

RUNNING HEAD: The evolution of offensive realism

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Survival under anarchy from the Pleistocene to the present

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ABSTRACT: Offensive realism, a theory of international relations, holds that states are disposed to competition and conflict because they are self-interested, power maximizing, and fearful of other states. Moreover, it argues that states are obliged to behave this way because doing so favors survival in the international system. Debate continues as to whether modern states actually do, or should, behave in this way, but we are struck by a different question. In this article, we ask whether the three core assumptions about behavior in offensive realism—self-help, power maximization, and outgroup fear—have any basis in scientific knowledge about human behavioral evolution. We find that these precise traits are not only evolutionarily adaptive but also empirically common across the animal kingdom, especially in primate and human societies. Based on these findings, we hypothesize that states behave as offensive realists predict not just because of anarchy in the modern international system but also because of the legacy of our evolution. In short, offensive realism may really be describing the nature of the human species more than the nature of the international system. If our hypothesis is correct, then evolutionary theory offers the following: (1) a novel ultimate cause of offensive realist behavior; (2) an extension of offensive realism to any domain in which humans compete for power; and (3) an

explanation for why individual leaders themselves, and not just states, seek power. However, a key insight from evolution is that the primacy of self-help, power maximization, and fear does not necessarily condemn individuals or groups to competition and conflict; rather, these traits can in themselves give rise to cooperation and alliances.

Recently, a 10-year conflict in the Kibale Mountains of Uganda came to an end. A larger, more powerful community from Ngogo launched a systematic campaign of aggressive and lethal attacks against its neighbors. A couple of times a month, groups of males would venture stealthily and deliberately into the periphery of their neighbors' territory, and, if the invaders found males wandering there alone, they brutally beat them to death. By 2009, after 18 such killings, the rival group had been all but destroyed. The Ngogo group annexed their newly captured area, increasing their territory by more than 20 percent.¹

This story might have come from any number of bloody human conflicts around the world. However, the Ngogo group and their neighbors are chimpanzees. Far from the original view of chimpanzees as boisterous but peaceful human cousins, researchers in recent decades have uncovered that these primates have a systematic tendency to kill males from rival groups.^{2,3,4} As primatologist Richard Wrangham put it, "violence between groups of chimpanzees is like a 'shoot-on-sight' policy."⁵ The strategic rationale is very simple: to eliminate rivals and increase territory. Chimpanzees with larger territories have higher body weights, and females in those territories give birth to more offspring. The motivation for such conquests does not, of course, involve conscious planning to attain larger territories or more offspring. Rather, chimpanzees appear to have evolved an innate aggression toward other groups, a tendency that causes them to attack neighboring males when the opportunity arises, and leads to greater Darwinian reproductive success over time. Under these conditions, such behavior will have been favored by natural selection and spread.

To an observant international relations scholar, the behavior of chimpanzees is remarkably like the behavior of states predicted by the theory of offensive realism. *Offensive realism* holds that states are disposed to competition and conflict because they are self-interested,

power maximizing, and fearful of other states. Moreover, theorists of offensive realism argue that states *should* behave this way because it is the best way to survive in the anarchy of the international system. This parallels the primatologists' argument that the efforts of chimpanzees to seek territorial expansion and as much power as possible represents an adaptive strategy to ensure survival and promote the success of future generations. In this article, we ask whether *human* nature may predispose us, like our nonhuman primate cousins, to behave as offensive realists. Of course, humans are not the same as chimpanzees, although we are close relatives and share a common ancestor around 5 million to 6 million years ago. More important, however, is that we both evolved in conditions of free-for-all competition—of anarchy—without any Leviathan to administer life-and-death struggles with rival groups, a situation well recognized in the study of international relations among states.

We do not propose a naïve transplant of “nature red in tooth and claw” (to quote Tennyson) into international politics. The modern understanding of human evolution rejects the simplistic stereotype that “selfish genes” equates to selfish organisms (Richard Dawkins carefully explained why that is *not* a logical consequence in *The Selfish Gene*⁶). Rather, we build on an accumulation of knowledge about human evolution and behavior derived from anthropology, evolutionary biology, experimental psychology, evolutionary game theory, genetics, and neuroscience. Natural selection has led to a variety of contingent, context-dependent adaptations for maximizing survival and reproduction that include cooperation and alliances as well as self-interest and aggression. So, while the natural sciences recognize the remarkable sociality and mutual dependence exhibited by the human species, these sciences are also unified in recognizing the selective advantages of self-interest and power. Humans may pursue self-interest and power by many means, including patience and reciprocity as well as

coercion and violence. Yet, it is notable that while humans are indeed a remarkably cooperative species, history shows that we have been remarkably good at cooperating in order to—among other things—dominate others and kill.

Note that we do not intend to make the full case for the role of evolution in human behavior. This has been done extensively many times elsewhere.^{7,8,9,10,11,12,13,14,15} Furthermore, we do not intend to make the full case for whether states do or do not act as predicted by offensive realism, which has also been done extensively elsewhere.^{16,17,18} The article focuses instead on our novel theoretical question: *Do the core behavioral assumptions underlying the theory of offensive realism map onto evolved human nature?*

Our argument may be useful for three reasons. First, to whatever extent anarchy deserves its place among realist presumptions, the evolution of human groups interacting in conditions of anarchy deserves study within realism. Previous work has explored the implications of evolved human behaviors for specific *aspects* of politics and international relations, such as ingroup/outgroup bias or risk-taking.¹⁹ However, we ask a bigger-picture question, identifying whether core assumptions underlying international relations theory match scientific knowledge about human evolution and behavior. Our ancestors not only *lived* in a state of anarchy for millions of years, but they also *evolved* in that state of anarchy and consequently developed cognitive and behavioral adaptations specifically to survive and reproduce effectively under conditions of anarchy. Strikingly, therefore, behavioral dispositions that enhanced success in the small-scale intergroup anarchy of humans' evolutionary past may have endowed us with behaviors that also enhance success in the anarchy of the international system.

Second, our argument makes two contributions to the theory of offensive realism: We ground the theory in human evolution (instead of the international system), and we extend it into

new domains (beyond the interaction of states as units of analysis). When grounded in evolutionary theory, offensive realism need not simplify structure to interpret behavior and can parsimoniously develop and test corollaries over the entire span of human history. Our approach also suggests that if offensive realism is a product of human nature, rather than merely a consequence of international anarchy, it can be broadened to explain human conflict at many levels, from tribal warfare, ethnic conflict, and civil wars to domestic politics, commercial competition, and international relations.

Third, by acknowledging that the social and natural sciences are both necessary to understand human behavior, we advance consilience. Incorporating ideas from the life sciences into the social sciences—rich in the study of culture and institutions and other influences on political behavior—will help scholars base their theories in rigorous scientific principles and subject their assumptions to empirical testing.^{20,21} Our approach draws heavily on evolutionary anthropology, which recognizes that human behavior is in large part the result of evolved cognitive, physiological, and behavioral mechanisms designed to solve recurrent problems confronted by our ancestors in the environment in which we evolved. The “environment in which we evolved” typically implies the Pleistocene era, lasting from 2 million years ago until around 10,000 years ago. It is important to appreciate, however, that some influences on human evolution have extended over a much longer timescale. Some of these date from the split with our last nonhuman primate ancestor at the beginning of the Pliocene, around 5 million years ago. Others are even older, such as the limbic system, hormones, and sexual dimorphism, which are shared by countless species extending across all mammals and beyond. The legacies of this long evolutionary history exert powerful influences on our behavior, including our political behavior, even today in large settled societies and in the global arena. Indeed, it is at these vast scales

where our evolved dispositions can have their greatest and most dangerous effects.

The remainder of the article proceeds as follows. First, we explain the theory of offensive realism and the place of anarchy in that theory. Second, we introduce key evolutionary concepts that explicate the human behaviors upon which offensive realism depends. Third, we illuminate offensive realism's new explanatory power when wedded to evolution.

What is offensive realism?

“What made war inevitable was the growth of Athenian power and the fear which this caused in Sparta.”

—Thucydides²²

The core idea of offensive realism is that a state most reliably ensures its security by maximizing its power. This seemingly straightforward idea is controversial, not least among realists themselves. *Defensive* realists argue that too much power—classically, too much military power—*decreases* a state's security because other states will balance against it. Let us begin, therefore, by situating offensive realism in the realist paradigm more generally.

Despite realism's long history as a theory of international politics and its widespread use by scholars and policymakers such as E.H. Carr, George Kennan, Henry Kissinger, and Hans Morgenthau, the traditional realist argument rests on weak foundations. The ultimate causation offered by Morgenthau, the major theorist of *classical realism*, is noumenal—outside the realm of what science can investigate and demonstrate.^{23,24} Morgenthau argued that an *animus dominandi* (desire for power) motivates humans, but he did not explain how such a spirit may be derived logically from his theory or how his theory could be tested scientifically. The result was that the theory lacked, and still lacks, a scientifically describable ultimate cause.

Kenneth Waltz placed realism on a more scientific foundation by introducing a new realist theory: *neorealism* or *structural realism*. Neorealism points to international anarchy, a phenomenon we can evaluate, as the ultimate cause of state behavior. This foundation permits us to reach realist conclusions about international politics, such as the importance of power in interstate relations, without having to believe in Morgenthau's *animus dominandi*.

Waltz's core concept in *Theory of International Politics* is the anarchy that reigns in world politics. That is, there is no ultimate authority in international politics comparable to a domestic government that can adjudicate disputes and provide protection for citizens.^{25,26} Without governmental authority, Waltz argues, the international system is a self-help system, where states must provide for their own protection through arms and alliances. Anarchy allows Waltz to argue that states must behave much the way Morgenthau expected, but for different reasons.

For Waltz, anarchy provides the ultimate cause of state behavior, but he also uses a structuralist analysis in his argument. *Structuralism* is a method of study that focuses on the interaction of the parts, or units of a system, seeing them as more useful to study than the individual units themselves.²⁷ Waltz uses structuralism to demonstrate how the distribution of power in international politics is critical for understanding whether war is more or less likely.²⁸ By wedding anarchy as an ultimate cause and structuralism as a method of analysis, Waltz's neorealism improves upon Morgenthau's realism in two ways. First, neorealism does not rely on noumenal ultimate causation, and, second, it explains and predicts variations in the likelihood of war in international politics—particularly among great powers.

John Mearsheimer's contribution to neorealism has also proved significant. He argues, like Waltz, that the anarchic international system is responsible for much trouble—suspicion,

fear, security competition, and great power wars—in international politics. Also like Waltz, Mearsheimer argues that bipolarity (where two states have the majority of power and international influence) is more stable than multipolarity for three reasons: First, bipolarity provides fewer opportunities for war between or among the superpowers; second, there will tend to be smaller imbalances of power between the superpowers; and, third, there is less potential for great power miscalculation.²⁹

However, unlike Waltz, who fears that too much power for a state will lead other states to seek to achieve a balance of power and thus actually threaten the state's security (the genesis of defensive realism),³⁰ Mearsheimer argues that the international system requires that states maximize their offensive power to be secure and keep rivals from gaining power at their expense.³¹ In fact, this systemic incentive is so powerful that states would become the most powerful of all if they could: "A state's ultimate goal is to be the hegemon in the system."³² Only by being the hegemon can the state be absolutely sure of its security. For Mearsheimer, states seek to maximize power not because they are aggressive, but because the system requires it—this behavior is the best way to maximize security in an anarchic world.

Mearsheimer's argument is a key contribution to the growing body of literature on offensive realism.^{33,34} In general, offensive realists argue that states are compelled to maximize their relative power because of competition in the international system.^{35,36,37} States will be secure only by acting in this way. Eric Labs captured this logic in his argument that, "a strategy that seeks to maximize security through a maximum of relative power is the rational response to anarchy."³⁸

As formulated by Mearsheimer, the theory of offensive realism is a type of neorealism because the principal causes of state behavior are rooted in the anarchic international system.

Mearsheimer outlines five “bedrock” assumptions on which offensive realism stands: (1) the international system is anarchic; (2) great powers inherently possess some offensive military capability; (3) states can never be certain about the intentions of other states; (4) survival is the primary goal of great powers; and (5) great powers are rational actors.³⁹ From these core assumptions, Mearsheimer argues “three general patterns of behavior result: fear, self-help, and power maximization.”⁴⁰ It is these three behaviors that are the focus of our article.

However, we argue that offensive realists need not depend on the anarchy of the state system to advance their argument. Due to the legacy of our evolutionary past, the anarchic state system is not required to obtain offensive realist behavior—only humans are. As a result of our evolution, humans will act like offensive realists even inside the state—that is, in conditions of hierarchy (as far as they are able to)—as well as in relations between states. All anarchy does is remove constraints on pursuing such behavior. By making implicit assumptions about human behavior explicit, offensive realism may become a more powerful theory. Indeed, given our approach, we submit that it is incumbent upon offensive realists to demonstrate why the anarchy of the international political system is necessary as a basis for their theory. We understand that this assertion may be a point of contention and look forward to engaging with our critics on this matter.

The anarchy of evolution

“The Yanomamo among whom I lived were constantly worried about attacks from their neighbors and constantly lived in fear of this possibility”

—Napoleon Chagnon⁴¹

Few principles unite the discipline of international relations, but one exception is *anarchy*—the absence of government in international politics. Anarchy is, ironically, the “ordering” principle of the global state system and the starting point for most major theories of international politics, such as neoliberalism and neorealism.^{42,43,44,45} Other theoretical approaches, such as constructivism, also acknowledge the impact of anarchy, even if only to consider why anarchy occurs and how it can be circumvented.^{46,47} Indeed, the anarchy concept is so profound that it defines and divides the discipline of political science into international politics (politics under conditions of anarchy) and domestic politics (politics under conditions of hierarchy, or government).

Given the prominence of the concept in present-day international relations theory, it is striking that anarchy only took hold as a central feature of scholarship in recent decades, since the publication of Kenneth Waltz’s *Theory of International Politics* in 1979. In fact, however, anarchy has been a constant feature of the entire multimillion year history of the human species (and indeed the 3.5 billion–year history of the evolution of all life on Earth before that). It is not just that we lack a global Leviathan today; humans *never* had such a luxury. The fact that human evolution occurred under conditions of anarchy, that we evolved as hunter-gatherers in an ecological setting of resource competition, predation, and intergroup conflict, and that humans have been subject to natural selection for millions of years has profound consequences for understanding human behavior, not least how humans perceive and act toward others. Scholars often argue over whether *historically* humans experienced a Hobbesian “state of nature,” but—whatever the outcome of that debate—it is certainly a much closer approximation to the *prehistoric* environment in which human brains and behavior evolved.^{48,49,50} This legacy heavily influences our decision-making and behavior today, even—perhaps especially—in the anarchy

of international politics.

We argue that evolution under conditions of anarchy has predisposed human nature toward the behaviors predicted by offensive realism: Humans, particularly men, are strongly self-interested, often fear other groups, and seek more resources, more power, and more influence (as we explain in full later). These strategies are not unique to humans and, in fact, characterize a much broader trend in behavior among mammals as a whole—and especially primates—as well as many other major vertebrate groups, including birds, fish, and reptiles. This recurrence of behavioral patterns across different taxonomic groups suggests that the behaviors characterized by offensive realism have broad and deep evolutionary roots. This perspective does not deny the importance of institutions, norms, and governance in international politics. On the contrary, it provides or adds to the reasons why we demand and need them, and indeed why they are so hard to establish and maintain.

Until recently, international relations theorists rarely used insights from the life sciences to inform their understanding of human behavior. However, rapid advances in the life sciences offer increasing theoretical and empirical challenges to scholars in the social sciences in general and international relations in particular, who are therefore under increasing pressure to address and integrate this knowledge rather than to suppress or ignore it. Whatever one's personal views on evolution, the time has come to explore the implications of evolutionary theory for mainstream theories of international relations.^{51,52}

The most obvious challenge that evolutionary theory presents to international relations concerns our understanding of human nature. Theories purporting to explain human behavior make explicit or implicit assumptions about preferences and motivations, and mainstream theories in international politics are no exception. Many criticisms of international relations

theories focus on these unsubstantiated or contested assumptions about underlying human nature. The parsimony of general theories depends on how well they explain phenomena across space and time; in other words, the more closely they coincide with empirical observations across cultures and throughout history. The most enduring theories of international relations, therefore, will be ones that are able to incorporate (or at least do not run against the grain of) evolutionary theory. Although Thomas Hobbes claimed to have deduced *Leviathan* scientifically from “motion” and the physical senses, he was writing two hundred years before Darwin and so had no understanding of evolution.⁵³ International relations scholars have tended to claim to deduce their own theories from Hobbes, or subsequent philosophers who followed him, and we suggest it is time to revisit the idea of foundational scientific principles. Starting with biology, or with human evolutionary history, has never been typical in international relations scholarship, but this approach is now less exotic than it once seemed as innovators in a range of social sciences, including economics, psychology, sociology, and political science, pursue this line of inquiry.^{54,55,56,57} International relations stands to gain from similar interdisciplinary insights.

At the dawn of the 21st century, an era that will be dominated by science at least as much as philosophy, we have the opportunity to move away from untested assumptions about human nature. Instead, we can make more concrete predictions about how humans tend to think and act in different conditions, based on new scientific knowledge about human cognition and behavior, and in particular a greater understanding of the social and ecological context in which human brains and behaviors evolved. But what was that context?

Human evolution under anarchy: predation, resource competition, and intergroup conflict

“It is hard to escape the conclusion from the ethnographic and archeological evidence from Europe, North America, South American, Australia, and New Guinea that hunter-gatherers both simple and complex engaged in socially sanctioned lethal conflict between independent polities, suggesting an extremely long history of warfare that can ultimately be traced back to early hominins.”

—Terry Jones and Mark Allen⁵⁸

Humans evolved as a distinct lineage principally in the Pleistocene era (from 2 million to 10,000 years ago), and our analysis therefore requires a discussion of the small-scale hunter-gatherer groups that formed the social and ecological context for that era of human evolution. Of the many features of hunter-gatherer society and organization, we focus on intergroup relations, since these are most relevant to the behaviors associated with international relations. While relations *within* groups might be characterized by coordination and cooperation (although internal conflict was important too), relations *between* groups were characterized by competition and conflict (although external cooperation and trade was also possible). A key debate in evolutionary anthropology has revolved around the origins and extent of intergroup conflict among hunter-gatherers, and the emerging consensus is that such conflict is (and has long been) significant and widespread, and that it serves adaptive functions.⁵⁹

Let us first consider these functional advantages. Why would hunter-gatherer groups fight at all? What is the logic for risking life and limb in engaging in violent aggression against other groups? Conflict may seem costly to all parties involved, winners and losers alike, but what matters for natural selection is whether fighting, despite its costs, can bring *net* benefits to Darwinian fitness. Evolutionary theory would expect that intergroup conflict contributes to fitness in certain circumstances if successful defense and offense against outgroups yield

resources and reduce competition in an environment defined by finite resources.^{60,61} A *resource* is any material substance that has the potential to increase the individual's ability to survive or reproduce, such as food, shelter, territory, status, coalition allies, and members of the opposite sex.⁶²

What an evolutionary perspective allows us to understand is that the *origins* of warfare and the *functions* of warfare are interconnected. The origins of warfare are rooted in the imperative to gain and defend resources necessary for survival and reproduction in dangerous and competitive conditions. Competition for resources results in situations where consumption by one individual or group diminishes the amount available for others, or where one individual or group controls the distribution of resources and thus can deny them to others.^{63,64}

In the Pleistocene era, any group facing a shortage of resources (or a need for more, as the group expands) could have adopted one or a combination of three basic strategies. First, the group could eliminate or reduce consumption to make the resource last. This strategy was clearly not an option for critical resources, such as food and water. Second, the group might seek an alternative for the resource, perhaps through technological innovation or by substitution. In the Pleistocene era, this strategy could have been an option with some resources but not others. Third, the group could acquire more of the resource from outside of their territory through migration to uninhabited areas, trade, theft, or warfare.^{65,66,67,68,69,70}

Although warfare is certainly costly to any member of a group who is killed or wounded, as well as in terms of the resources and time expended, it can become the sole (or least bad) choice for a group if migration is risky due to factors such as inhospitable or unproductive terrain or hostile neighboring groups, and where trade is difficult or impossible. For example, a group seeking a fixed source of water may be unable to trade for it if the group lacks adequate

resources to offer in exchange. Warfare might then be necessary for offensive purposes, to plunder resources from others. Aggression may be a risky strategy, but it is a more attractive option than starvation or other lethal dangers. Any given individual's Darwinian fitness will be increased if they can successfully seize the resources of others at sufficiently low cost.⁷¹ Of course, warfare also may be waged for defensive reasons, such as to defend critical resources from the advances of others.⁷² E.O. Wilson captures the evolutionary logic succinctly, saying that humans would fight wars "when they and their closest relatives stand to gain long-term reproductive success," and he continues, "despite appearances to the contrary, warfare may be just one example of the rule that cultural practices are generally adaptive in a Darwinian sense."⁷³ An evolutionary approach allows the expectation that contemporary humans possess specific behavioral traits that contributed to fitness in the past, including the willingness to fight to retain or gain the resources necessary so that the individual, the family, and the extended family group would continue to survive and reproduce.⁷⁴

Unsurprisingly, direct evidence of human behavior from the Pleistocene era is rare, but in addition to archeological finds, we have evidence from recent and contemporary indigenous societies that offer a model for the behavior of our distant ancestors, who lived under similar social and ecological conditions. Napoleon Chagnon's work among the Yanomamo of the Amazon revealed that indigenous groups had a constant need to find new territory as they expanded and split, and they experienced a constant fear of other groups because violent conflict was a recurring strategy used to stake out a livelihood.⁷⁵ The Yanomamo are just one example of a pattern that extends to a wide range of indigenous societies around the world.^{76,77} Across such societies, around 15 percent of male deaths occurred in warfare, which compares to a figure of around 1 percent for the United States and Europe in the so-called bloody 20th century (and in

many of those small-scale indigenous societies, the rate of male deaths from warfare is much higher than **the** average figure of 15 percent).^{78,79}

It has been argued that such high levels of conflict among indigenous societies might have been caused by pressure from more developed societies encroaching on their territories and way of life from the outside. However, a study by Wrangham and Glowacki, which explicitly looked at warfare among hunter-gatherers who were surrounded by other hunter-gatherers, found that warfare was just as common in this more “natural” setting.⁸⁰ Evidence from across the cumulative research of archeologists and anthropologists indicates that violence is a widespread feature of small-scale foraging societies and follows a pattern that is consistent as far back as we can see in the ethnographic and archeological record.⁸¹

Wrangham’s and Glowacki’s work has also established empirical support for the evolutionary logic in the patterns of intergroup conflict. Hunter gatherers have recurrent tendencies in warfare, including hostility toward members of different societies, and for killing to be carried out in relative safety—that is, only when there is a strong asymmetry in power between subgroups, such as in a raid or ambush (the “imbalance of power” hypothesis). By contrast, as “rational actor” theorists would expect, hunter-gatherers are averse to the risk of fighting symmetric battles with roughly equivalent numbers on each side.⁸² Importantly, sustained instances of imbalances of power over evolutionary history would have led to the selection of contingent aggression. In other words, since imbalances of power offer systematic opportunities for low-cost aggression over time, then we should expect human groups to have developed a disposition to act aggressively against others when they have the opportunity, because opportunistic aggression is a strategy that pays off on the average. Indeed, Wrangham and Glowacki find evidence that after “warriors killed members of a neighboring society, the

killer's group benefited as a whole via territorial expansion"⁸³—precisely as has been shown for intergroup killings by chimpanzees.

Chagnon, Wrangham and Glowacki and others have also shown that individuals, as well as the group, may gain significant reputational and reproductive advantages of participation in warfare. Although warfare is a high-stakes collective action problem, warriors are willing to participate because over evolutionary time the dividends have tended to outweigh the costs.^{84,85}

These findings may be surprising for those who hold to the popular notion of a harmonious and peaceful past in which humans were at one with nature and each other, but the evidence suggests the opposite. Aggression is not a cultural accident, but an evolutionary adaptation for acquiring and securing resources—just as it is for other species. We do not, however, need to rely on mere analogies linking animal and human behavior. Looking at the environment in which our own species evolved, we find significant empirical evidence for, and a Darwinian logic favoring, intergroup aggression. Whether or not humans and chimpanzees inherited warlike propensities from a common ancestor, there was nevertheless a strong selection pressure in both species to develop them.

The evolution of adaptive behavioral strategies: Egoism, dominance, and ingroup/outgroup bias

How does the evolutionary perspective outlined above relate to offensive realism? As we have noted, offensive realism contains explicit assumptions about how states behave in international politics: Given the hostile environment, states are (and ought to be if they are to survive) self-interested, power maximizing, and fearful of others. Our argument is that evolution produced a human brain and human behaviors that closely match the implicit behavioral patterns

on which Mearsheimer's theory of offensive realism depends: *Egoism* (self-help) captures why we want resources and resist their loss. *Dominance* (power maximization) explains why we want power to control resources for ourselves and our relatives and why we seek to defend them from or deny them to others. *Ingroup/outgroup bias* (fear of others) explains why we perceive other human groups as threats and rivals. We now explore the adaptive logic of these behaviors in turn.

Egoism (self-help)

Evolutionary theory offers a powerful explanation for the trait of egoism (by which we mean the nonpejorative definition of “self-regarding, prompted by self-interest”).⁸⁶ Given competition for limited resources and threats from predators and the environment, an individual organism is primed to seek its own survival and—the Darwinian bottom line—reproductive success. The organism has to ensure that its physiological needs—for food, water, shelter, and so on—are satisfied so that it can survive and reproduce. The imperative for survival in a hostile environment also requires that an individual organism places its survival, especially in a time of danger or stress, above the survival of others. The genes of egoistic individuals survive and spread at the expense of those that fail to effectively put their own interests first. Of course, cooperation and helping behaviors are common in nature, but such behaviors persist only where they help the genes causing that behavior to spread. Genes obviously do not “want” or “try” to spread, but the machinery of natural selection means that self-serving alleles will generally increase in relative frequency in the population over time, at the expense of alleles that are neutral or self-sacrificing for no return benefit.

Evolutionary theorists now recognize, following William Hamilton's concept of “inclusive fitness,” that egoism has complexities. Darwin himself envisioned these nuances, even though he did not know the biological mechanisms at work. Hamilton used genetic models to

show that, while individual organisms are egoistic, they should be less so in their behavior toward genetic relatives, especially in parent-offspring and sibling relationships.^{87,88} This decrease in egoism is because close relatives share many of the same genes—one-half for siblings and parents, one-quarter for aunts, uncles, and grandparents, and one-eighth for cousins. An individual's Darwinian fitness therefore includes the success of related others (hence the phrase *inclusive* fitness). The preeminent evolutionary theorist J.B.S. Haldane thus quipped that he would give his life to save two of his brothers (each sharing half of his genes) or eight of his cousins (each sharing one-eighth of his genes).^{89,90} Inclusive fitness provides a biological basis for the common intuition that individuals favor those who are close genetic relatives.⁹¹

Evolutionary theory accounts for egoism and explains why cooperation can extend to the family or close kin group but remains difficult between unrelated individuals. Cooperation among unrelated individuals is possible but only as the result of interactions that help genes replicate in the long run, through mechanisms such as reciprocal altruism, indirect reciprocity, and signaling.⁹² Even cooperation and helping behavior, therefore, are strategies that increase an individual's Darwinian fitness—indeed, that is precisely why they evolved.⁹³ In nature, genetic egoism is the basis of natural selection.

Dominance (power maximization)

Evolutionary theory can also explain dominance. Like egoism, the desire to dominate is a trait of human nature (which, as with egoism, we stress does not necessarily apply to every individual or situation but is a statistical tendency underlying behavior). As evolutionary economist Robert Frank has explained, “Evidence suggests that we come into the world equipped with a nervous system that worries about rank. Something inherent in our biological makeup motivates us to try to improve, or at least maintain, our standing against those with

whom we compete for important positional resources.”⁹⁴ In the context of evolutionary theory, *dominance* usually means that particular individuals in a social group have priority of access to resources in competitive situations.⁹⁵ A wide variety of animals exhibit a form of social organization called a *dominance hierarchy*, in which members of a social group each have a status rank descending from the alpha male down through all the other individuals to the lowliest subordinates. A dominance hierarchy is created competitively, often violently, and is maintained forcefully, but it can serve to prevent or reduce conflict within a group because it establishes a pecking order that is generally respected.

As with all things in nature, dominance hierarchies vary considerably. Hierarchies may be weak or strong, and “alpha” males may sire nearly all offspring or just more than others. However, what is striking is the prevalence and potency of dominance in social organization, despite variations in the specifics. Dominance behavior occurs in thousands of taxonomic groups ranging from fish and reptiles to birds and mammals.

Of particular note regarding the impact of dominance on human behavior are the roles of both *phylogeny* (a species’ ancestral lineage) and *ecology* (its adaptations to local conditions). With regard to phylogeny, most primates and all the great apes (the group to which humans belong) have strong social dominance hierarchies, and humans are no exception—dominance hierarchies have been extensively documented among humans in a wide variety of settings and eras.^{96,97,98} With regard to ecology, dominance hierarchies are a common form of social organization in the kind of ecological settings in which humans evolved (social groups with competing interests, variation in power, and finite resources).

The strength of dominance hierarchies in humans is debated and varies empirically, but such hierarchies are always evident in some form or other. Even where dominance hierarchies

are actively suppressed, such as in more egalitarian small-scale societies, suppression itself is evidence of the competition for status that simmers beneath the surface.⁹⁹ In historical and contemporary societies, competition for power is all too obvious, and the quest for status, dominance, and leadership is ancient and ever present.^{100,101,102,103}

Males of most mammal species are particularly competitive with each other over females. Indeed, the competition for mates is subject to a special type of evolutionary selection process—*sexual selection*, as opposed to standard natural selection. Reproductive access to females tends to be highly skewed, with a few males responsible for a large proportion of progeny. This is because a single male can reproduce with multiple females, whereas females can usually only reproduce and rear the offspring of one male at a time, with a long delay before becoming reproductively available again. In some species, reproductive access is settled by coercion, in which the strongest male defeats rivals to dominate a harem. In other species, males cannot coerce females, but the females are choosy about with whom they mate, leading to selection pressures for males to demonstrate or signal their quality as attractive partners. In either case, it is females rather than males that are the limiting factor in sexual competition, making male competition for available females intense. Sexual selection has led to costly biological adaptations, such as fighting, the growth of heavy “weapons” (e.g., antlers), risky courtship displays, or adornments that signal genetic quality (e.g., gigantic tails). These types of adaptations not only consume precious time and energy but can also decrease survival in other, nonreproductive domains of life (for example, the plumage of male peacocks limits their ability to fly). Thus, the power of sexual selection can lead to the evolution of traits that actually damage survival in order to achieve superiority over other males.^{104,105} Reproduction trumps survival in evolution.

Sexual selection is typically responsible for the hierarchical nature of group-living animal species, including humans, as males fight for rank and the reproductive benefits it brings. As we would expect, this leads to sex differences in the desire for status. Both laboratory experiments and real-world observations have identified empirical differences between men and women in a range of social behaviors, not least that men tend to have relative-gains, or “zero-sum” motivations (wanting to get ahead at the expense of others), whereas women tend to favor payoff-maximization, or “variable-sum” motivations (content to do well even if others also do well in the process).^{106,107,108,109}

It is well established that dominance and status-seeking behaviors in humans are based on many of the same biochemical and neurological processes as in other mammals, such as the secretion and uptake of testosterone and serotonin, which modify status-challenging behavior.^{110,111} However rational we may like to think we are, our judgments and decision-making are nevertheless influenced by cognitive mechanisms and biochemicals circulating in our bodies and brains that relate to dominance behavior.^{112,113,114,115}

Dominance hierarchies need not only benefit those at the top. An organized social structure can help promote the harvesting of resources, coordinate group activity, and reduce within-group conflict. Although alphas in the hierarchy tend to have the highest reproductive success, other males may benefit from group membership by gaining protection from other groups, or by biding their time for a chance to challenge the alpha male when they become strong enough or old enough. Ethological studies have shown that hierarchical dominance systems within a primate group’s social network can reduce overt aggression, although aggression increases again when the alpha male is challenged.^{116,117,118}

To summarize, a species that lives communally could have two broad forms of social

organization. The group can accept organization with some centralization of power (dominance hierarchies), or it can engage in perpetual conflict (“scramble competition”), which incurs costs in terms of time, energy, and injuries, as well as depriving the group of many benefits of a communal existence, such as more efficient resource harvesting.¹¹⁹ Among social mammals, and primates in particular, dominance hierarchies have emerged as the primary form of social organization.

Thus far, we have emphasized a state of “anarchy” in evolutionary history, in which there was no overarching power to provide protection from predators, rivals, or other threats. Egoism and dominance arose as strategies that provided solutions to achieving survival and reproduction in this environment. However, dominance hierarchies were in some sense a mechanism by which this anarchy could be suppressed—at least *within* the group—to the benefit of all group members since they share at least some common interests (such as avoiding conflict). This collective benefit points to the special and much more significant role of anarchy at a higher level—*anarchy between* groups. As we show in the next section, competition between groups is especially significant for human evolution, and for international politics, precisely because it is at the intergroup level where anarchy reigns supreme and is much harder to suppress.

Ingroup/outgroup bias (fear of others)

Egoism and dominance are important mechanisms for attaining security, but also important is attaining security from members of other groups. In fact, interactions with people from other groups—unrelated others that may not have shared interests—may be especially costly or lethal compared to within-group interactions. Evolutionary theory provides an important framework for understanding the ingroup/outgroup distinction commonly noted by anthropologists, sociologists, and political scientists, and perhaps most prominently by

psychologists.^{120,121} Of the many biases identified in the so-called cognitive revolution in psychology, the ingroup/outgroup bias is one of most pervasive, pernicious, and powerful. The key finding is that humans quickly adopt an “us” (ingroup) versus “them” (outgroup) worldview. We are positively biased toward our own groups and negatively biased toward other groups. Psychologists argue that the ingroup/outgroup distinction develops from a need for social identity. Identification with a specific group provides individuals with meaning and purpose, encouraging them to become part of a community with common interests, values, and goals.^{122,123,124} One also knows what one is not—the outgroup, which is stereotyped and homogenized as the “Other.” Among the many different possible ingroup categories, the most common and significant include family, friends, age, sex, class, ethnicity, politics, religion, and nationality.

The ubiquity and strength of the ingroup/outgroup bias across history and across human cultures suggest it is an ingrained aspect of human nature, and evolutionary theory explains why such a mechanism would evolve.^{125,126,127} First, considerable evidence from both archeological and ethnographic research on preindustrial societies points to intensive intergroup conflict in our past.^{128,129,130,131,132,133} As we noted earlier, around 15 percent of male populations in indigenous small-scale societies died in warfare (and, in some such societies, war-related mortality rates were considerably higher).^{134,135} War also remains a significant influence on the social organization and physical distribution of these societies even when they are not actually *at war*. In human history and prehistory, other human groups were commonly the most dangerous threat in the environment, and the ingroup/outgroup bias is likely to have helped the ingroup remain cohesive, avoid and be wary of outgroups, solve the collective action problem in emergencies, and kill outsiders.^{136,137,138}

Second, the ingroup/outgroup bias offers a rapid heuristic to weigh the various threats when encountering other humans. Will the outsider be a threat to oneself or to one's family? Will an outsider compete for the current or future resources that the insiders need to survive or expand? Will a male from the outgroup present competition for mates, or will his presence threaten the ingroup male's position in the extended family or group? In environments where resources are highly contested, outgroup fear can become extreme. For example, Wrangham recounts that among the Inuit of the Arctic, "unfamiliar men would normally be killed even before questions were asked."¹³⁹

Such wariness of individuals from other groups is paralleled among animals. For example, among wolves, lions, and chimpanzees, when members of rival groups are found alone, they are extremely vulnerable and risk being killed.^{140,141,142} We discussed intergroup killing in chimpanzees earlier, but the pattern is notable among social carnivores, too: Studies of undisturbed wolf populations in Alaska have found that 39 to 65 percent of adult deaths were due to intergroup killing.¹⁴³

Of course, the ability to assess threats is much more complex in humans than it is in other animals, and human intelligence gives us a greater repertoire of behavior. Thus, humans may consider other variables, such as the possibility of future trade or cooperation, when assessing outgroups. Still, humans exhibit an instinctive fight or flight response, just as other animals do, which operates below (and faster than) conscious awareness.^{144,145} Befriending or cooperating with a stranger may have benefits, but those benefits are uncertain and limited whereas the costs of trusting an outsider may be lethal. It is therefore no surprise, as psychologists have argued, that evolution has favored a bias to be fearful of strangers to avoid the costlier error.^{146,147}

Summary: The legacy of evolution

In this section, we have presented standard biological arguments that egoism, dominance, and ingroup/outgroup bias are deeply rooted behavioral adaptations common among mammals in general and primate species in particular. Of course, human behavior is not a direct extension of the behavior of other animals, but, as we have explained, the ecological setting in which our own species evolved made these same traits as or even more important for humans. Egoism, dominance, and ingroup/outgroup bias are widespread because they increased survival and reproductive success compared with other strategies and were therefore favored by natural selection. The cognitive mechanisms underpinning the three traits were established in an environment very different from the one in which humans now live, but they persist because our brains, biochemistry and nervous systems, which evolved over many millions of years, have remained the same despite the rapid sociological and technological advances of the last few centuries. The fact that these evolved behaviors are not always beneficial today does nothing to undermine their evolutionary logic or empirical presence.

Note that we did not pick the traits of egoism, dominance, and ingroup/outgroup bias out of a hat. As well as being the key behavioral traits identified by Mearsheimer, self-interest, social stratification, and groupish behavior are three of the most prominent behavioral features of social animals. That natural selection should have drawn out the same three traits as Mearsheimer may seem a remarkable coincidence. However, because anarchy is a problem both in nature and in international politics, it is no coincidence at all. Rather, we suggest it is an example of what biologists call “evolutionary convergence”—similar traits arising in different settings because they are good solutions to a common problem.

One reason why an evolutionary explanation of egoism, dominance, and

ingroup/outgroup bias is useful is because alternative explanations for these empirical traits have failed. Egoism, dominance, and ingroup/outgroup distinctions have previously been attributed to variables such as culture, economics, or religion.^{148,149} For example, Karl Marx and his followers identified egoism as a result of capitalism and called for its suppression and the triumph of class consciousness. Likewise, many other religious and utopian theorists attribute egoism, dominance, and ingroup/outgroup bias to special, or at least changeable, circumstances. The fact that all prior utopian visions have failed to come to fruition does not prove that current ones will fail too. However, the persistence of these three traits across domains and over time casts doubt on arguments like these, and strongly counts in favor of an evolutionary explanation instead.

We recognize that humans are influenced by culture, norms, rational calculation, and moral principles. Nevertheless, overwhelming evidence shows that people *also* behave in ways that can be predicted from the biological knowledge outlined above. The impact of these biological factors on social and political behavior will vary depending on context. However, our contention is that significant aspects of political behavior could be given a stronger foundation if we acknowledge the powerful and basic biological principles that are chronically ignored in the political science literature, as well as the conditions under which they become exacerbated or suppressed.

Evolution and offensive realism: New insights

Evolutionary theory makes three major contributions to the offensive realist theory of international politics: (1) a novel ultimate cause of the primary traits of offensive realist behavior (self-help, power maximization, and fear); (2) an extension of offensive realism to any domain in which human actors compete for power (e.g., civil war, ethnic conflict, or domestic politics); and

(3) an explanation for why individual leaders themselves, not just states, behave as they do.

Novel ultimate cause and theoretical foundation

Our theory advances offensive realist arguments without seeking an ultimate cause in the anarchic international state system. Offensive realism based on evolutionary theory makes the same *predictions* for state behavior, but the *ultimate causal mechanism* is different: human evolution in the anarchic, dangerous, and competitive conditions of the late-Pliocene and Pleistocene eras. Evolutionary theory explains why humans are egoistic, strive to dominate others, and make ingroup/outgroup distinctions. These adaptations in turn serve as a foundation for offensive realism—what Mearsheimer independently identified as self-help, power maximization, and fear.

The central issue raised by our theory is what causes states to behave as offensive realists predict. Mearsheimer argues that anarchy is the fundamental cause of such behavior. The fact that there is no world government compels the leaders of states to take steps to ensure their security, such as striving to have a powerful military, forging and maintaining alliances, and acting aggressively when necessary. This is what neorealists call a *self-help* system: Leaders of states are forced to take these steps because nothing else can guarantee their security in the anarchic world of international politics.

We argue that evolutionary theory also offers a fundamental cause for offensive realist behavior (see Table 1). Humans evolved in a state of nature where competition for resources and dangers from other humans and the environment were great. Humans survived (and note that several other Hominin species did not) by virtue of evolved behavioral traits—among them egoism, dominance, and the ingroup/outgroup bias—which were adaptations to competitive ecological conditions. These traits help to explain why humans (including political leaders) will

behave, in the proper circumstances, as offensive realists expect them to behave. In sum, evolutionary theory offers realist scholars a natural-scientific behavioral foundation for offensive realism. Human evolution explains why people seek control over resources, why some of us (particularly males) will seek to dominate others in order to achieve and maintain a privileged position in a dominance hierarchy, and why we are suspicious and wary of other groups.¹⁵⁰ Since the leaders of states are human, they too will be influenced—perhaps especially influenced—by this evolutionary legacy as they react to the actions of other states and decide how to respond.^{151,152,153}

[Insert Table 1 about here]

Table 1. Major realist theories and their predictions,¹⁵⁴ plus predictions from human evolution.

| | Classical realism | Defensive realism | Offensive realism | Human evolution |
|--|---|--|---|---|
| What causes states to compete for power? (What is the ultimate cause of behavior?) | Lust for power inherent in states due to <i>animus dominandi</i> | Anarchy | Anarchy | Evolved dispositions |
| What is the proximate cause of behavior? | Balance of power | Security through power sufficiency | Security through power maximization | Security through power maximization |
| How much power do states want? | All they can get. States maximize relative power, with hegemony as their ultimate goal. | Not much more than what they have. States concentrate on maintaining the balance of power. | All they can get. States maximize relative power, with hegemony as their ultimate goal. | All they can get. States (and individuals) maximize relative power, with hegemony as their ultimate goal. |

Note: The unit of analysis varies among the theories (*states* for defensive and offensive realism, *humans* for classical realism and human evolution), but all predictions are for state behavior. Our evolutionary approach predicts the same behavior as offensive realism but derives from a different ultimate cause.

Extensions of offensive realism to other domains

The second contribution of our theory is that it offers an explanation of the behavior of humans in a wide variety of contexts extending beyond international politics. Our evolutionary theory of offensive realism is unlimited in *time*, explaining behavior from the ancestral environment to the present day, whereas offensive realism is conventionally inapplicable prior to 1648, when the Treaty of Westphalia established the European state system. Our theory is also unlimited in *domain*, explaining behavior wherever there are human actors and weak external constraints on their actions, from ancestral human groups, ethnic conflict, and civil wars to domestic politics, free markets, and international relations. The theory might thus be extended to explain the behavior and actions of many phenomena: the Roman Empire, warfare among Papua New Guinean or Native American tribes, the European conquest of South America, the race for the American west and the failed Mormon and Confederate secessions, the imperialist scrambles over African colonies, institutions like the medieval Catholic Church, commercial organizations from the East India Company to Coca-Cola, the struggles of rival ethnic groups the world over, and the ruthlessness of electoral campaigns.

Table 2 illustrates the range of domains to which an evolutionary theory of offensive realism applies. Note that the table captures key patterns, not universal behavior. Clearly, not all individuals or businesses or states act the same way all the time or in all circumstances. Behavior varies considerably, just as standard offensive realism predicts for states, and countervailing forces would sometimes mitigate power-maximization strategies—although the very need for and difficulties of those countervailing forces help to demonstrate the fact that offensive realist behavior remains an underlying problem. Indeed, part of the beauty of evolutionary approaches is their ability to predict *sources of variation*—the socio-ecological conditions under which we

should expect to see humans acting (in this case) more fearful and more self-interested, and pursuing more power maximization, rather than less. Older versions of evolutionary theory sometimes presented strategies and behaviors as fixed or “hard wired.” Modern biology stresses the contingent, context-dependent nature of behavioral adaptations, which generates finer predictions for *when* we should expect to see different types of behavior.¹⁵⁵ This is an important point to which we will return.

[Insert Table 2 about here.]

Table 2. Behavior under anarchy in different domains.

| Domain | Actors | Source of anarchy | Time period | Predictions |
|------------------------|----------------------------------|--------------------------------------|-------------------|--------------------------------------|
| Human evolution | Individuals (primarily males) | No high-level political organization | Evolutionary past | Self-help behavior to maximize power |
| International politics | States | No world government | Today | Self-help behavior to maximize power |
| Domestic politics | Individuals, parties | Limited constraints on power | Today | Self-help behavior to maximize power |
| Civil wars | Individuals, factions | No government in control | Today | Self-help behavior to maximize power |
| Free markets | Firms | Weak regulation | Today | Self-help behavior to maximize power |

Note: In all cases, we argue, holding onto the status quo is not always good enough to ensure survival. Instead, the best strategy is a constant effort to maximize power to stay ahead of rivals. Even if this strategy is never successful, it motivates individuals to achieve the maximum possible. We invoke anarchy in all situations in the table because, while our core argument is that evolved dispositions (egoism, dominance, groupishness) give rise to offensive realist behavior today *even in the absence of anarchy*, these evolved dispositions will be more prominent and influential where regulation is lax. Under an iron fist, even the most egotistical, dominating, and xenophobic actor will be prevented from realizing his or her goals.

Wherever actors are left to compete with each other by relying on their own devices (whether in the human evolutionary past or today), we predict that actors within those systems will exhibit similar behavior, not least self-help behavior to maximize power. Offensive realists can thus explain more than the behavior of states or great powers. If anchored on evolutionary theory, offensive realism allows new insights to elucidate why individuals and substate groups are self-interested, vie for power, and fear each other, and it can explain political behavior and war that occurred long before the creation of the modern state system in 1648.

Explaining leaders' lust for power

The third contribution of our theory is that it identifies a more explicit role for leaders (see Table 3). Mearsheimer's offensive realism argues that states gain power to ensure security. That certainly may be, as he attempts to demonstrate. However, an overtone of this argument is that power or domination is distasteful for leaders—that they tolerate it only for the sake of their state's security. Leaders are forced to maximize power when perhaps they would rather cooperate or share power with others. By contrast, our theory posits that a tendency toward offensive realist behavior, however modulated by other tendencies, would have conferred a fitness advantage in the environment in which humans evolved and should thus have led to dispositions to seek and like power. Indeed, a wide range of empirical evidence from psychology and neuroscience suggests instead that humans, especially men, not only want to be leaders but also enjoy the pursuit of power (as well as its material fruits).^{156,157,158} The force of this motivation is frequently revealed in victors' expressions of the satisfaction of conquest. As Chinggis Khan is purported to have said: "The greatest happiness is to vanquish your enemy, to drive him before you, to see his cities reduced to ashes."¹⁵⁹ Although not usually expressed in such stark terms, the pleasure of competition and victory has been widely recognized as a feature

of human nature from classical times to the present day, and success in competitive interactions and the domination of others are known to increase testosterone and dopamine responses in men—the so-called victory effect.¹⁶⁰ Such dominance behavior is, we suggest, exaggerated among leaders because they are generally ambitious and competitive, and usually male. Moreover, the very acquisition and exercise of power itself is known to inflate dominance behavior further.¹⁶¹

[Insert Table 3 about here]

Table 3. Who wants power? A comparison among alternative realist theories.

| | Classical realism | Defensive realism | Offensive realism | Human evolution |
|-------------|-------------------|-------------------|-------------------|-----------------|
| Individuals | Yes | No | No | Yes |
| Leaders | Yes | Sometimes | Sometimes | Yes |
| States | Yes | Sometimes | Yes | Yes |

Criticisms of an evolutionary approach

Scope conditions: Human behavior is contingent, not fixed

We recognize that a challenge to the theory of offensive realism is the empirical mix of cooperation and conflict in the real world. Offensive realists and other theorists of international relations may see more or less of each. However, an evolutionary perspective is particularly useful here because it predicts that behavior is contingent, not fixed. Individuals may follow generalized decision rules, but these rules give rise to different behaviors in different contexts. Individuals fight when benefits are expected to exceed costs (on average), and not otherwise. Chimpanzees, for example, will attack others when they have a numerical advantage, but they will retreat if they are outnumbered.¹⁶² This behavior makes perfect sense from an evolutionary perspective, because a decision-making mechanism that takes account of the probability of winning will spread at the expense of a decision-making mechanism that does not. As such, an evolutionary account does not necessarily expect animals, humans, or states to act as offensive realists all the time and in all situations. Offensive realism also does not have such expectations. Rather, as Mearsheimer points out, states do best if they expand only when the opportunity for gains presents itself—they “try to figure out when to raise and when to fold.”¹⁶³ Evolution has been doing this for a long time.

Our point is therefore not that humans are naturally “good” or naturally “bad” at all times and in all circumstances, but rather that people have evolved mechanisms for egoism, dominance, and groupishness that are activated and amplified in certain settings. Under conditions of anarchy, when there is the threat of predation and resource competition (as in many eras and locales in history), cognitive and physiological mechanisms of egoism, dominance, and groupishness are triggered. Where these conditions are tempered, such as in the modern peaceful

democracies of Western Europe, these cognitive and physiological mechanisms are likely to be more subdued. For example, Western Europeans feel relatively secure (at least while the United States provides for its security). In general, humans cooperate where we can (e.g., within groups or within alliances deriving mutual benefit), but the anarchy of international relations is a hostile environment that, like the one in which humans evolved, tends to trigger our egoism, dominance, and group bias. In short, our theory is one of *behavioral ecology*—human and animal behaviors are not constants, but are contingent strategies that become engaged or elevated in order to best seek payoffs depending on the particular circumstance or environment. This insight has important implications for international politics because it suggests that we can potentially create—at least in principle—environments that take account of our human nature so we can turn them to our advantage, such as designing institutions that elicit cooperative rather than conflictual tendencies.^{164,165}

Meet the family: Chimpanzees versus bonobos

Debates about evolved human propensities have often centered on whether human behavior more closely resembles the behavior of common chimpanzees or that of bonobos (pygmy chimpanzees that live in central Africa and are somewhat less aggressive than common chimpanzees). Such comparisons are not central to our argument. As we have stressed, the human traits of egoism, dominance, and ingroup/outgroup bias are adaptations to the ecological conditions prevalent in *human* evolution. We do not assume that humans and our primate cousins simply inherited these traits wholesale from a common ancestor. Clearly, when it comes to the many distinctive physiological and behavioral changes humans have undergone, ecology has been as or more important than phylogeny (hence, the field of evolutionary anthropology focuses on hunter-gatherer analogues, not nonhuman primate analogues). The particular socio-ecological

setting in which humans evolved meant that egoism, dominance, and groupishness were important behavioral adaptations, irrespective of the traits found in related species.

Nevertheless, in evolutionary biology, the attribution of traits to common ancestry (a species' phylogenetic history) can be important too. Therefore, to the extent that it matters, let us address the bonobo-chimpanzee issue briefly here, because certain phylogenetic and socio-ecological factors suggest that we are more like chimpanzees than bonobos.

The key observation is that bonobos are less aggressive than chimpanzees. However, it is important to make clear that humans did not descend from either species. All three species descended from an (unknown) common ancestor. Some evidence suggests that the separation between common chimpanzees and bonobos was quite recent, occurring perhaps only 0.86 million to 0.89 million years ago, although it remains possible that the separation occurred much earlier, between 1.5 million to 2.5 million years ago.¹⁶⁶ Either way, humans separated from our common ancestor with both chimpanzee species long before, about 5 million to 6 million years ago. In short, on the basis of the family tree, there is little reason to assume that humans should be more or less like bonobos or chimpanzees.

What is more important is the ecological differences and similarities that we shared with the two species. Humans and chimpanzees shared some features of their socio-ecological environment, such as spatially and temporally variable food resources, that required that individuals leave the protection of the group to forage in open or bordering areas, often alone or in small groups, subjecting them to greater risks of predation or ambush from conspecifics.¹⁶⁷ In contrast, the ecology of bonobos has been relatively benign. They have enjoyed an absence of competition from gorillas (bonobos only live south of the Congo River, while gorillas only live on the north side of the river), high-quality foliage for food, and dense forest, which reduced

vulnerability to ambush and thus, it is thought, the utility of aggression in males.^{168,169}

Accordingly, bonobos may not be a good model for understanding human behavior, for reasons of both phylogenetic history and shared ecology. Chimpanzees do at least have some important ecological similarities to humans. We reiterate the point above, however, that it is the context of our own evolution as hunter-gatherers in the socio-ecological conditions of the Pleistocene era that offers the crucial evidence on human behavioral adaptations.

What about the prevalence of cooperation in nature?

Given the considerable cooperation evident in the natural world, one might think that evolution provides a foundation for cooperative behavior rather than selfish, power-maximizing behavior. The fact is that evolution explains and predicts both (under the relevant circumstances). Indeed, there is a considerable literature on animal and human adaptations for cooperation.^{170,171,172} However, while cooperation is frequent and widespread, this empirical observation does nothing to dent the evolutionary logic that cooperation helps the helper—it evolved to occur only where it brings return benefits.^{173,174} This is precisely why the cooperation literature has remained so heated. Theorists have had to explain how cooperation could occur in the face of significant individual self-interest, the difficulties of collective-action, and the free-rider problem.^{175,176,177} Special conditions are needed for cooperation to emerge and remain stable among unrelated individuals.^{178,179} Typically, those special conditions are ones that make helping advantageous to the genes responsible for the behavior.

Similarly formidable obstacles to cooperation exist in international relations. Cooperation is extremely hard to achieve and requires special conditions. Even optimists acknowledge that remarkable mechanisms and institutions are required to generate and sustain cooperation, and the identification and implementation of these conditions occupies many of our

colleagues.^{180,181,182,183} The European Union, to give one flagship example, is often put forward as a vision of the future, demonstrating that democratic states are willing to subordinate self-interest for a greater good, and that war is becoming obsolete. However, the European project was set up precisely to respond to centuries of European powers competing and fighting for power at great cost. We are also yet to see how European states will cooperate or compete when the U.S. security umbrella is removed. The recent crises of the Euro and migration have shown in stark terms that individual states continue to exploit the opportunity to free-ride on others if they can, and even the most powerful states, such as Germany, France, and the United Kingdom, have been reluctant or unwilling to make sacrifices to protect other states. When the stakes are high and one's livelihood or survival is threatened, the traits of egoism, dominance, and fear of outgroups come to the fore—a conclusion we can draw from any number of conflicts in the Balkans, Northern Ireland, Ukraine, Syria, Iraq, Nigeria, India, and elsewhere.

If intergroup conflict is so important, might evolution favor the most cooperative groups?

Evolution is sometimes argued to operate on groups rather than individuals (“group selection”). This idea is important because, if individuals are working for the good of the group rather than only for themselves, then groups composed of more-cooperative individuals may do better than less-cooperative groups, meaning that genuinely altruistic traits (sacrificing one's own interests for the good of others) can spread in the population.^{184,185} However, there are several reasons why this possibility does not affect our argument.

First, group selection is a controversial hypothesis, which has been rejected by many prominent evolutionary biologists.¹⁸⁶ While selection at the level of groups is possible in principle, it requires special conditions to overcome what are generally agreed to be the much more powerful forces of competition and selection acting on individuals, and these forces are

always in play whether groups are in competition with each other or not. Therefore, even the strongest advocates of group selection, such as David Sloan Wilson, argue that, in any given case, it remains an empirical question as to whether or not the selection pressures acting at the level of individuals are outweighed by selection pressures potentially acting at the level of the group (so called *multi-level selection*). While biological group selection in humans is possible in theory, there have not been any published empirical examples.

Second, even if group selection does occur, it can only increase altruism *within* groups. *Between* groups, group selection would do the opposite, maintaining or even exacerbating conflict.¹⁸⁷ Because the premise is that selection operates at the level of groups, altruistic traits can only spread if altruism helps spread the genes responsible for it at the expense of other genes, and that must occur via intergroup competition or conflict. Therefore, to advocate group selection over individual selection does nothing to reduce predictions regarding human conflict or aggression. If anything, group selection would tend to *increase* violence, since between-group competition (conflict among strangers) can be more brutal than within-group competition (conflict among kin and fellow group members). In Matt Ridley's words, to prefer group selection over individual selection "is to prefer genocide over murder."¹⁸⁸ Group selection can promote cooperation and altruism, but only within the group. The dark side of group selection is the unfettered conflict it presupposes and predicts between groups in competition with each other.

Third, it is important to remember that the empirical observation of altruism in nature does not imply or demand group selection. Given group selection's theoretical constraints, it should be a last-resort explanation (subject to empirical testing), not a first point of call. As we have explained, there are several mechanisms by which altruistic or helping behavior can (and

have) evolved because of the benefits of helping others *that accrue to oneself*—not least, altruistic behavior among kin, reciprocity, and reputation formation. In short, you do not need group selection to explain altruism. In the right contexts, helping others can help oneself. The strategic allocation of resources to others often advances one's own Darwinian fitness. We do not need to resort to group selection unless altruism cannot be explained by more conventional mechanisms based on individual selection. George C. Williams famously made this point in response to so called naïve group selectionists of the time, and his insight has continued to be reiterated to biology students ever since.¹⁸⁹

While biological group selection among humans is unlikely, the selection of *cultural* traits among groups is possible. The constraints on biological group selection, such as significant differences in a given trait between groups and low migration, are relaxed in the case of cultural traits, since groups actively promote cultural distinctions and have many mechanisms to prevent flows between them.¹⁹⁰ Therefore, it is not just likely but quite apparent that many *cultural* traits have evolved out of group-level competition—sometimes referred to as *memes*, as opposed to genes. (Examples include the spread of Christianity or Islam at the expense of traditional religions over the last 2,000 years.) However, once again, the potential for cultural group selection does not change or challenge our argument. To the extent that cultural group selection extends back into our evolutionary past, cultural traits have not been consistently or powerfully contrary to the evolved traits of egoism, dominance, and ingroup/outgroup bias. Indeed, cultural selection has often reinforced, not reduced, these very behaviors over human history. Moreover, and lastly, cultural differences have themselves represented an additional cause and consequence of conflict. In addition to fighting over resources, we can now fight over ideology as well.

Leaders and offensive realist behavior

A crucial extension of our theory concerns how leaders may differ from the average person in the population. Up to now, our claims have focused on traits that are common to all humans. However, there is, of course, considerable variation in egoism, dominance, and ingroup/outgroup bias. As we have been at pains to explain, much of this variation stems from contextual differences (behavioral ecology)—that is, a given individual's behavior can change across circumstances. However, another important source of variation is individual differences—that is, specific people exhibit these traits to greater or lesser degrees. Individual differences are important because political leaders may be more likely than the average person to display egoism, dominance, and groupishness.

A state's elites—its captains of industry and media and its military and political leaders—may be more likely than average to show these traits in abundance for five reasons. First, ambitious leaders self-select themselves into seeking high-profile roles in the first place.¹⁹¹ Second, strong leaders are selected into power over weak-willed or hesitant candidates.^{192,193} Third, leaders rise to the top of their respective hierarchies through an intensively competitive process that compels them to be increasingly attentive to self-interest and self-preservation.¹⁹⁴ Fourth, once in power, decision-makers tend to heed hawkish rather than dovish advice.¹⁹⁵ Fifth, the experience of power itself is well known to corrupt, precisely because being a leader elevates one's sense of worth and power.¹⁹⁶ Taking these phenomena together, a skeptic of our argument that humans are generally egoistic, dominance-seeking and groupish may nevertheless concede that the small subset of humans that become political leaders tend to express these traits. Again, the political world mirrors nature: Not everyone can be the alpha male.

Sex differences and offensive realist behavior

Men, more often than women, lead states. If women led them, or were better represented in legislative or executive branches of government, a logical prediction of our theory is that egoistic, dominant, and groupish tendencies—being primarily male traits—would be less likely to influence state behavior. A caveat to this prediction is that women in power may tend to act like men, either because selection effects trump stereotypical sex differences (female leaders may have personalities similar to male leaders), or because egoism and dominance are necessary traits in order to survive in the system of international anarchy (or on Capitol Hill).^{197,198}

Combining the previous two considerations (leaders and sex) raises another problem: If leaders are especially egoistic and domineering, and if sex is a primary cause, does this not mean that we predict state leaders will undertake actions (consciously or subconsciously) that serve to maximize their own personal reproductive opportunities—perhaps at the expense of state interests? Historically, evidence has often supported this hypothesis.^{199,200,201} However, we take the position that, on average, state leaders' personal interests have significant and genuine overlap with national security interests, not least of which is the survival and prosperity of the state for themselves and their progeny.

Levels of analysis: Individual and state behavior

A recurrent criticism of any theory of international relations based on the role of individuals is why we should expect *individual* behavior to tell us anything about *state* behavior. We recognize that many factors may affect the behavior of states, including bureaucracies, types of government, culture, international institutions, or the international system itself, but we also recognize, as traditional theories of international politics have from the time of Thucydides, that humans affect state behavior as well.²⁰² Many factors come between an individual leader and the

behavior of a state, but that does not mean leaders have no effect at all.

We see several reasons why human behavior is an important predictor of state behavior in the context of this article. First, the preferences of individual citizens are, at least to a degree, represented in those elected to—or tolerated in—office, and those preferences may also be seen in the goals of the state. Second, bureaucracies and organizations are designed, run, and led by human beings, whose own dispositions influence how they function. Third, state leaders are the actors who make important strategic decisions from a set of options, and they are potentially affected by their human dispositions and those of their advisers, even if their actions are tempered by checks and balances. Fourth, group decision-making may actually amplify the influence of human dispositions; it is groups of men that are especially prone to behaviors associated with dominance, aggression, and coalitionary psychology.^{203,204,205,206,207}

Novel solutions to weaknesses in offensive realism

We recognize that offensive realism remains controversial, and we would like to address three fundamental problems with the theory. Although it is not our intention to resolve offensive realism's theoretical lacunae, an evolutionary account can help to explain them.

First, offensive realism fails to explain why costly wars sometimes occur against the interests of the states that initiate them. As Mearsheimer and others acknowledge, power maximization may not always be a good strategy, and, indeed, it has led a number of states into disaster. Conventional offensive realism cannot explain such events well. However, if actors seek dominance at least partly because of evolved behavioral dispositions (of which actors may not even be aware), then we may expect sometimes to observe power-maximizing behavior whether or not it is a good strategy. Although we have stressed that evolved behavior is often contingent on circumstances, this matching is not perfect, especially when human decision-

makers are faced with an evolutionarily novel environment—as witnessed today with mass societies, modern technologies, and interactions with distant peoples—for which the human brain was not designed. We should therefore expect instances of “evolutionary mismatch” in which evolved behaviors lead to poor decisions in modern settings. The brain may be responding exactly as it was designed to do, given informational inputs from the environment. However, while the resulting behavior may have been adaptive in our ancestral environment, it may be maladaptive, or even disastrous, today. Evolutionary theory is especially helpful here because it advances our understanding of the proximate (biological) causes of offensive realist behavior and the conditions under which mistakes are more likely to be made (i.e., conditions that exacerbate egoistic, dominating, and groupish behaviors even where such behaviors may not help to achieve strategic goals).

Second, critics of offensive realism point to countering factors such as the “democratic peace” or international institutions. However, an evolutionary perspective raises new doubts about the significance of such evidence. The very existence of these phenomena, not to mention the extreme efforts and expense they continually require to function, only supports the point that international politics needs very special and powerful arrangements to prevent people from acting as offensive realists—predisposed as they are to do so. And, even then, these arrangements often fail to work. When the stakes are high enough, individuals as well as states all too easily revert to egoism, dominance, and fear.

Third, critics point to international cooperation among states as evidence against offensive realism. We realize international cooperation is prevalent, but that does not mean such cooperation is easy to obtain. On the contrary, it is famously hard to initiate and maintain from both a theoretical and empirical perspective, which is why this topic continues to fill huge

volumes of scholarly literature in economics and political science.^{208,209} As we have emphasized, cooperation is easy to explain where it brings clear mutual benefits to the self-interest of those involved, such as trade or military alliances (in which case offensive realism is as good an explanation of cooperation as any other theory). Collective action to attain public goods, however, is much harder to attain because of the threat of free-riders (as demonstrated, for example, by the slow response to climate change, the reluctance of states to accept Syrian refugees, and Eurozone fiscal responsibility). Where extensive international cooperation does occur, it is often only by virtue of a hegemon willing to sustain it, and cooperation quickly breaks down if core interests and security are put at risk. Furthermore, cooperation is often itself a means to power maximization in the formation of military and security alliances—and thus, cooperation can be a prediction of, not a challenge to, offensive realism. Where a state's own security is threatened or the state becomes vulnerable to exploitation, alliances offer one means of increasing or preserving power. Similar patterns are evident in nature. Animals do not constantly fight. Natural selection generates contingent behavior because it is more effective than blind aggression. Individuals bide their time, form coalitions and alliances, and cooperate with others, but they also seize power where the opportunity arises. States are much the same. In international politics, the bigger problem may be aspiring hegemons—states that do not need to cooperate to obtain what they want.

Conclusions

Offensive realism, more than other major theories of international relations, closely matches what we know about human nature from the evolutionary sciences. Reading the literature of offensive realism can be hauntingly analogous to reading ethnographies of warfare

among preindustrial societies such as the Yanomamo in the Amazon, the Mae Enga in New Guinea, or the Shuar in the Andes. An evolutionary foundation offers a major reinterpretation of the theory of offensive realism and permits its broader application to political behavior across a wide range of actors, domains, and historical eras.

Evolutionary theory also allows realist scholars to explain the intellectual foundations of offensive realism: Why individuals and state decision-makers are egoistic and strive to dominate others when circumstances permit, and why they make strong ingroup/outgroup distinctions. These adaptations were favored by natural selection over the course of evolution and remain a significant cause of human behavior.

The fundamental differences and similarities between our theory of offensive realism and Mearsheimer's are captured in Table 4. The abundance of intergroup threats, which cause the fear and uncertainty Mearsheimer identifies, are deeply rooted in human evolution under conditions of anarchy over millions of years, and not just in the anarchy of the modern state system in recent history. Thus, if theories of international relations are to accurately account for human nature, they must acknowledge how human behavior has been shaped by the ancestral environment, rather than (or as well as) contemporary international politics.

[Insert Table 4 about here]

Table 4. Two theories of offensive realism

| | Mearsheimer's theory (applies primarily after 1648) | Johnson and Thayer's theory (applies to all eras and domains) |
|-----------------------------------|--|--|
| Environment | Anarchy | Anarchy Predation Finite resources Intergroup conflict |
| Problems caused by environment | Insecurity | Lack of protection Ubiquity of threats and dangers Competition for resources |
| Resulting strategies | Emergent behavioral patterns: • Self-help • Power maximization • Fear | Evolved behavioral dispositions: • Egoism • Dominance • Group bias |
| Core solution | Power maximization | Power maximization |
| Outcome | Offensive realist behavior (for states) | Offensive realist behavior (for individuals, groups, organizations, and states) |

The optimistic message of our argument is that understanding human nature will make efforts toward international institutions, democracy, and cooperation more effective. Cooperation and peace efforts often fail precisely because people have too rosy a view of human nature and thus fail to structure incentives effectively. Efforts to make positive political change may be more effective if we view humans as offensive realists and intervene accordingly. At worst, this perspective will make us err on the side of caution.

No theory is perfect. None captures all salient issues. However, offensive realism is one of the most compelling current theories for explaining major phenomena across the history of international politics, such as great power rivalries and the origins of war. Part of the reason for its intuitive and explanatory success is, we suggest, its close match with human behavior. This match, in turn, should be no surprise because human behavior evolved under conditions of anarchy, which pervaded throughout our evolution as well as in international politics today. Self-help, power maximization, and fear are strategies to survive nature, not just contemporary international politics. It is also worth noting that offensive realism may often be derided because we do not want it to be true. We prefer a more positive picture of human nature, perhaps one that accords with comfortable modern life in developed states. However, we need to see the world as it is, not as we would like it to be. When the stakes are high, such as in 1914, 1939, 1941, or 1962, or today in the Middle East, Ukraine, or the East and South China Seas, offensive realism does not seem so foreign. Indeed, the possibility of even more intense security competition in the Sino-American relationship, between India and Pakistan, and in the Middle East highlights the importance of making the theory's logic explicit and revealing and testing its foundations.

Finally, evolution may make significant contributions to other theories of international relations. Studies from an evolutionary perspective of the fundamental assumptions of

neoliberalism, constructivism, poststructural approaches, Marxist and dependency theories, and other theories of international relations would be welcomed for four reasons. First, such studies would complement and critique the present study. Second, the evolutionary approach helps make a given theory's assumptions about human nature explicit, exposing them to empirical validation. Third, exploring how evolution intersects with other theories of international relations would advance the goal of consilience, fusing theoretical and empirical knowledge drawn from both the social and natural sciences. Fourth, we have argued that evolutionary insights closely match offensive realism *among existing theories* of international relations. However, if unconstrained from having to fit evolutionary insights into any particular existing school of thought, evolutionary theory may offer its own, unique theory of international relations that shares features of offensive realism (and perhaps other theories too) but is distinct from them all.

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References

1. John C. Mitani, David P. Watts, and Sylvia J. Amsler, "Lethal intergroup aggression leads to territorial expansion in wild chimpanzees," *Current Biology*, 2010, 20(12): 507–508.

-
2. Michael L. Wilson, Christophe Boesch, Barbara Fruth, Takeshi Furuichi, Ian C. Gilby, Chie Hashimoto, Catherine L. Hobaiter, Gottfried Hohmann, Noriko Itoh, Kathelijne Koops, Julia N. Lloyd, Tetsuro Matsuzawa, John C. Mitani, Deus C. Mjungu, David Morgan, Martin N. Muller, Roger Mundry, Michio Nakamura, Jill Pruett, Anne E. Pusey, Julia Riedel, Crickette Sanz, Anne M. Schel, Nicole Simmons, Michel Waller, David P. Watts, Frances White, Roman M. Wittig, Klaus Zuberbuhler, and Richard W. Wrangham, “Lethal aggression in Pan is better explained by adaptive strategies than human impacts,” *Nature*, 2014, 513(7518): 414–417.
 3. Richard W. Wrangham, “The evolution of coalitionary killing,” *Yearbook of Physical Anthropology*, 1999, 42: 1–30.
 4. Joseph H. Manson, and Richard W. Wrangham, “Intergroup aggression in chimpanzees and humans,” *Current Anthropology*, 1991, 32(4): 369–390.
 5. Richard W. Wrangham, *Catching Fire: How Cooking Made Us Human* (New York: Basic Books, 2009), p. 106.
 6. Richard Dawkins, *The Selfish Gene*, 2nd ed. (Oxford: Oxford University Press, 1989).
 7. Jerome H. Barkow, *Missing the Revolution: Darwinism for Social Scientists* (New York: Oxford University Press, 2006).
 8. Geoffrey M. Hodgson and Thorbjørn Knudsen, *Darwin’s Conjecture: The Search for General Principles of Social and Economic Evolution* (Chicago: University of Chicago Press, 2010).
 9. Jerome H. Barkow, Leda Cosmides, and John Tooby, eds. *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* (Oxford: Oxford University Press, 1992).
 10. Bradley A. Thayer, *Darwin and International Relations: On the Evolutionary Origins of War*

-
- and Ethnic Conflict* (Lexington: University Press of Kentucky, 2004).
11. Jim Sidanius and Robert Kurzban, "Evolutionary approaches to political psychology," in *Handbook of Political Psychology*, David O. Sears, Leonie Huddy, and Robert Jervis, eds. (Oxford: Oxford University Press, 2003), pp. 146–181.
 12. John R. Alford and John R. Hibbing, "The origin of politics: An evolutionary theory of political behavior," *Perspectives on Politics*, 2004, 2(4): 707–723.
 13. Azar Gat, *War in Human Civilization* (Oxford: Oxford University Press, 2006).
 14. Stephen Peter Rosen, *War and Human Nature* (Princeton, NJ: Princeton University Press, 2004).
 15. Steven Pinker, *The Blank Slate: The Modern Denial of Human Nature* (New York: Penguin Putnam, 2002).
 16. Christopher Layne, *The Peace of Illusions: International Relations Theory and American Grand Strategy in the Post–Cold War Era* (Ithaca, NY: Cornell University Press, 2005).
 17. John J. Mearsheimer, *The Tragedy of Great Power Politics* (New York: Norton, 2001).
 18. Eric Labs, "Beyond victory: Offensive realism and the expansion of war aims," *Security Studies*, 1997, 6(4): 1–49.
 19. Thayer, 2004; Rosen, 2004
 20. Edward O. Wilson, *Consilience: The Unity of Knowledge* (London: Abacus, 1999).
 21. Barkow.
 22. Thucydides, *History of the Peloponnesian War*, Rex Warner, trans. (Harmondsworth, UK: Penguin 1954), Book 1, Chapter 23.
 23. Hans J. Morgenthau, *Politics Among Nations* (New York: Alfred Knopf, 1956).
 24. Hans J. Morgenthau, *Scientific Man Versus Power Politics* (Chicago: University of Chicago

-
- Press, 1946).
25. Kenneth N. Waltz, *Theory of International Politics* (New York: McGraw-Hill, 1979), pp. 114–116.
 26. Kenneth N. Waltz, “The stability of a bipolar world,” *Daedalus*, 1964, 93(3): 881–909.
 27. Waltz, 1979, pp. 73–74, 77–101.
 28. Waltz, 1979, pp. 161–193.
 29. Mearsheimer, 2001, pp. 338–344.
 30. Waltz, 1979, Chapter 8.
 31. Mearsheimer, 2001, pp. 1–8.
 32. Mearsheimer, 2001, p. 21.
 33. For an analysis of offensive realism and defensive realism, see Sean M. Lynn-Jones, “Realism and America’s rise: A review essay,” *International Security*, 1998, 23(2): 157–182.
 34. An exceptional study of realism, and in some respects the fountainhead of offensive realism is Ashley Joachim Tellis, *The Drive to Domination: Towards a Pure Realist Theory of Politics*, Ph.D. dissertation (Chicago: University of Chicago, 1994).
 35. John J. Mearsheimer, “The false promise of international institutions,” *International Security*, 1994–1995, 19(3): 5–49.
 36. Mearsheimer, 2001, pp. 1–5.
 37. Layne.
 38. Labs, p. 12.
 39. Mearsheimer, 2001, p. 30–31.
 40. Mearsheimer, 2001, p. 32.

-
41. Napoleon Chagnon, *Noble Savages: My Life Among Two Dangerous Tribes—The Yanomamo and the Anthropologists* (NY: Simon and Schuster, 2014), p. 8.
42. Waltz, 1979.
43. Robert O. Keohane, *Neorealism and Its Critics* (New York: Columbia University Press, 1986a).
44. Robert Jervis, “Cooperation under the security dilemma,” *World Politics*, 1978, 30(2): 167–174.
45. Joseph S. Nye, “Neorealism and neoliberalism,” *World Politics*, 1988, 40: 235–251.
46. Alexander Wendt, *Social Theory of International Politics* (Cambridge: Cambridge University Press, 1999).
47. Nicholas Greenwood Onuf, *World of Our Making: Rules and Rule in Social Theory and International Relations* (Columbia: University of South Carolina Press, 1989).
48. Barkow et al.
49. David M. Buss, ed., *The Handbook of Evolutionary Psychology* (New York: Wiley, 2005).
50. M. Mirazón Lahr, F. Rivera, R.K. Power, A. Mounier, B. Copsey, F. Crivellaro, J.E. Edung, J.M. Maillo Fernandez, C. Kiarie, J. Lawrence, A. Leakey, E. Mbua, H. Miller, A. Muigai, D.M. Mukhongo, A. Van Baelen, R. Wood, J.L. Schwenninger, R. Grün, H. Achyuthan, A. Wilshaw, and R.A. Foley, “Inter-group violence among early Holocene hunter-gatherers of West Turkana, Kenya.” *Nature*, 2016, 529: 394–398.
51. Iver B. Neumann, “International relations as a social science,” *Millennium: Journal of International Studies*, 2014, 43(1): 330–350.
52. Dominic D.P. Johnson, “Survival of the disciplines: Is international relations fit for the new millennium?” *Millennium: Journal of International Studies*, 2015, 43(2): 749–763.

-
53. Thomas Hobbes, “Part 1: Of man,” in *Leviathan* (Cambridge: Cambridge University Press, 1991 [1651]), pp. 1–115.
54. James H. Fowler and Darren Schreiber, “Biology, politics, and the emerging science of human nature,” *Science*, 2008, 322(5903): 912–914.
55. Barkow.
56. Hodgson and Knudsen.
57. Alford and Hibbing.
58. Mark W. Allen, and Terry L. Jones, eds., *Violence and Warfare among Hunter-Gatherers* (Walnut Creek, CA: Left Coast Press, 2014), p.362.
59. Gat 2006 and Azar Gat, “So why do people fight? Evolutionary theory and the causes of war,” *European Journal of International Relations*, 2009, 15(4): 571–599. For a recent review, see Allen and Jones.
60. Wrangham, 1999.
61. Gat, 2009.
62. Bobbi S. Low, “An evolutionary perspective on war,” in *Behavior, Culture, and Conflict in World Politics*, William Zimmerman and Harold K. Jacobson, eds. (Ann Arbor: University of Michigan Press, 1993), pp. 13–55.
63. Mervyn Meggitt, *Blood Is Their Argument: Warfare Among the Mae Enga Tribesmen of the New Guinea Highland* (New York: McGraw-Hill, 1978).
64. Lawrence H. Keeley, *War Before Civilization: The Myth of the Peaceful Savage* (Oxford: Oxford University Press, 1996).
65. Gat, 2006.

-
66. Keeley.
67. Jean Guilaine and Jean Zammit, *The Origins of War: Violence in Prehistory* (Oxford: Blackwell, 2004).
68. Steven LeBlanc, and Katherine E. Register, *Constant Battles: The Myth of the Peaceful, Noble Savage* (New York: St. Martin's Press, 2003).
69. Richard W. Wrangham and Dale Peterson, *Demonic Males: Apes and the Origins of Human Violence* (London: Bloomsbury, 1996).
70. Allen and Jones.
71. Also noting this are David M. Buss and Todd K. Shackelford, "Human aggression in evolutionary psychological perspective," *Clinical Psychology Review*, 1997, 17(6): 605–619.
72. John Strate emphasizes the importance of defense from attack by conspecifics, other humans; he argues that it caused the growth of human societies. "The role of war in the evolution of political systems and the functional priority of defense," *Humboldt Journal of Social Relations*, 1985, 12: 95–110.
73. Edward O. Wilson, *On Human Nature* (Cambridge, MA: Harvard University Press, 1978), p. 112.
74. For an excellent review of the logic for, and evidence of, adaptations for war, see Anthony C. Lopez, "The evolution of war: theory and controversy," *International Theory*, 2016, 8(1): 97–139.
75. Napoleon A. Chagnon, "Life histories, blood revenge, and warfare in a tribal population," *Science*, 1988, 239: 985–992.
76. Meggitt.

-
77. Keeley.
78. Keeley.
79. Samuel Bowles, “Group competition, reproductive leveling, and the evolution of human altruism,” *Science*, 2006, 314: 1569–1572.
80. Richard W. Wrangham and Luke Glowacki, “Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers: Evaluating the chimpanzee model,” *Human Nature*, 2012, 23: 5–29.
81. Allen and Jones.
82. Wrangham and Glowacki, 2012.
83. Wrangham and Glowacki, 2012, p. 19.
84. Chagnon, 1988.
85. Richard W. Wrangham and Luke Glowacki, “Warfare and reproductive success in a tribal population,” *Proceedings of the National Academy of Sciences*, 2015, 112(2): 348–353.
86. “Egoism,” in *Oxford English Dictionary*,
<http://www.oed.com/view/Entry/59922#eid5780558>.
87. William D. Hamilton, “The genetical evolution of social behavior. I,” *Journal of Theoretical Biology*, 1964a, 7(1): 1–16
88. William D. Hamilton, “The genetical evolution of social behavior. II,” *Journal of Theoretical Biology*, 1964b, 7(1): 17–52.
89. J.B.S. Haldane, “Population genetics,” *New Biology*, 1955, 18: 34–51.
90. Inclusive fitness has recently been the subject of a heated debate in the biological literature; see M.A. Nowak, Corina E. Tarnita, and Edward O. Wilson, “The evolution of eusociality,” *Nature*, 2010, 466(7310): 1057–1062. However, it is primarily a debate

-
- about alternative methods of accounting for genetic fitness, not a criticism of the types of behaviors we expect to see in nature. Both approaches lead to the same conclusions. See David Sloan Wilson, “Clash of paradigms,” *Huffington Post*, July 15, 2012.
91. There is copious evidence from historical and contemporary times that such nepotism is a significant influence in politics. See Laura Betzig, *Despotism and Differential Reproduction: A Darwinian View of History* (New York: Aldine, 1986).
92. Martin A. Nowak, “Five rules for the evolution of cooperation,” *Science*, 2006, 314: 1560–1563.
- 45 S.A. West, C. El Mouden, and A. Gardner, “16 common misconceptions about the evolution of cooperation in humans,” *Evolution and Human Behavior*, 2011, 32: 231–262.
94. Robert H. Frank, *Choosing the Right Pond: Human Behaviour and the Quest for Status* (Oxford: Oxford University Press, 1985), pp. 7–8.
95. See, for example, Manfred Milinski, and Geoffrey A. Parker, “Competition for resources,” in *Behavioural Ecology: An Evolutionary Approach*, John R. Krebs and Nick B. Davies, eds. (Oxford: Blackwell Scientific Publications, 1991), pp. 137–168.
96. Paul K. Wason, *The Archaeology of Rank* (Cambridge: Cambridge University Press, 2004).
97. Allan Mazur and Alan Booth, “Testosterone and dominance in men,” *Behavioural and Brain Sciences*, 1998, 21: 353–397.
98. Frank.
99. Christopher Boehm, *Hierarchy in the Forest: The Evolution of Egalitarian Behavior* (Cambridge, MA: Harvard University Press, 2001).
100. Allan Mazur, *Biosociology of Dominance and Deference* (Lanham, MD: Rowman and Littlefield, 2005).

-
101. Betzig.
102. Arnold M. Ludwig, *King of the Mountain: The Nature of Political Leadership* (Lexington: University Press of Kentucky, 2002).
103. Andrew J. King, Dominic D.P. Johnson, and Mark Van Vugt, “The origins and evolution of leadership,” *Current Biology*, 2009, 19(19): 1591–1682.
104. Gerald A. Lincoln, “Teeth, horns and antlers: The weapons of sex,” in *The Differences Between the Sexes*, Roger V. Short and Evan Balaban, eds. (Cambridge: Cambridge University Press, 1994), pp. 131–158.
105. Robert L. Trivers, “Parental investment and sexual selection,” in *Sexual Selection and the Descent of Man*, Bernard Campbell, ed. (Chicago: Aldine, 1972), pp. 136–179.
106. Anthony C. Lopez, Rose McDermott, and Michael Bang Petersen, “States in mind: Evolution, coalitional psychology, and international politics.” *International Security*, 2011, 36(2): 48–83.
107. Lee Ellis, Scott L. Hershberger, Evelyn M. Field, Scott Wersinger, Sergio Pellis, Amir Hetsroni, David Geary, et al., *Sex Differences: Summarizing More Than a Century of Scientific Research* (New York: Psychology Press, 2008).
108. Shelley E. Taylor, Laura C. Klein, Brian P. Lewis, Tara L. Gruenewald, Regan A.R. Gurung, and John A. Updegraff, “Biobehavioral responses to stress in females: Tend-and-befriend, not fight-or-flight.” *Psychological Review*, 2000, 107: 411–429.
109. Mark Van Vugt and Brian R. Spisak, “Sex differences in leadership emergence during competitions within and between groups,” *Psychological Science*, 2008, 19(9): 854–858.
110. Rosen.
111. Mazur and Booth.

-
112. Rose McDermott, “The feeling of rationality: The meaning of neuroscientific advances for political science,” *Perspectives on Politics*, 2004, 2(4): 691–706.
- 113 Antonio R. Damasio, *Descartes’ Error: Emotion, Reason and the Human Brain* (New York: Avon, 1994).
114. Rosen.
115. For an excellent general analysis of the genetic origins of aggression and its chemical mediators in humans such as the hormone testosterone, its derivative dihydroxytestosterone (DHT), neurotransmitters such as serotonin, and some of the differences in behavior caused by these factors in men and women, see William R. Clark and Michael Grunstein, *Are We Hardwired? The Role of Genes in Human Behavior* (New York: Oxford University Press, 2000).
116. Bruce M. Knauft, “Violence and sociality in human evolution,” *Current Anthropology*, 1991, 32(4): 391–409.
117. J.C. Flack, M. Girvan, F.B. de Waal, and D.C. Krakauer, “Policing stabilizes construction of social niches in primates,” *Nature*, 2006, 439(7075): 426–429.
- 118 F.B.M. de Waal, *Chimpanzee Politics: Power and Sex Among Apes* (Baltimore, MD: Johns Hopkins University Press, 1998).
119. In this respect, too, international politics resembles animal behavior. As an alpha male provides stability to the group, so too a hegemon in international politics, as many scholars recognize, may provide stability for lesser states both in the realm of international security and for international political economy. On the importance of resource harvesting for the development of dominance hierarchies, see James L. Boone, “Competition, conflict, and the development of social hierarchies,” in *Evolutionary*

-
- Ecology and Human Behavior*, Eric Alden Smith and Bruce Winterhalder, eds. (New York: Aldine de Gruyter, 1992), pp. 301–337.
120. Robert Kurzban and Steven Neuberg, “Managing ingroup and outgroup relationships,” In *The Handbook of Evolutionary Psychology*, David M. Buss, ed. (New York: Wiley 2005), pp. 653–675.
121. Sidanius and Kurzban.
122. Miles Hewstone, Mark Rubin, and Hazel Willis, “Intergroup bias,” *Annual Review of Psychology*, 2002, 53: 575–604.
123. Susan T. Fiske, “What we know about bias and intergroup conflict, problem of the century,” *Current Directions in Psychological Science*, 2002, 11(4): 123–128.
124. Jim Sidanius and Felicia Pratto, *Social Dominance: An Intergroup Theory of Social Hierarchy and Oppression* (New York: Cambridge University Press, 2001).
125. Richard D. Alexander, *The Biology of Moral Systems* (Aldine, NY: Hawthorne, 1987).
126. R.A. Hammond and Robert Axelrod, “The evolution of ethnocentrism,” *Journal of Conflict Resolution*, 2006, 50(6): 926–936.
127. J.K. Choi and S. Bowles, “The coevolution of parochial altruism and war,” *Science*, 2007, 318: 636–640
128. Gat, 2006.
129. Keeley.
130. Guilaine and Zammit.
131. LeBlanc and Register.
132. Allen and Jones.
133. Wrangham and Peterson.

-
134. Keeley.
135. Bowles.
136. Sidanius and Kurzban.
137. Alexander.
- 138 John Tooby and Leda Cosmides, “Groups in mind: The coalitional roots of war and morality,” in *Human Morality and Sociality: Evolutionary and Comparative Perspectives*, Henrik Høgh-Olesen, ed. (New York: Palgrave MacMillan, 2010), pp. 191–234.
139. Wrangham, 2009, p. 169.
140. Manson and Wrangham.
141. Wrangham, 1999.
142. M.L. Wilson et al, 2014.
143. LD Mech, LG Adams, TJ Meier, JW Burch, and BW Dale, *The Wolves of Denali* (Minneapolis: University of Minnesota Press, 1998).
144. Robert Axelrod, *The Evolution of Cooperation* (London: Penguin, 1984).
145. Lee Cronk and Beth L. Leech, *Meeting at Grand Central: Understanding the Social and Evolutionary Roots of Cooperation* (Princeton, NJ: Princeton University Press, 2013).
146. Martie G. Haselton, and Daniel Nettle, “The paranoid optimist: An integrative evolutionary model of cognitive biases,” *Personality and Social Psychology Review*, 2006, 10(1): 47–66.
147. Paul Rozin, and Edward B. Royzman, “Negativity bias, negativity dominance, and contagion,” *Personality and Social Psychology Review*, 2001, 5(4): 296–320.
148. We thank Robert Jervis for bringing this point to our attention.

-
149. Gat, 2009.
150. Gat, 2006.
151. Rosen.
152. Rose McDermott, *Presidential Leadership, Illness, and Decision Making* (Cambridge: Cambridge University Press, 2007).
153. Rose McDermott, *Political Psychology in International Relations* (Ann Arbor: University of Michigan Press, 2004).
154. Mearsheimer, 2001, p. 22.
155. Nick B. Davies, John R. Krebs and Stu A. West, *An Introduction to Behavioural Ecology* (Chichester, UK: Wiley Blackwell, 2012).
156. Frank.
157. I.H Robertson, *The Winner Effect: How Power Affects Your Brain* (London: Bloomsbury, 2012).
158. Mazur.
159. Gat, 2006, p. 427; see also Elizabeth Knowles, ed., *Oxford Dictionary of Quotations* (Oxford: Oxford University Press, 1999), p. 333.
160. Rosen.
161. Robertson.
162. Michael L. Wilson, Nick F. Britton, and Nigel R. Franks, "Chimpanzees and the mathematics of battle," *Proceedings of the Royal Society of London, Series B*, 2002, 269: 1107–1112.
163. Mearsheimer, 2001, p. 40.
164. Robert O. Keohane, *After Hegemony: Cooperation and Discord in the World Political*

-
- Economy* (Princeton NJ: Princeton University Press, 1986b).
165. Arthur Stein, *Why Nations Cooperate: Circumstance and Choice in International Relations* (Ithaca, NY: Cornell University Press, 1990).
166. Yong-Jin Won and Jody Hey, “Divergence population genetics of chimpanzees,” *Molecular Biology and Evolution*, 2005, 22(2): 297–307.
167. Richard W. Wrangham and David Pilbeam, “African apes as time machines,” in *All Apes Great and Small. Volume 1: Chimpanzees, Bonobos, and Gorillas*, Birute M.F. Galdikas, Nancy E. Briggs, Lori K. Sheeran, Gary L. Shapiro, and Jane Goodall, eds. (New York: Kluwer Academic/Plenum, 2001), pp. 5–18.
168. Wrangham and Peterson.
169. Wrangham and Pilbeam.
170. Ernst Fehr and Urs Fischbacher, “The nature of human altruism,” *Nature*, 2003, 425: 785–791.
171. L.A. Dugatkin, *Cooperation in Animals* (Oxford: Oxford University Press, 1997).
172. Cronk and Leech.
173. Robert Trivers, *Natural Selection and Social Theory: Selected Papers of Robert Trivers* (Oxford: Oxford University Press, 2002).
174. Hamilton, 1964a and Hamilton, 1964b.
175. Robert Boyd, “The puzzle of human sociality,” *Science*, 2006, 314(5805): 1555.
176. Mancur Olson, *The Logic of Collective Action: Public Goods and the Theory of Groups* (Cambridge, MA: Harvard University Press, 1965).
177. Elinor Ostrom, *Governing the Commons: The Evolution of Institutions for Collective Action* (Cambridge: Cambridge University Press, 1990).

-
178. Nowak.
179. K. Sigmund, “Punish or perish? Retaliation and collaboration among humans,” *Trends in Ecology and Evolution*, 2007, 22(11): 593–600.
180. Mearsheimer, 1994–1995.
181. Helen V. Milner, *Interests, Institutions, and Information: Domestic Politics and International Relations* (Princeton, NJ: Princeton University Press, 1997).
182. Ostrom.
183. Keohane, 1986b.
184. David S. Wilson, “Evolutionary biology: Struggling to escape exclusively individual selection,” *Quarterly Review of Biology*, 2001, 76(2): 199–205.
185. David Sloan Wilson and Elliott Sober, “Reintroducing group selection to the human behavioural sciences,” *Behavioral and Brain Sciences*, 1994, 17(4): 585–654.
186. See, for example, the recent articles and responses here: Steven Pinker, “The false allure of group selection. *Edge*, 2012 (12 July), http://edge.org/conversation/steven_pinker-the-false-allure-of-group-selection.
187. Bowles.
188. M. Ridley, *The Origins of Virtue: Human Instincts and the Origins of Cooperation* (London: Penguin, 1996).
189. G.C. Williams, *Adaptation and Natural Selection* (Princeton, NJ: Princeton University Press, 1966).
190. P.J. Richerson and R. Boyd, *Not by Genes Alone: How Culture Transformed Human Evolution* (Chicago: University of Chicago Press, 2004).
191. Alan Ehrenhalt, *The United States of Ambition: Politicians, Power and the Pursuit of Office*

-
- (New York: Times Books, 1992).
192. A. Todorov, A.N. Mandisodza, A. Goren, and C.C. Hall, “Inferences of competence from faces predict election outcomes,” *Science*, 2005, 308: 1623–1626.
193. Mark Van Vugt and Anjana Ahuja, *Selected: Why Some People Lead, Why Others Follow, and Why It Matters* (New York: Harper Business, 2011).
194. Richard Shenkman, *Presidential Ambition: Gaining Power at Any Cost* (New York: Harper Collins, 1999).
195. Daniel Kahneman and Jonathan Renshon, “Why hawks win,” *Foreign Policy*, 2007, 158: 34–38.
196. Robertson, 2012.
197. Francis Fukuyama, “Women and the evolution of world politics,” *Foreign Affairs*, 1998, 77(5): 24–40.
198. Eleanor Clift and Tom Brazaitis, *Madam President: Women Blazing the Leadership Trail* (New York: Routledge, 2003).
199. Ludwig.
200. Betzig.
201. Gat, 2009.
202. Jack S. Levy, “Misperception and the causes of war: Theoretical linkages and analytical problems,” *World Politics*, 1983, 36(1): 76–99.
203. R.F. Baumeister and J.M. Boden, “Aggression and the self: High self-esteem, low self-control, and ego threat,” in *Human Aggression: Theories, Research, and Implications for Social Policy*, R.G. Geen and E. Donnerstein, eds. (San Diego, CA: Academic Press, 1998), pp. 111–137.

-
204. Irving L. Janis, *Victims of Groupthink: Psychological Studies of Policy Decisions and Fiascoes* (Boston: Houghton Mifflin, 1972).
205. McDermott, 2007.
206. Kahneman and Renshon.
207. Richard W. Wrangham and Michael L. Wilson, "Collective violence: comparisons between youths and chimpanzees," *Annals of the New York Academy of Sciences*, 2004, 1036: 233–256.
208. Olson.
209. Ostrom.