al., 2017), this will be no small task.

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Notes

1. From an evolutionary perspective, the focus herein on animal aggression is somewhat arbitrary. After all, even bacteria have means of hurting their competition (e.g., Hawlena, Bashey, & Lively, 2010; Hawlena, Bashey, Mendes-Soares, & Lively, 2010; Inglis et al., 2009; Riley et al., 2003). Still, to the extent that aggression suggests a state of *motivation*—one that triggers a suite of coordinated physical and psychological responses—animals are ideally suited to empirical investigation of the topic.

2. Determining the number of sexes in a species is a surprisingly nuanced affair that depends on what, exactly, is being counted. Biologists may measure sex by genetic information exchange, gamete size, genitalia, or even mating type (Fusco & Minelli, 2019). Here, the focus is on the effects of genetic information exchange and gamete size in animals, in which case there are typically two sexes. Sex is, of course, also distinct from the concept of gender (Haig, 2004).

3. There are, however, some notable *intraspecific* exceptions to this rule, particularly well-known in spiders. For instance, male redback spiders (*Latrodectus hasselti*) “somersault” into the mouths of their mates (Andrade, 2003), and female black lace-weavers (*Amaurobius ferox*) actively encourage their newborn offspring to consume them (Kim & Horel, 1998). These examples should give pause to anyone attempting to define aggression by the *appearance* of harm to the recipient rather than by the historical inclusive fitness effects of the behavior.

4. For an alternative perspective in which humans have evolved adaptations for homicide, see Duntley and Buss (2011).

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