The Origin of Politics: An Evolutionary Theory of Political Behavior

John R. Alford and John R. Hibbing

In this article we propose that evolutionary biology can supply political science with a theory of the ultimate causes of human preferences and behaviors that it otherwise lacks. For the most part, political scientists are either unfamiliar with the social side of evolutionary theory or misidentify its key features. Far from being genetically deterministic or leading exclusively to predictions that all human behavior will be selfish, modern evolutionary theories stress that adaptive behavior is frequently characterized by a guarded sort of cooperation. We describe modern biological theory, offer our own version of it, discuss new and potentially useful interpretations of political attitudes and public policies, and present scientific evidence, drawn from research on autistic individuals and monozygotic and dizygotic twins, of the startlingly important role genetics plays in shaping politically relevant attitudes and behaviors.

Why do people hold the political attitudes they do? Despite the centrality of this question, the two guiding theoretical orientations of modern political science, rational choice and behavioralism, are surprisingly unhelpful. Rational choice is content to take preferences as given and is not particularly motivated to explore their origins or grounding in reality. Behavioralism is based on the untested assertion that preferences can be understood by an exclusive focus on environmental variables; it largely ignores the fundamental issue of why people respond to the environment as they do. It is quite common (and accurate) for adherents of both positions to admit that their favored approaches are not theories at all.

Our goal is not to criticize rational choice and behavioralism. Indeed, political scientists working within both theoretical frameworks have produced impressive findings and insights, thereby revealing the value in identifying influential environmental factors and in outlining the actions that a rational individual holding a given preference takes. Nonetheless, the fact remains that, as early proponents of rational choice correctly noted, behavioralism is limited by its lack of a real theory to being a largely inductive mode of research. Rational choice, in turn, as many of its proponents have come to realize, is reaching the limits of what can be accomplished by deductive research based on assumed rather than actual preferences. To fully understand, connect, and transcend the extant research requires an empirically sustainable theory of the source of preferences and of the reasons people respond as they do to environmental stimuli.

Such a theory exists and is being employed with increasing regularity in the social sciences, especially experimental economics, behavioral anthropology, and social psychology. Certainly, some political scientists are familiar with this theory, but it has not been the basis for original research in political science. Yet theories of the origins of preferences (and therefore behaviors) may offer the ability to unite the individual social sciences—and even the social sciences as a group—with the natural sciences.

Political scientists may find the theory we describe wanting. But it should not be dismissed without due consideration of the evidence for and against it. Most important, the theory should not be dismissed because of an unscientific aversion to its implications.

The central tenet of this theory is that preferences and behaviors are at least partially shaped by evolutionary forces and therefore by genetic heritage. Just as evolutionary pressures shaped genes governing the physical traits of humans, they also shaped genes governing behavioral traits. If this is true, research in the social sciences will be furthered by taking into account evolutionarily advantageous behaviors and by increased attention to the connection between human biology and social behavior. This evolutionary-biological approach incorporates valuable insights from both behavioralism and rational choice. In fact, the most substantial current applications of this theory are seen in the two disciplines, psychology and economics, from which political scientists borrow most heavily—and from which we

John R. Alford is associate professor of political science at Rice University (jra@rice.edu). John R. Hibbing is Foundation Regents University Professor of Political Science at the University of Nebraska–Lincoln (jhibbing@unl.edu). *The authors are grateful to Chris Larimer, Levente Littvay, David Rapkin, Kevin Smith, Jeff Spinner-Halev, Elizabeth Theiss-Morse, and anonymous reviewers for their helpful comments and suggestions.*

borrowed behavioralism and rational choice, respectively. If a single theoretical approach can make headway in disciplines as disparate as economics and social psychology, it surely merits some attention in a discipline like ours, which has internalized the conflict between psychology and economics.

In what follows, we provide a general description of modern evolutionary theory and our own more sociopolitically focused behavioral theory, which we call "wary cooperation." We then draw out the direct implications of this theory for interpretations of politics and public policy. Finally we direct our attention to evidence supporting the assertion that is most likely to trouble political scientists: that political orientations are to a significant extent genetically influenced.

An Evolutionary Theory of Political Behavior

While "survival of the fittest" is often automatically associated with Hobbesian self-interest, the Darwinian account of human behavior is not nearly as depressing as is typically imagined. As is often the case, a disciple took a much harder line, which has colored popular interpretations of the original message. In Charles Darwin's case, Thomas H. Huxley was the individual largely responsible for creating a story of social evolution characterized by unceasing and often violent self-interest.[1] Darwin himself recognized the incredible variety of adaptive behaviors and the value and prevalence of behavior designed, at least in the near term, to benefit other organisms.[2]

To the extent that evolutionary theory has influenced the thinking of political scientists, it has been primarily in the equation of natural selection with narrow self-interest. Deviations from self-serving behavior are typically explained by humans' limited cognitive abilities,[3] or by humans' socialization and ultimate internalization of societal norms. As Leda Cosmides and John Tooby put it, most economists and social scientists assume that "rational behavior is the state of nature, requiring no explanation."[4] This sentiment is evident in the work of political scientists. For example, Elinor Ostrom asserts that "our evolutionary heritage has hardwired us to be boundedly self-seeking at the same time that we are capable of learning heuristics and norms, such as reciprocity."[5] From this perspective, self-serving behavior is genetically driven and can only be countered by the decidedly nongenetic teaching of societal niceties.

In equating natural selection with inherent selfishness, political scientists reflect views held by mainstream biologists from Huxley's time through about a quarter century ago. The overwhelming focus of evolutionary theorists then was largely compatible with what came to be the rational choice view of the appropriate starting assumption for human behavior. In a well-known work, biologist Richard Dawkins observed: "If we were told that a man lived a long and prosperous life in the world of Chicago gangsters, we would be entitled to make some guesses as to the sort of man he was. . . . Like successful Chicago gangsters, our genes have survived, in some cases for millions of years, in a highly competitive world. . . . If you look at the way natural selection works, it seems to follow that anything that has evolved by natural selection should be selfish."[6]

In this view, human beings are merely "survival machines," constructed by the genes to help the genes continue into the next generation. The interactions of survival machines are hardly expected to be warm and fuzzy. Dawkins continues: "To a survival machine, another survival machine is part of its environment, like a rock or a river or a lump of food. It is something that gets in the way or something that can be exploited."[7] One need not search long to find parallel views in social science. In one of the founding works of rational choice, James M. Buchanan and Gordon Tullock declared that when two people interact, each will always seek "more rather than less" and will "exclude from consideration" the interests of their "opposite number."[8]

Evolutionary theory has undergone fundamental changes in recent decades, particularly as it relates to social behavior. Renewed enthusiasm for an earlier, but largely ignored, insight—that of multilevel selection—offers an ingenious explanation for the emergence of cooperation from a nuanced pattern of self-interest. Selection pressure itself is, after all, a law of nature, not an evolved mechanism: over time, things that last longer and/or reproduce themselves more successfully will come to dominate numerically. This is not limited to living things, and genetic evolution is only one mechanism that expresses this natural law. Traditional evolutionary theory has focused largely on the role of selection pressure at the level of the gene, and this is what most political scientists think of when the topic of evolution comes up.[9]

Multilevel selection begins by recognizing the ubiquity of selection pressure. Focusing at any single level will highlight selection pressure and the associated narrowly self-interested modes of activity at that level. For example, focusing at the level of the gene highlights the fact that the behavior of human genes is ultimately a consequence of self-interest at that level. This has led scholars such as Dawkins to think of organisms as nothing more than machines built and utilized by selfish genes, genes which "care" nothing for the ultimate welfare of the organism itself.[10]

Taking a step back alters this picture substantially. The genes themselves are, after all, merely survival machines for the complex proteins that make up genetic material. At this deeper level, it is the complex proteins that are selfish, and their survival machines—the genes—may behave in ways that seem highly inconsistent with selfishness.[11] In terms of human behavior, if we think of groups as survival machines for collections of individuals, then selection pressures that lead individuals to behave selfishly may well be in conflict with selection pressures that favor groups of individuals that behave in concert. Whenever working in groups allows for advantages stemming from specialization, division of

labor, or even mere numerousness itself, groups characterized by cooperative behavior at the individual level have the potential to out-compete and hence dominate groups characterized by selfish behavior at the individual level. Thus individuals are subject to conflicting selection pressure. At the individual level, pressure favors entirely self-regarding behavior, but self-regarding individuals may have a better chance of survival if they are members of cooperative groups. The parameters that characterize the equilibrium of these conflicting pressures will often yield behavior that is selfish; however, under some realistic conditions the result will be the evolution of mechanisms for cooperation. The cooperation evident among proteins in creating living cells, among cells in creating tissues, among tissues in creating organs, and among organs in creating complex living structures like plants and animals, are all examples of this balance of competition and cooperation within the evolutionary process.[12]

The important insight for human behavior comes from continuing this Russian doll analogy of competition within cooperation to the level of families, extended kin groups, clans, political parties, and nation states—all of which are potentially subject to selection pressure at the individual and collective levels. Environmental conditions that offer substantial advantages to clans that cooperate easily and efficiently will tend to produce at equilibrium an environment filled largely with relatively cooperative clans. The selfish interest of the clan vis-à-vis other clans thus acts to reduce the selfish behavior of individuals within a clan, but only to the degree that that reduction in within-clan selfishness improves the survival chances of individuals in cooperative clans relative to less cooperative clans. Thus it is not that evolution itself favors cooperation or operates in anything but a selfish fashion; it is simply that evolution is agnostic about the methods (e.g., competition or cooperation) by which overall survival advantages are achieved.

Humans are cooperative, but not altruistic; competitive, but not exclusively so. We have an innate inclination to cooperate, particularly within defined group boundaries, but we are also highly sensitive to selfish actions on the part of other group members.

Our Theory: Wary Cooperation

New theories of political behavior can be built on this current and subtle version of Darwinian selection theory. In that spirit we offer our own theory of "wary cooperation" drawn from the work of leading scholars in evolutionary psychology and experimental economics. The theory may be summarized as follows. Humans are cooperative, but not altruistic; competitive, but not exclusively so. We have an innate inclination to cooperate, particularly within defined group boundaries, but we are also highly sensitive to selfish actions on the part of other group members. This sensitivity leads us to cease cooperating when that cooperation is not reciprocated, to avoid future interaction with noncooperators, and even to engage in personally costly punishment of individuals who fail to cooperate.

Perhaps the easiest way to see wary cooperation in action is to summarize findings from the ultimatum game. In this widely used experimental scenario two anonymous players are brought together for a single interaction.[13] One is given the task of dividing a sum of money between the two of them. The other can either accept or reject the proposed allocation but if it is rejected neither player receives any money. Of course, from a rational point of view, no player should ever make a generous offer to a receiving player and no receiving player should ever reject a positive offer. In practice, however, the modal offer is 50 percent of the pot, and offers of less than one-third are rejected by receiving players more than 50 percent of the time, meaning that a remarkably high percentage of people are willing to sacrifice their own monetary rewards to share with another player or to punish an allocator who kept a large portion of the pot.[14] The latter practice is sometimes called, for obvious reasons, costly or altruistic punishment.[15]

On the one hand, pure self-interest cannot explain either our willingness to cooperate or our willingness to punish at our own expense in this scenario.[16] On the other hand, pure altruism cannot explain our willingness to punish noncooperators or, in multiple-play games, to cease cooperating with noncooperators. Wary cooperation does account for these behaviors. Moreover, unlike short-term self-interest or altruism, our theory is grounded in an evolutionary view of human behavior, for it is likely that wary cooperation is a product of innate and genetically heritable behavioral predispositions, and that these predispositions are the result of identifiable selection pressures.[17]

What are the evolutionary underpinnings of our theory? Evolution is a slow process, and much of the environmental pressure favoring human cooperation has existed for a long time. Our genetic composition is to some extent the product of conditions faced by our hunter-gatherer predecessors of perhaps 100,000 years ago. One of the keys to an individual's survival was being a respected part of a viable group. The central insight of a behavioral theory built on evolutionary biology is that the desire for group life is a fundamental human preference. What kinds of behaviors optimally promote belonging to a viable group? These tend

to be primitives as opposed to elaborated behaviors since specific, genetically determined behaviors are less likely to be adaptive. Space precludes a complete list; we mention just six of the most important default behaviors for members of a viable group. To sustain group membership, individuals must

1. cooperate with others in their in-group;
2. dislike those in out-groups;
3. punish or banish uncooperative in-group members;
4. encourage others through norms, institutions, or moral codes to (1), (2), and (3);
5. be ever sensitive to status, payoffs, and reputation relative to other in-group members;
6. cease cooperating if the noncooperation of other members goes unpunished.

Since these behaviors foster valued membership in viable groups, and since being an accepted member of a properly functioning group facilitates survival, we believe these six behaviors will be common, though perhaps not universal, genetic endowments.

Wary cooperation is the most social of theories, since it is built around other people. In this sense it affords another contrast with existing approaches. According to rational choice (and old school evolutionary theory), for example, other people get in the way. According to the theory of wary cooperation, other people *are* the way. But this does not mean that behavior is altruistic. Social behavior is often taken to be good and its polar opposite—egocentric behavior—bad. But social behavior is not synonymous with altruistic behavior.[18] Rather, social behavior is centered on other people but not necessarily concerned with the welfare of other people. In so saying, we are in complete accord with Kristen Renwick Monroe's recent emphasis on "interactions with others," on "sociability" and on "an innate need for human connection" as well as Marilyn Brewer's account of behavior relevant to in- and out-groups.[19]

In addition to expecting cooperative behavior in some circumstances, our theory also expects—and empirical studies have proven it to be the case—that people mindlessly conform,[20] passively obey authority figures,[21] are competitive to the point of taking pleasure in the misfortunes of others,[22] initiate hostilities toward those people in out-groups,[23] construct out-groups for the sake of having them,[24] and are disconcertingly enthusiastic about punishing those not perceived as living up to the group's behavioral standards, especially when personally victimized.[25] The theory of wary cooperation predicts the construction of moral codes that conditionally value cooperative behavior; it does not predict altruistic behavior.

Thus human behavior seems to be remarkably consistent with the behaviors expected by our theory—an issue future scholarship will continue to address.[26] Here we must defend the claim that the behaviors listed above are indeed advantageous for humankind—or at least were in the past. Since no one has the ability to recreate the Pleistocene, evolutionary psychology is vulnerable to charges that it merely spins "just-so" stories by observing modern human behavior and then offering post-hoc and perhaps even tortured accounts of why those behaviors might have been valuable in our species' distant past.[27] These charges should be taken seriously because, as is the case with any theory, proponents have occasionally made overstatements.

Having said this, there is intriguing support for the notion that behaviors and traits consistent with the theory of wary cooperation are precisely those that lead to success in a harsh and competitive environment. Much of this support comes from computer simulations used to test models developed in evolutionary game theory. These simulations allow observation of the relative success of groups of individuals who follow various behavioral rules. Some groups in these simulations are populated by altruists, some by egoists, and some by wary cooperators. When groups with these different characteristics are allowed to compete with one another, those composed of wary cooperators survive the evolutionary test. Groups composed mainly of altruists fail because they have no protection against the occasional egoist in their midst. But egoist groups also fail because they are groups in name only and lack the bonds that lead to the benefits of group behavior.[28] We submit that it is not a coincidence that wary cooperation wins in computer simulations of the evolutionary process *and* is so frequently observable in real human society.

Evidence suggests that even humans' alleged mental frailties serve a purpose. Ralph Hertwig and Peter M. Todd demonstrate that cognitive "limitations in processing capacity, as well as in other resources such as knowledge, can actually enable rather than disable important adaptive functions."[29] For example, it is now thought that children learn languages more quickly than adults in part due to their limited memories. Limitations constrain solution space, allow a scaffolding to guide learning, and suggest patterns. Neural networks designed to simulate language learning actually learn more quickly with less memory—more is not always better.[30] The same is true of rationality. As stated by Cosmides and Tooby, " '[R]ational' decision-making methods . . . are computationally very weak; incapable of solving the natural adaptive problems our ancestors had to solve reliably in order to reproduce."[31] They conclude that, from an evolutionary point of view, human mental capacities, far from preventing rational thought,[32] actually allow us to be "better than rational."[33] Related evidence that there is method to human madness comes from identification of the tasks that humans do not do well. Humans are not particularly good at calculation, storage and retrieval of facts, and pure logical problems.

On the other hand, humans (even very young ones) are amazingly good at language recognition; intuitively comprehending the physics of movement (e.g., throwing an

object accurately at something while it and the thrower are both moving); reading facial expressions for honest, as opposed to contrived, emotion; making inferences about plants and animals (as opposed to similarly distinguishable man-made objects); and identifying others likely to be noncooperators, especially cheaters—even though these tasks are as, or more, demanding than many we do poorly.[34] For example, when experimental subjects are shown pictures of individuals and told their names along with a single fact about them, subjects are better at remembering the names of those who had been connected with a social fact (Sally helped a neighbor paint his house) than a nonsocial fact (Tom has an old refrigerator), and they are best at remembering those who had been connected to a negative social fact (Harry did not return a CD he borrowed from his friend).[35] These very activities—accurately reading social situations, intuiting the physics of the world around us, perceiving food sources, and especially identifying those who might harm us or our group status—are those that would have been quite useful to our ancestors as they roamed the savannah in small bands. As biologist William Hamilton put it, "The tabula of human nature was never rasa."[36]

The idea that human nature exists should not be confused with the belief that it is fixed. In fact, humans must be sensitive to environmental surroundings to achieve objectives. For example, levels of trusting behavior vary widely around the world and even within a country.[37] If natural selection over hundreds of thousands of generations has weeded out the altruists and the egoists, leaving only wary cooperators, why is cooperative behavior present in such vastly different proportions around the world? The answer is simple but important: wary cooperation is a conditional behavior and thus fundamentally different from strategies of "always act in your own interest" or "always act in the interest of the other person." The wary cooperator acts with a glance over the shoulder and adjusts behavior as needed. Thus the behavior of a wary cooperator in Lombardy will be quite unlike that of the same genotype transplanted to Sicily, merely because these two individuals are likely to encounter different levels of cooperative behavior.

Most contributions of rational choice and behavioralist scholarship are in no way compromised but rather enhanced by the acceptance of evolutionary theories. The previously content-free "preference structures" of rational choice can find a source of clear and potentially falsifiable content, and the "incoherent environmentalism"[38] of behavioralism can be given theoretical coherence. The message is not that nature trumps nurture but rather that nurture is in our nature—and that the precise nature of our nurturing tendencies depends upon environmental conditions.[39] Our theory subsumes a wide range of behavior—as any successful social theory must. Work that takes evolution seriously opens a broad range of cooperative opportunities across methodologies and approaches that in the past have created lines of conflict within political science; it draws on and encourages more theory-driven research in fields as diverse as game theory, traditional field work in anthropology, and economic and social psychological experiments, with worldwide human (and nonhuman) subjects.[40]

Implications for Politics and Public Policy

Buchanan and Tullock are undeniably correct to assert that "the only final test of a model lies in its ability to assist in understanding real phenomena."[41] We believe our theory of wary cooperation has practical applications in a variety of areas in politics and political science.

Death, taxes, and welfare

Perhaps not surprisingly, a theory that highlights our innate willingness to engage in costly punishment sheds considerable light on policies that relate to criminal justice. In the death penalty debate, the theory of wary cooperation suggests that support for such draconian punishments derives more from a desire for retribution than from an effort to discourage potential murderers. This explains why, with research consistently finding that the death penalty has no deterrent value, the American public largely supports it. Historically, executions have been public events, and while their public nature is certainly compatible with the goal of deterrence, it is difficult to see why anyone without a general interest in punishment would attend.

Tax law provides another example. Do we punish tax evaders because we all wish to be tax evaders and must be frightened into compliance, or are we willing to pay our fair share only assuming others do the same and evaders face swift and certain consequences? Wary cooperation suggests the latter reason.

Turning to the positive side of government, welfare programs are often poorly regarded, in large part, apparently, because it is believed they provide benefits to unworthy recipients. Why are people so willing to help the downtrodden, and why are they even more willing to stop helping when they suspect even a handful of undeserving recipients? Our theory provides a ready explanation for both tendencies. People are initially helpful and cooperative, even at some personal expense, but they are hypersensitive to the possibility that someone might take advantage of their generosity.

The wary cooperation theory also has something to say about the viability of strategies for dealing with cheaters in general. In the welfare debate, for example, policy makers commonly argue that increased effort to eliminate cheating is simply inefficient, as the amount spent on detecting each additional cheat will exceed, often substantially, the cost that the cheater was imposing. This rational appeal typically serves only to further outrage those whose tax contributions finance welfare benefits. But does anyone actually think that it would be a good idea to send a cheat to live in

luxury in the Caribbean for what we would otherwise pay to bring him to justice for his noncompliant behavior? In this and related policy matters, we see clear evidence that people are willing to support and engage in costly punishment—and also to comply themselves—as long as they remain confident that noncontributors are routinely punished. The perception of a general failure to punish others, rather than the perception that we are personally unlikely to be punished, is the proximate cause of noncompliance.

War

The phrase "millions for defense, not a penny for tribute," popularized in the United States during the days of the Barbary pirates but just as relevant to today's mood (if a few zeroes are added), nicely captures the role wary cooperation has played in the history of international affairs. The fact that wary cooperation helps account for humans' innate capacity to cooperate on a large social scale is by no means equivalent to a notion that the social side of human nature is benign in its aims and impacts. Perhaps the most striking example of this is war. The most apparent characteristic of war at the group level is conflict, but we should not miss the fact that at the individual level warfare is among the most cooperative and self-sacrificing of all human ventures. In no other arena are humans as likely to set aside their personal health, well-being, comfort, and even life itself, in favor of group success. Selfless participation in warfare remains, even in modern societies, at the center of our notions of heroism and ennobling actions. While the savagery of war clearly derives from innate human features, it is clear that the explanation of group-level savagery is not simply an aggregation of individual-level aggression. While the importance of cooperation for peace may seem self-evident, cooperation is no less critical to war. This seeming contradiction is troubling to many. As Kenneth Waltz notes, for example, "While human nature no doubt plays a role in bringing about war, it cannot by itself explain both war and peace."[42]

War is, of course, only an extreme example of the apparent contradiction within an explanation for both cooperation and competition that focuses on human nature. In some ways, avoiding this contradiction may be the greatest value of the wary cooperation theory. Though our theory posits a simple baseline explanation of human nature, it does not assume that human nature must be either competitive or cooperative; rather, it explains one source of the relative importance of competitive and cooperative drives within a given behavioral context.[43] Similarly, it frees competition from a necessary tie to self-interest just as it frees cooperation from any necessary association with altruism. We do not have a gene for combativeness any more than we have a gene for cooperation, or indeed a gene for wary cooperation. What we have is a set of innate behavioral repertoires that allows wary cooperation to emerge and dominate in a variety of fairly common social environments. Rational actor models would predict universal free-riding in the face of the overwhelming costs to individual participation in warfare.[44] While some individuals do indeed seek to avoid participation and sanctions against deserters are necessary, the modal behavior is often voluntary participation, particularly when perceptions of group membership and expectations of cooperation by other group members are present. Behavioralists' explanations fare no better, as neither the level of self-sacrificing cooperation nor the level of violent competition find any natural parallels in the average individual's peacetime behavioral repertoire. Both cooperation and conflict reach their zenith in the same behavior.

What other features of war does an evolutionary view like ours highlight? Since in this view, the conflict of war is a group-level phenomenon, group-level factors become particularly salient. Markers of in-group–out-group boundaries, for example (e.g., borders, language, ethnicity, race, religion, citizenship) should assume exaggerated importance in both the development and prosecution of war.[45] Similarly, the intergroup pressure of competition should lead to an exaggerated intragroup focus on cooperation, group solidarity, and potential internal betrayal (witness the public mood in the United States after the terrorist attacks of September 11, 2001). Human behavior in war is a bundle of seemingly intractable contradictions. Nevertheless, our theory can account for the inherent human willingness in wartime to risk one's life for a chance to take the life of an out-group member, or save the life of an in-group member while simultaneously supporting the killing of in-group members who are unwilling to kill out-group members.

Political institutions

Why do political institutions exist? This question has bedeviled political thinkers for quite some time. If people prefer the kind of societal life that is made possible by political institutions, why do they not merely lead that life in the first place? The infinite regress problem immediately scuttles most attempted explanations, but wary cooperation offers a way out: the existence of political institutions may in large part be attributed to people's intense desire for sanctions to be brought against noncooperators. People may believe that, if left to their own devices, most of their compatriots would be cooperative good citizens, but the possibility of even a very small number of bad apples is enough to drive them to create institutions.

Do people not realize that those elevated to positions of power in institutions have great potential to take advantage of their positions for personal gain? Indeed they do, and thus it should come as no great surprise that public opinion research finds that Americans' primary source of dissatisfaction with government is not that it makes bad decisions, but rather that it makes decisions for self-serving rather

than common-good reasons.[46] Government is typically disliked not because it is perceived to do the wrong things, but because it is perceived to do things for the wrong reasons. Ascribed motive is the main determinant of responses to the actions of others in any societal interaction, but it becomes acutely important when we are dealing with people possessing substantial clout.[47] In this sense, the theory of wary cooperation holds that those staffing political institutions should be subject to special vigilance not because they are fundamentally different life forms but because their ambition for authority raises suspicions, and their possession of authority makes them potentially dangerous.[48]

What does the theory say about the specific manner in which political institutions should be constructed? For starters, it points out the prescience of the architects of the U.S. political system in making it difficult for decision makers to further their own ends. Separation of powers across institutions, frequent elections, federal arrangements, and a strong judiciary—all facilitate the balancing of one group's powers against another's, which is, not coincidentally, extremely popular with the mass public.

This does not mean, however, that the American political system is a perfect fit with the institutional preferences flowing from the theory of wary cooperation. In the people's view, far too many opportunities still exist for elected officials to feather their own nests. Think of the ire evoked by matters relating to congressional salary, pension plans, and perquisites, not to mention the perceived unholy alliance of well-heeled interest groups and politicians. Wary cooperators like to cooperate, but they are also predisposed to be wary of the actions of others—especially those eager to make decisions for the group. Reformers would do well to realize that people do not wish to be in control of the political system; they only want those who *are* in control to be unable to take advantage of their positions. If people were confident that existing constraints prohibited such self-interested actions, they would pay even less attention to the political arena than they do now. For most people, involvement in politics is driven not by a desire to be heard but by a desire to limit the power of others. Current American foreign policy might be improved, for example, if decision makers realized that, like Americans, people in Afghanistan and Iraq do not crave democratic procedures. Kurds simply do not want to be dominated by Sunnis; Sunnis do not want to be dominated by Shiites; Uzbekis by Tajiks; and Tajiks by Pashtuns. People often express a desire for participatory democracy when they really just want to avoid being victimized by a more powerful group.

The Genetic Inheritance of Political Orientations

To this point, we have asserted that the modal human behavioral tendency is neither self-interested nor altruistic, but, rather, warily cooperative. Further, we claim that the prevalence of wary cooperators is the result of evolutionary pressures that reward humans skilled at creating and existing in viable social units. Our theory is only one of many possible theories that take seriously the connection between biology, natural selection, and human behavior. Evidence supporting this connection can be found in the literature on genetics and human behavior that has flourished, as new fields of inquiry often do, with the acceptance of a new methodology. In this section we explore one such methodology—twin studies.

Charles Darwin and Alfred Russel Wallace worked out the details of natural selection at roughly the same time and were in remarkable agreement—with one vital exception. Darwin was completely consistent and contended that natural selection applied to behavioral as well as physical traits. Wallace, on the other hand, drew a bold line between the two, positing that the mental realm was immune to evolution and was instead the purview of ethereal religious uncertainties. Wallace's position is still favored by groups as diverse as religious fundamentalists and many in the social science community who refuse to believe that behavior is innate. The natural sciences have sided almost unanimously with Darwin. Wallace spent the last years of his life largely ignored, a religious mystic who thought it possible to communicate with the dead and who tried desperately to hold on to the fiction that our brains, behaviors, and beings constitute something more than just another step along the evolutionary path.[49]

If political scientists believe, with Darwin, that genetics influences social attitudes and behavior, it is not evident in their research. Certainly no recent article in a leading political science journal has used genetics as an independent variable.[50] Perhaps most believe that, while genetics may play some nebulous role in politics, environmental complexities and human cognitive capabilities overwhelm genetic effects, allowing the discipline's research agenda to completely ignore biology. Contrary to popular belief, however, the link between genes and political attitudes and behaviors is strong. In this section we hope to convince readers that genetic variables are more influential than is generally conceded by political scientists. To do so we summarize recent research on twins, on autism, and on genetic-environmental interactions.

Twins

Monozygotic (MZ) twins have virtually identical genetic codes; dizygotic (DZ) twins, like other full siblings, share as little as 50 percent of the genetic material that varies in human beings.[51] This makes the study of the adult characteristics of these two types of twins of special value in computing the relative influence of heredity and environment—especially when augmented by a comparison of twins reared separately and those reared together. Such studies typically identify a substantial amount of genetic influence and a

surprisingly paltry amount of parental influence operating through the environment.[52] To take a single example, the correlation in general intelligence between MZ twins is much greater than the correlation in general intelligence between DZ twins. While general intelligence appears to be the most highly heritable behavioral trait discovered to date,[53] thousands of twin studies have documented the heritability of numerous other traits, from susceptibility to drinking problems to manners of talking and from likelihood of divorce to religiosity. Those who believe genetic composition is irrelevant to behavior must offer an alternative explanation for the persistent findings from twin studies; otherwise, the unavoidable conclusion has to be that an exclusive focus on environmental factors misses a major source of the variance in attitudes and behavior.

As interesting and challenging as these findings may be, do they relate to the concerns of political science? While, to our knowledge, there are no political scientists currently performing twin studies, much of what is being done in other disciplines is surprisingly relevant to a variety of political science subfields. The most developed examples come from studies of the heritability of traits such as conservatism and altruism. These behaviors have been studied in different twin populations in different countries by different researchers over the last twenty years. All of the studies reach the same conclusion: *a predisposition to conservatism is genetically heritable*.

This is an empirical assertion that should startle and intrigue any political scientist. Thus far the pertinent research has been done largely by psychologists, and there is considerable work ahead in this field for political scientists. Social psychologists treat conservatism as a broad personality trait, roughly equivalent to other personality traits, such as introversion or authoritarianism. For most political scientists this is not the first thing that comes to mind when someone mentions a specific ideology like conservatism. Conservatism as a belief system, a bundle of policy preferences, or a nascent group identification are all examples of common political science conceptualizations of conservatism that differ, often substantially, from the view of conservatism as a personality trait. Fortunately, the details of at least one method by which social psychologists measure conservatism allow us a glimpse at some component characteristics that are more compatible with our conceptions of it. Before proceeding to the details of conservatism, we must discuss in more detail the methodology of twin research.

The value of twins to genetic research does not come from the distinctiveness of their attitudes and behaviors compared to the population of nontwins. In fact, the lack of distinctiveness is a salient and empirically established prerequisite for generalizing twin findings to the general population.[54] Nor is the value of twins the obvious fact that they are genetically closer than nontwin siblings. The real research power comes from the fact that the two distinct types of twins differ genetically in known ways. For any trait that is at least partly heritable the tendency for monozygotic (MZ) twins to share that characteristic should be stronger than the tendency for dizygotic (DZ) twins to share it. In contrast, characteristics that arise from the environment, whether shared by the twins, as would typically be the case for parental socialization, or not shared by the twins, as would be the case for many adult experiences, should not generate any significantly different patterns when we contrast MZ and DZ twins.[55]

This assertion—that the effect of genetics is measurably distinct for MZ and DZ twins while the effect of the environment is either equivalent or at least randomly distributed around equivalence—is crucial to everything that follows from twin research. It is important therefore to consider criticisms of this fundamental assumption, which appear in two essential varieties. The first is that MZ twins, genetics aside, experience a similar environment because they are treated more alike than are DZ twins. This could be particularly telling for childhood socialization if, for example, parents of MZ twins tended to treat them less as individuals than do parents of DZ twins. The second basic criticism is that MZ twins, genetics aside, interact with each other more throughout life than do DZ twins. This could be particularly important for adult socialization; close adult contact between MZ twins might lead us to expect a higher degree of environmentally induced similarity than we would expect in DZ twins.

Both criticisms have been subject to sustained and varied investigation, and neither has been found to hold up under empirical scrutiny. The argument of more similar treatment fails on several fronts. Parents frequently miscategorize their twins (DZ twins are often believed by their parents to be MZ twins) and the differential correlation persists in these instances of miscategorization. In other words, the degree of correspondence between MZ twins surpasses that of DZ twins even in a subpopulation of twins all of whom were thought by their parents to be MZ twins.[56] The speculation that MZ twins have closer or more frequent contact than DZ twins turns out to be, at best, irrelevant. The correlation between interpair contact, for example, and interpair differences in conservatism is in fact slightly negative.[57] That is, the more contact, the less ideological similarity. But the most powerful refutation of both criticisms comes in recent studies that compare MZ and DZ twins raised apart. These studies uniformly validate MZ and DZ differences found in earlier studies of twins raised together. Arguments about the relative degree of shared environmental effects between MZ and DZ twins simply offer no credible explanation if the twins in question have been raised apart.[58] In effect, this naturally occurring, if uncommon, condition provides precisely the sort of laboratory control that we want in an experimental setting.[59]

Empirical evidence also suggests that identical twins reared together are often *less* likely to share behavioral traits than are identical twins reared apart, perhaps because of parents'

extra efforts to help the twins living together establish distinct identities. In addition, as adult MZ twins living apart age, they tend to become more, not less, similar,[60] a finding difficult to reconcile with the belief that only the environment matters. Interestingly, this precise effect is predicted in an early landmark criticism of behavioralism and the conditioned-response research on animal behavior at its core. Over time, substantial anomalies accumulated in this research, pointing toward a primacy for some nonenvironmental behaviors. As Keller and Marian Breland summarized this tendency, "Learned behavior drifts toward instinctive behavior."[61]

While the twin-study methodology has yet to be applied by political scientists, a variety of social psychology studies use this methodology to assess conservatism as a personality trait. The measure of most interest to political scientists is the Wilson-Patterson Attitude Inventory. This inventory is administered by presenting subjects with a short stimulus term, such as death penalty, and eliciting a simple response of agree, disagree, or uncertain. The broadest version of the W-P inventory includes 50 items, half of which contribute positively to the conservatism score and half of which contribute negatively. While some of the items relate heavily to conceptions of social conservatism—for example, pajama parties, casual living, nudist camps, computer music, and horoscopes—others are more directly political—for example disarmament, legalized abortion, socialism, patriotism, and death penalty.

Studies typically use reduced sets of W-P items or tailor individual items to the country in which the studies are being administered. For political scientists, this is frustrating on two counts. The list of politically relevant items is tantalizing but limited and unfocused; moreover, the results are often presented only for the entire combined scale, making it difficult to assess the contribution of the directly political items to the overall index of heritability. Heritability estimates for overall conservatism as measured by the W-P inventory are quite high, usually around 0.60. Furthermore, the models typically show little or no effect for shared environment (the rest is likely the result of nonshared environmental factors, including the prenatal environment). These findings come from studies of twins in settings as disparate as Australia, Virginia, and Minnesota. The Minnesota findings, based on twins reared apart, conform well to the other studies, based on twins raised together.[62]

Our concern at this point is not to quibble over whether in fact genetics accounts for more than half of the variation in individual levels of conservatism. The important point is that our discipline currently believes that the state of the world would yield an environmental (i.e., socialization) component greater than 50 percent and a genetic component of essentially zero.[63] Whatever the precise numbers, the durable and stark results of twin studies are completely at odds with current thinking in our discipline. At the very least, political science can no longer dismiss genetics as some minor or distant precursor to important political orientations. Taken at full face value, these results suggest that virtually everything we have supposed to be true about the *origins* of broad political orientations is false.

As strong as this assertion may seem, it does not indicate that most of the extant empirical results concerning political socialization are incorrect, only that the interpretations commonly applied to those results are incorrect. In fact, it strongly reinforces the most salient empirical findings.[64] We know, for example, that if both parents share a political orientation and find politics to be important, their offspring will likely have that same political orientation and also value politics.[65] Nothing in this description contradicts the twin-based contention that political orientations are largely the result of genetic inheritance. In fact, this is precisely the pattern we would expect to find if the twin studies are correct. The challenge of the twin research is only to our assumption that, unlike shared physical traits, shared behavioral traits must be purely a function of enculturation.

At this point, the careful reader is undoubtedly thinking that we are getting ahead of ourselves. As we mentioned earlier, the 50-item W-P inventory contains both items that we would recognize as having substantive political content and others about which we would entertain substantial doubt. If the overall degree of heritability is largely a function of attitudes toward modern art and pajama parties, the direct relevance to political science may be minimal. What then do we find in the limited studies that report heritability for individual items? A 1986 study by Martin and colleagues of over 3,800 Australian and British twin pairs reported the following estimates of heritability (on a scale of 0 to 1.0) for the following items: death penalty, 0.51; white superiority, 0.40; royalty, 0.44; apartheid, 0.43; disarmament, 0.38; censorship, 0.41. The heritability estimate for pajama parties, on the other hand, was a mere 0.08. The comparable estimates for the influence of shared environment were: death penalty, 0.00; white superiority, 0.09; royalty, 0.14; apartheid, 0.05; disarmament, 0.00; censorship, 0.03 (but pajama parties, 0.44).[66]

These findings are powerful yet incomplete. As political scientists, we could all provide our own list of items that we would want to see included in this sort of inventory. Party identification, for example, is probably an obvious item.[67] In any case, the implication for political science is clear: we must take seriously the possibility that at least some part of what we have attributed to active socialization is a function of genetic inheritance. Equally important—and even more urgent—is the need to adapt twin-study methodology to our specific disciplinary research agendas.

We invite dubious readers to indulge us in a thought experiment. Suspend disbelief and think seriously about what this might mean for our entire conception of political attitudes and orientations. Daniel Elazar characterized the American South as having what he called a traditionalist orientation toward politics, and argued further that these presumably

learned cultural orientation had been brought to the South through patterns of European migration.[68] If white attitudes toward issues as diverse as the death penalty, white supremacy, apartheid, disarmament, and censorship are highly heritable, then we might have a deeper explanation for the durability of a characteristically southern orientation toward politics in the relatively closed breeding population of much of the traditional white South. This is not incompatible, and in fact substantially supports Elazar's basic thesis; moreover, it could help account for the fact that, unlike purely learned orientations, these deeply rooted attitudes might prove surprisingly resistant to the rise of a generic national culture in an era of mass communication and rapid travel.

Autism

Thus far we have merely suggested that political scientists become acquainted with the relatively distant fields of evolutionary biology and genetics, but it is difficult to move from distal to proximate causes without also equipping ourselves with tools from the areas of brain science and cognitive psychology. One relevant thread of research in these areas has been on autism and related syndromes. While most of us are familiar with the more extreme and debilitating forms of childhood autism, there is a great deal of interesting recent research on a much milder form variously referred to as Asperger's Syndrome, or high-functioning autism. This condition leads to a variety of physical and behavioral manifestations. Among the most salient, and the most relevant for our purposes, is a deficiency in what psychologists term "theory of mind" and an apparently related tendency toward a rule-based approach to understanding the behavior of others. One of the most prolific and respected researchers in this area has recently suggested that rather than being a distinct brain abnormality there is instead an autism spectrum running from systematizers to empathizers along which we could array the entire population.[69]

The details of theory of mind are beyond the scope of this discussion, but essentially it says that at an early age, approximately three, most individuals develop the ability to consciously place themselves in the mind of another individual and thus not only predict what that individual might do but also intuit that individual's motivations and likely reactions. Armed with this capability, children develop an increasingly extensive capability to read the minds of others in social situations and adjust their own behavior accordingly. This allows neurotypical individuals to understand seemingly without effort very subtle distinctions in the orientations of others. In a simple verbal compliment, for example "nice hat," neurotypicals might quickly discern either approval, flattery, condescension, sarcasm, admiration, or banality. Lacking this ability to read minds leaves the autistic with little more than the literal spoken words. What most people can instinctively intuit, the mildly autistic must deduce from other contextual and circumstantial information combined with an elaborate set of remembered past experiences and carefully applied rules of judgment.

As odd as this way of understanding other humans might seem, it should be immediately familiar to all of us as a close analogue to the intellectual investigation of the physical world. In fact, individuals afflicted with mild autism are often relatively gifted in fields such as mathematics, engineering, and computer science, where their proclivity for rule-based experiential learning offers them an advantage over more intuitive thinkers. The mildly autistic are sometimes described as weak in folk psychology and strong in folk physics. While much remains to be learned about the autistic spectrum of behavior, psychologists agree that these characteristics are genetically heritable and implicate relatively specific functional differences in the brain.

If what we see at the extreme is merely an exaggeration of what is present to a greater or lesser degree across the range of human brains, political scientists must orient themselves accordingly. For example, our diverse and often contradictory views of "human nature" may all be correct. Those at opposite ends of the systematizing-empathizing spectrum approach basic human interaction in fundamentally different ways, and explain human interaction in fundamentally different terms. At the systematizing end of the spectrum we should find individuals increasingly likely to interact socially with a relatively elevated focus on self-interest, a correspondingly diminished sensitivity to the wishes of others, and a tendency toward relatively structured and rule-based patterns of interaction. At the empathizing end of the spectrum we should find individuals who behave in social situations with a high, perhaps even excessive, degree of concern for the wishes of others, a relatively weak emphasis on their own self-interest, and a tendency toward relatively fluid and situational patterns of interaction.[70]

Researchers' explanations of human social and political behavior depend in large part on which type of individual predominates in groups under study. Moreover, researchers' own placement on the spectrum will significantly shape both their ability to understand their subjects' behaviors and their own explanations of those behaviors. For example, the closer an individual is to the systematizer end of the spectrum, the more prone that person would be to seeing the social world in a highly individualized way, and the more likely he or she would be to explain this individualized behavior on the basis of a system of relatively powerful rules. An observer from the empathizer end of the spectrum will, through both introspection and theory of mind, see a world of highly interdependent utilities, and would be more likely to offer explanations involving complex contingencies, with an emphasis on context. If these two individuals happen to be political scientists, we would not be surprised if we found that because they viewed and explained human behavior in starkly different terms, they would largely be talking past each other—as has all too frequently been the case for behavioralists and rational choicers. This suggests

that differences in methodology within and across disciplines may derive at least in part from heritable differences in brain physiology. When Morris Fiorina writes that he is "rational choice down to [his] DNA," he could be literally correct.[71] Likewise, seemingly incompatible conceptions of basic human nature may in fact be equally correct when applied to the proper subset of the population: fundamental behavioral differences may also derive from heritable differences in brain physiology.

Genes

For a variety of reasons, skepticism persists regarding estimates of heritability derived from twin studies. But the case for genetics playing a role in shaping behavior is based on much more than twin research. Since much of the resistance among social scientists to genetic independent variables stems from unfamiliarity with modern biology, it is essential that we offer some indication of the manner in which genetics connects to behavior.

The most interesting and numerous genes in human beings are not structural (blue eyes or brown), but regulatory. Regulator genes allow an organism to respond to its environment; they are the genes that turn on and off the transcription of other genes (or themselves). They are the body's thermostats. Consider, for example, biological responses to fear and threat. The amygdala, a primitive part of the lower brain, sounds an alarm, adrenaline and stress hormones are released, extra blood is sent to the muscles, breathing quickens, glucose is disgorged by the liver, blood pressure skyrockets, and nonessential bodily functions stop. While this general pattern is always in evidence, sensitivity, rapidity, and depth of response vary widely. Some people experience a full-fledged panic attack at the slightest provocation; others display quite muted physiological reactions to even life-threatening events. Why? Just as people display physical differences partly because of differences in structural genes, they display behavioral differences partly because of difference in regulator genes. People's regulator genes encourage them to react to environmental conditions in certain ways, whether those conditions involve danger, lactose, alcohol, an uncooperative individual, or sexual stimulation. These on-off switches shape much of our personalities.[72]

Regulator genes are not merely theoretical constructs. They have been seen, and behavior has been accurately predicted merely by knowing the shape of an individual's key regulator genes. Consider a gene called D_4DR, which can be found on the short arm of chromosome 11. This gene influences the reception of dopamine, a chemical needed by portions of the brain. Individuals with a long version of D_4DR are less efficient at collecting dopamine, so they need to take more risks and seek more thrills in order to generate as much dopamine as others acquire from more sedentary lifestyles.[73]

None of this is to say that environmental factors are irrelevant.[74] In fact, surprisingly, and perhaps for many, reassuringly, current biological thinking unites genetic and environmental influences in a complicated but compelling interactive fashion. For example, recent work on violence has found a connection to a blood transmitter called monoamine oxidase A (MAOA), but the connection is not simply that those with genetic deficiencies in MAOA production are more violent. Rather, those individuals who have low MAOA production *and* experienced violence as children are much more likely to be violent as adults.[75] Acting alone, MAOA deficiencies or a violent childhood have little predictive power, but the interaction of genetic and environmental factors is disconcertingly powerful. A similar pattern has been found in studies attempting to predict those individuals likely to suffer from clinical depression. There is a gene on chromosome 17 called 5-HTT. This gene also comes in a long form and a short form. An extensive study of nearly 1,000 New Zealanders found that clinical depression was associated not just with the presence of the short form of 5-HTT and not just with the presence of many high-stress events in a subject's life, but with a combination of high-stress events and the short-form of 5-HTT.[76]

If we generalize this pattern to predispositions more central to political concerns, such as conservatism and cooperation, it suggests that the eventual genetic-level explanation may fit surprisingly well with much of what we already know and much of what we have suggested here with regard to genetics and evolution. Perhaps for a substantial portion of the population the short form of a yet-to-be-identified gene allows their degree of cooperation/retaliation to vary with regard both to the specific current context and to their broader experience over time. We might call these individuals wary cooperators. For another portion of the population, those with the long form of the gene, context seems to make little difference. While we believe our theory of wary cooperation discussed earlier accurately describes the behavior of the majority of the population, it needs to and does leave room for a minority that behaves in a predictably different fashion. This minority may be fixed in either cooperative or noncooperative modes, or may alternate between these modes with no apparent regard for the cooperation or lack of cooperation evidenced by those in their environment. This could provide a rough genetic sketch of the biological underpinnings for the starkly different social abilities and orientations discussed above in the section on autism. And that discussion in turn provides the cognitive underpinnings for the theory of wary cooperation that was the starting point for this piece. Interestingly, the computer simulations that we discussed above have demonstrated that (under reasonable assumptions) a population consisting of two types roughly compatible with mildly autistic individuals and wary cooperators, respectively, can reach a stable equilibrium with the larger part of the final population

composed of wary cooperators and the smaller remainder behaving more like the mildly autistic.[77]

Conclusion

We began by noting the usefulness to the social sciences of greater attention to biological evolution. Part of the problem may be that the last time biology came to the attention of political scientists (in the 1970s, after the publication of E. O. Wilson's *Sociobiology*), they believed that advocates were saying that behavior was determined by biology.[78] If that was ever the position of biology proponents, it is no longer. A research program focused on genetic factors to the exclusion of environmental factors would be deeply misguided—perhaps as misguided as a research program focused on environmental factors to the exclusion of genetics,

We believe that modern biological theory, properly understood, holds the promise of unifying political science and integrating political science with other social sciences—and even with the natural sciences. Concepts borrowed from evolutionary biology can provide the theoretical guidance both rational choice and behavioralism need to become even more useful than they have been to date. Scholars operating in the behavioral tradition can certainly continue to identify aspects of the environment that seem more influential than others and the conditions under which these environmental influences vary. Though we are convinced that it is necessary to understand original causes, this understanding would be useless if behavioralists did not link these causes to more proximate environmental factors. Scholars operating in the rational choice tradition are similarly advantaged by the incorporation of biological theory, since preferences can be derived from an understanding of evolutionary pressures acting on individuals and groups. Baselines of behavior no longer have to be questionable assumptions that people pursue short-term tangible gains or largely tautological assumptions that people must prefer whatever they pursue.

We are not suggesting that all political scientists become evolutionary theorists or adopt a certain methodological approach. We need a healthy disciplinary division of labor in service of a genuine theory of political and social behavior. To date in the social science disciplines that *have* embraced evolutionary theory, everything from participant-observation to pure mathematical game theory to laboratory (and field) experiments has been employed with fruitful results. As the old saw goes, "If you are looking in the right place there is no wrong way to look."[79] Evolutionary theory has the potential to render obsolete our intradisciplinary conflicts over approach, method, and theory. It is more than a replacement for existing political science theories, since rational choice and behavioralism are simply not capable of supplying an account of ultimate causes. It is a true theory of the origins of behavior and as such provides a basis for bringing together the remarkably diverse and useful ongoing research in political science and beyond.

Notes

1 Huxley 1989. For an intriguing counterpoint to Huxley, see Kropotkin 1972.
2 Darwin 1968; Darwin 1981.
3 Simon 1957; Simon 1985; Simon 1997.
4 Cosmides and Tooby 1994, 327.
5 Ostrom 1998, 2. See also Jones 2001.
6 Dawkins 1976, 2–4.
7 Ibid., 66. At a later point, Dawkins clearly recognizes that genes occasionally engage in cooperative behavior.
8 Buchanan and Tullock 1962, 18.
9 See, for example, Dawkins 1976; Dawkins 1982.
10 Such "selfish" genes have been used to explain the self-destructive behavior of organisms such as salmon, which leave the comforts of the ocean to swim upstream, spawn, and die, and male mantises, which sometimes celebrate the end of copulation by throwing themselves back into the open, waiting jaws of the much larger females.
11 For a description of the biology of cooperation at this level, see Mark Ridley 2003.
12 Frank 1988; Sober and Wilson 1998. The claim that selection pressures can be profitably viewed at levels other than the gene, while increasingly accepted by students of evolutionary psychology, has had a checkered past, and many scholars remain unpersuaded. Wynne-Edwards's 1962 account of rooks voluntarily curtailing their clutch size for the welfare of the flock was roundly criticized by the biological community and gave related notions much to overcome. Moreover, so-called group selectionists occasionally envisioned an ethereal, almost inexplicable, and somewhat magical devotion to the group. As emphasized in our description above, mysticism is not needed, and modern thinking is firmly embedded in the logical consequences of selection pressures at different levels. The switch in common phraseology from group selection to multilevel selection is more than semantic.

In addition, continuing advances in genetics cast more and more doubt on genes as stand-alone, clearly distinct actors in the evolutionary drama. Instead, we now know from Gibbs 2003 and others that many traits are epigenetic, that is, influenced by chemical marks outside the DNA sequence. Today, much of the dispute centers on the relative importance of multilevel selection rather than the fact of its existence. For some sense of the opposing arguments, see the exchange in the 1994 issue of *Behavioral and Brain Sciences*, in which Wilson and Sober make the case for multilevel selection, and which is commented on by numerous scholars. See also Sober and Wilson 1998.
13 For a good summary, see Guth and Tietz 1990.
14 See Nowak, Page, and Sigmund 2000. Lest it be thought that the generosity of allocators is merely strategic, when the game is changed to a dictator game, in

which the receiving player has no chance to veto the proposed allocation, anonymous allocators still make generous offers, albeit typically less generous than in ultimatum games. See Fehr and Fischbacher 2003 for a useful summary. See Van Dijk and Vermunt 2000 for research suggesting players in the dictator game are actually more generous than those in the ultimatum game.

15 Boyd and Richerson 1992; Gintis 2000; Henrich and Boyd 2001; Price, Cosmides, and Tooby 2002.

16 Thus the discipline's theoretical basis for explaining self-interested and non-self-interested behavior is much as Ostrom, Gardner, and Walker (1994) describe it with regard to the specific instance of abusing or not abusing common pool resources. "No existing theory provides a consistent explanation for how and why many appropriators extricate themselves from common pool resource dilemmas [and] why this is not universally the case" (p. 18). The theory of wary cooperation, in contrast, does explain these puzzles.

17 The main reason for opening up social science to the role of biology is not that it can better explain variations of human behavior around the mean but rather that it can help us to better understand the mean itself. We do not, however, believe all individuals possess in the same degree the biological materials that push us toward wary cooperative behavior. In fact, as discussed below, we believe that a minority of humans are genetically predisposed toward insensitivity to the cooperation levels of people around them.

18 For a thorough treatment of altruistic behavior, see Monroe 1996.

19 Monroe 2002, 203; Brewer 2000.

20 Asch 1951.

21 Milgram 1974.

22 Frank 1999.

23 Sherif et al. 1961.

24 Barash 1994.

25 Price, Cosmides, and Tooby 2002.

26 Extant research roughly consistent with our theme includes Kahneman and Tversky 1984; Kahneman, Knetsch, and Thaler 1986; Orbell and Dawes 1991; Thaler 1992; Kahn and Murnighan 1993; Komorita and Parks 1996; Ostrom, Gardner, and Walker 1994; Hoffman, McCabe, and Smith 1996; Wedekind and Milinski 1996; Thompson, Kray, and Lind 1998; Smith 2000; Lubell and Scholz 2001; and Fehr and Fischbacher 2003.

27 See Gould 1981; Gould 2000.

28 See Maynard Smith 1982; Axelrod 1984; Brewer 2000; Hammond 2000; Fehr and Gächter 2002; Rauch 2002. See also Putnam1993 and Putnam 2000 for a real-world description of this problem.

29 Hertwig and Todd 2003. See also Gigerenzer and Selten 2001.

30 Elman 1993.

31 Cosmides and Tooby 1994, 329.

32 As posited by Simon 1957; Simon 1985; Simon 1997.

33 Cosmides and Tooby 1994, 327.

34 See Pinker 1997; Tooby and Cosmides 1992; Cosmides and Tooby 1992; Frank 1988.

35 See Chiappe, Brown, and Rodriquez 2002. See also Baron and Burnstein 2002.

36 Quoted in Sanderson 2001,120; elaborated in Pinker 2002.

37 See, for example, Putnam 1993.

38 Tooby and Cosmides 1992, 37.

39 Matt Ridley 2003.

40 For recent creative evidence involving nonhuman primates, see Brosnan and de Waal 2003.

41 Buchanan and Tullock 1962, 21. See also Selten 1999.

42 Waltz 2001, 29. For a more positive take on the value of an evolutionary approach to understanding war, see Strate 1983 and 1985, and Alexander 1987.

43 This is a point that critics such as Waltz seem to miss. As Wrangham (1999) points out, it is a gross "misconception" to believe that "the only behavioral patterns explainable by biology are instincts, i.e., behaviors that are obligatory and/or inevitable. . . . [T]his error seems remarkable because behavioral ecologists have long stressed that psychological adaptations are expected to respond in a contingent way to appropriate contexts" (p. 21).

44 See Olson 1965.

45 Proponents of rational choice such as Rabushka and Shepsle (1972) admit they are "unable to explain … the preeminence of ethnicity" (p. 64). They do, however, attempt to do so by claiming this preeminence is entirely the result of elites pushing their followers to view the world through ethnic lenses, a contention that flies in the face of even casual observation of rank-and-file people. According to Varshney (2003), the ability of rational choice to explain why so much conflict is organized along ethnic, religious, and linguistic rather than economic lines has not improved in the decades since Rabushka and Shepsle wrote.

46 Hibbing and Theiss-Morse 2002.

47 Hibbing and Alford 2004.

48 From an evolutionary point of view, what could be worse than being a part of a group in which leaders are bent on personal gain at the expense of the welfare of other members of the group?

49 Raby 2001 and Pinker 2002.

50 Sullivan and Masters 1988 may be the closest to an exception to this statement. Several other essays have called for original research using biological and genetic principles. Examples include Wahlke 1979; Masters 1993;

Somit and Peterson 1996; Ostrom 1998; and Somit and Peterson 1999.

51 Approximately 98 percent of all human genetic material is estimated to be shared by all members of the species.

52 See Eaves, Eysenck, and Martin 1989; Plomin 1990; Plomin, Owen, and McGuffin 1994; Bouchard 1998; and Plomin et al. 2000. Adoption studies deal with cases in which the varying portion of the genotype shared by siblings approaches zero but the portion of the environment shared by them is substantial. These studies come to the same conclusion as twin studies. For a good summary, see Plomin et al. 2000.

53 See Plomin 1990; Plomin et al. 2000.

54 See Bouchard and McGue 2003.

55 See Plomin et al. 2000 for a thorough discussion of the relevant statistical techniques.

56 Plomin 1990; Bouchard et al. 1990; and Bouchard and McGue 2003.

57 See Martin et al. 1986.

58 See Bouchard et al. 1990; Bouchard and McGue 2003.

59 To explain this finding, opponents would need to argue that adoption agencies are more likely to place MZ twins in similar homes than they are to place DZ twins in similar homes. In fact, information on twin zygosity is typically unavailable to those making placement decisions. Even if it were, it seems highly unlikely that it would factor into their decisions, even if agencies were generally more likely to place twins than nontwin siblings in similar homes.

60 See Bouchard and McGue 2003.

61 Breland and Breland 1961, 684.

62 Conservatism is not unusual in this regard. Rushton, Littlefield, and Lumsden (1986), find that approximately 50 percent of the variance in altruism is the result of "direct genetic inheritance" (p. 7340), with family environment responsible for 0 percent.

63 To take just one example, a leading text on political behavior states without equivocation that "attitudes, beliefs, and values are learned predispositions, and the various forms of political participation are learned behaviors." See Conway 2000, 61. The twin studies suggest this assertion is quite wrong.

64 Though clearly the phrase "political socialization" is a misnomer since much of the correlation between the attitudes of parents and children is not due to a socialization process at all.

65 See, for example, Jennings and Niemi 1968; Tedin 1974.

66 A listing of the heritability of all items can be found in Martin et al. 1986. Our own analysis of twin pairs in the United States produces similar results. See Alford, Funk, and Hibbing 2004.

67 Twin researchers have not focused directly on party affiliation. The closest they have come may be some unpublished research by Lykken, referenced by Pinker 2002. Our expectation is that just as affiliation with a particular religious denomination is heavily environmental, while the tendency to be religious at all is heavily inherited (Bouchard and McGue 2003), particular political identifications, like party identification, are much more environmental than the tendency to be interested in and involved with politics in any fashion. The tendency of traits like religious affiliation to not be shared by MZ twins any more than DZ twins is further evidence against the argument that differences in correlation between the two types of twins are due to environmental factors. If this alternative explanation were true, religiosity should produce the same pattern as religion and this simply is not the case.

68 Elazar 1984.

69 Baron-Cohen 2003; see also Baron-Cohen, Tager-Flusberg, and Cohen 2000.

70 Baron-Cohen 2003 further suggests that the mean placement for males and females on such a spectrum is distinct, with males located closer to the autistic pole. This conception could account for the fact that four out of five individuals clinically diagnosed with autism are males.

71 Fiorina 1996, 85.

72 For more, see Plomin, Owen, and McGuffin 1994.

73 See Hamer and Copeland 1998; Ridley 1999.

74 At the broadest level the interaction between genes and the environment includes not only the natural environment but the man-made environment as well. With the recognition that culture, a key component of the manmade environment, can also develop along lines quite similar to evolution and natural selection, scholars have recently begun attempts to conceptualize and empirically study what is commonly termed "gene-culture coevolution." For an early application see Boyd and Richerson 1985; for a more recent application, see Fehr and Fischbacher 2003.

75 Caspi et al. 2002.

76 Caspi et al. 2003.

77 See Fehr and Fischbacher 2003; Boyd et al. 2003.

78 Wilson 1975.

79 Einstein said, "Without theory observation is impossible," to which we would only add that with theory all methods of observation are useful.

References

Alford, John R., Carolyn L. Funk, and John R. Hibbing. 2004. The source of political attitudes: Assessing genetic and environmental contributions. Paper presented at the annual meeting of the American Political Science Association, Chicago, September 2–5.

Asch, Solomon E. 1951. Effects of group pressure upon the modification and distortion of judgment. In *Groups, leadership and men: Research in human relations*, ed. Harold Guetzkow, 177–90. Pittsburgh: Carnegie Press.

Alexander, Richard D. 1987. *The biology of moral systems*. New York: Aldine.

Axelrod, Robert. 1984. *The evolution of cooperation*. New York: Basic Books.

Barash, David P. 1994. *Beloved enemies: Our need for opponents*. Amherst, NY: Prometheus Press.

Baron, Andrew Scott, and Eugene Burnstein. 2002. Are humans equipped with a specific cheater-detection module or a more general person-impression module? Paper presented at the annual meeting of the Human Behavior and Evolution Society, New Brunswick, NJ, June 8.

Baron-Cohen, Simon. 2003. *The essential difference: The truth about the male and female brain*. New York: Perseus.

Baron-Cohen, Simon, Helen Tager-Flusberg, and Donald J. Cohen. 2000. *Understanding other minds: Perspectives from developmental cognitive.* 2nd ed. New York: Oxford University Press.

Bouchard, T. J., Jr. 1998. Genetic and environmental influences on intelligence and special mental abilities. *Human Biology* 70 (2): 257–59.

Bouchard, T. J., Jr., and Matt McGue. 2003. Genetic and environmental influences on human psychological differences. *Journal of Neurobiology* 54 (1): 4–45.

Bouchard, T. J., Jr., D. T. Lykken, M. McGue, N. L. Segal, and A. Tellegen. 1990. Sources of human psychological differences: The Minnesota study of twins reared apart. *Science* 250 (4978): 223–28.

Boyd, Robert, Herbert Gintis, Samuel Bowles, and Peter J. Richerson. 2003. The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences* 100 (6): 3531–35.

Boyd, Robert, and Peter J. Richerson. 1985. *Culture and the evolutionary process*. Chicago: University of Chicago Press.

———. 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13 (3): 171–95.

Breland, Keller, and Marian Breland. 1961. The misbehavior of organisms. *American Psychologist* 16 (9): 681–84.

Brewer, Marilyn B. 2000. Superordinate goals vs. superordinate identity as bases of cooperation. In *Social identity processes,* ed. Dora Capozza and Rupert Brown, 117–32. London: Sage.

Brosnan, Sarah F., and Frans B. M. de Waal. 2003. Monkeys reject unequal pay. *Nature* 425 (6955): 297–99.

Buchanan, James M., and Gordon Tullock. 1962. *The calculus of consent: Logical foundations of constitutional democracy*. Ann Arbor: University of Michigan Press.

Caspi, Avshalom, Joseph McClay, Terrie E. Moffitt, Jonathan Mill, Judy Martin, Ian W. Craig, Alan Taylor, and Richie Poulton. 2002. Role of genotype in the cycle of violence in maltreated children. *Science* 297 (5582): 851–54.

Caspi, Avshalom, Karen Sugden, Terrie E. Moffitt, Alan Taylor, Ian W. Craig, HonaLee Harrington, Joseph McClay, Jonathan Mill, Judy Martin, Antony Braithwaite, and Richie Poulton. 2003. Influence of life stress on depression: Moderation by a polymorphism in the 5-HTT gene. *Science* 301 (5631): 386–89.

Chiappe, Dan, Adam Brown, and Marisela Rodriquez. 2002. Remembering the faces of potential cheaters and cooperators in social contract situations. Paper presented at the annual meeting of the Human Behavior and Evolution Society, June 8, New Brunswick, NJ.

Conway, M. Margaret. 2000. *Political participation in the United States*. Washington, DC: CQ Press.

Cosmides, Leda, and John Tooby. 1992. Cognitive adaptations for social exchange. In *The adapted mind: Evolutionary psychology and the development of culture*, ed. Jerome H. Barkow, Leda Cosmides, and John Tooby, 163–228. New York: Oxford University Press.

———. 1994. Better than rational: Evolutionary psychology and the invisible hand. *American Economic Review* 84 (2): 327–32.

Darwin, Charles. 1968. *The origin of species*. New York: Penguin Books. (Orig. pub. 1859.)

———. 1981. *The descent of man, and selection in relation to sex*. Princeton: Princeton University Press. (Orig. pub. 1871.)

Dawkins, Richard. 1976. *The selfish gene*. New York: Oxford University Press.

———. 1982. *The extended phenotype: The gene as the unit of selection*. New York: Oxford University Press.

Eaves, L. J., H. J. Eysenck, and N. G. Martin. 1989. *Genes, culture, and personality: An empirical approach*. San Diego: Academic Press.

Elazar, Daniel. 1984. *American federalism: A view from the states*. 3rd ed. New York: Harper and Row.

Elman, J. L. 1993. Learning and development in neural networks: The importance of starting small. *Cognition* 48 (1): 71–99.

Fehr, Ernst, and Urs Fischbacher. 2003. The nature of human altruism. *Nature* 425 (6960): 785–91.

Fehr, Ernst, and Simon Gächter. 2002. Altruistic punishment in humans. *Nature* 415 (6868): 137–40.

Fiorina, Morris P. 1996. Rational choice, empirical contributions, and the scientific enterprise. In *The rational choice controversy: Economic models of politics reconsidered*, ed. Jeffrey Friedman, 85–94. New Haven: Yale University Press.

Frank, Robert H. 1988. *Passions within reason: The strategic role of emotions*. New York: W. W. Norton.

———. 1999. *Luxury fever: Why money fails to satisfy in an era of excess*. New York: Free Press.
Gibbs, W. Wayt. 2003. The unseen genome: Beyond DNA. *Scientific American* (December): 106–13.
Gigerenzer, Gerd, and Reinhard Selten, ed. 2001. *Bounded rationality: The adaptive toolbox*. Cambridge: MIT Press.
Gintis, Herbert. 2000. Strong reciprocity and human sociality. *Journal of Theoretical Biology* 26 (2): 169–79.
Gould, Stephen Jay. 1981. *The mismeasure of man*. New York: W. W. Norton.
———. 2000. More things in heaven and earth. In *Alas, poor Darwin: Arguments against evolutionary psychology*, ed. Hilary Rose and Steven Rose, 101–26. New York: Harmony Books.
Guth, Werner, and Reinhard Tietz. 1990. Ultimatum bargaining behavior: A survey and comparison of experimental results. *Journal of Economic Psychology* 11 (3): 417–49.
Hamer, Dean, and Peter Copeland. 1998. *Living with our genes: Why they matter more than you think*. New York: Doubleday.
Hammond, Ross. 2000. *Endogenous transition dynamics in corruption: An agent-based computer model*. Unpublished manuscript. Brookings Institution, Washington, DC.
Henrich, Joseph, and Robert Boyd. 2001. Why people punish defectors. *Journal of Theoretical Biology* 208 (1): 79–89.
Hertwig, Ralph, and Peter M. Todd. 2003. More is not always better: The benefits of cognitive limits. In *The Psychology of Reasoning and Decision Making: A Handbook*, ed. L. Macchi and D. Hardman, 1–19. Chichester, UK: Wiley.
Hibbing, John R., and John R. Alford. 2004. Accepting authoritative decisions: Humans as wary cooperators. *American Journal of Political Science* 48 (1): 62–76.
Hibbing, John R., and Elizabeth Theiss-Morse. 2002. *Stealth democracy: Americans' beliefs about how government should work*. New York: Cambridge University Press.
Hoffman, Elizabeth, Kevin McCabe, and Vernon L. Smith. 1996. Social distance and other-regarding behavior in dictator games. *American Economic Review* 86 (2): 653–60.
Huxley, Thomas H. 1989. *Evolution and ethics*. Princeton: Princeton University Press. (Orig. pub. 1894.)
Jennings, M. Kent, and Richard G. Niemi. 1968. The transmission of political values from parent to child. *American Political Science Review* 62 (1): 169–83.
Jones, Bryan D. 2001. *Politics and the architecture of choice: Bounded rationality and governance*. Chicago: University of Chicago Press.
Kahn, Lawrence M., and Keith Murnighan. 1993. General experimentation bargaining in demand games with outside options. *American Economic Review* 83 (5): 1260–80.
Kahneman, Daniel, Jack L. Knetsch, and Richard H. Thaler. 1986. Fairness and the assumptions of economics. *Journal of Business* 59 (4): S285–S300.
Kahneman, Daniel, and Amos Tversky. 1984. Choices, values, and frames. *American Psychologist* 39 (5): 341–50.
Komorita, Samuel S., and Craig D. Parks. 1996. *Social dilemmas*. Boulder, CO: Westview Press.
Kropotkin, Peter. 1972. *Mutual aid: A factor of evolution*. London: Allen Lane. (Orig. pub. 1902.)
Lubell, Mark, and John Scholz. 2001. Cooperation, reciprocity, and the collective-action heuristic. *American Journal of Political Science* 45 (1): 160–78.
Martin, N. G., L. J. Eaves, A. C. Heath, Rosemary Jardine, Lynn M. Feingold, and H. J. Eysenck. 1986. Transmission of social attitudes. *Proceedings of the National Academy of Sciences* 83 (12): 4364–68.
Masters, Roger D. 1993. *Beyond relativism: Science and human values*. Hanover, NH: University Press of New England.
Maynard Smith, John. 1982. *Evolution and the theory of games*. New York: Cambridge University Press.
Milgram, Stanley. 1974. *Obedience to authority: An experimental view*. New York: Harper and Row.
Monroe, Kristen Renwick. 1996. *The heart of altruism: Perceptions of a common humanity*. Princeton: Princeton University Press.
———. 2002. Interdisciplinary work and a search for shared scientific standards. *PS* 35 (2): 203–5.
Nowak, Martin A., Karen M. Page, and Karl Sigmund. 2000. Fairness versus reason in the ultimatum game. *Science* 289 (5485): 1773–75.
Olson, Mancur. 1965. *The logic of collective action*. Cambridge: Harvard University Press.
Orbell, John M., and Robyn M. Dawes. 1991. A cognitive miser theory of cooperators' advantage. *American Political Science Review* 85 (2): 515–28.
Ostrom, Elinor. 1998. A behavioral approach to the rational choice theory of collective action. *American Political Science Review* 92 (1): 1–22.
Ostrom, Elinor, Roy Gardner, and James Walker. 1994. *Rules, games, and common-pool resources*. Ann Arbor: University of Michigan Press.
Pinker, Steven. 1997. *How the mind works*. New York: W. W. Norton.
———. 2002. *The blank slate: The modern denial of human nature*. New York: Viking Books.
Plomin, Robert. 1990. The role of inheritance in behavior. *Science* 248 (4952): 183–248.
Plomin, Robert, John C. DeFries, Gerald E. McClearn, and Peter McGuffin. 2000. *Behavioral genetics*. 4th ed. New York: Worth.
Plomin, Robert, Michael J. Owen, and Peter McGuffin.

1994. The genetic basis of complex human behaviors. *Science* 264 (5166): 1733–39.
Price, Michael E., Leda Cosmides, and John Tooby. 2002. Punitive sentiment as an anti-free rider psychological device. *Evolution and Human Behavior* 23 (3): 203–31.
Putnam, Robert D. 1993. *Making democracy work: Civic traditions in modern Italy*. Princeton: Princeton University Press.
———. 2000. *Bowling alone: The collapse and revival of American community.* New York: Simon and Schuster.
Rabushka, Alvin, and Kenneth A. Shepsle. 1972. *Politics in plural societies: A theory of democratic instability*. Columbus, OH: Charles E. Merrill.
Raby, Peter. 2001. *Alfred Russel Wallace: A life*. Princeton: Princeton University Press.
Rauch, Jonathan. 2002. Seeing around corners. *Atlantic Monthly* 289 (4): 35–48.
Ridley, Mark. 2003. *The cooperative gene: How Mendel's demon explains the evolution of complex beings.* New York: Free Press.
Ridley, Matt. 1999. *Genome: The autobiography of a species in 23 chapters.* New York: Harper Collins.
———. 2003. *Nature via nurture: Genes, experience, and what makes us human*. New York: Harper Collins.
Rushton, J. Philipe, Christine H. Littlefield, and Charles J. Lumsden. 1986. Gene-culture coevolution of complex social behavior: Human altruism and mate choice. *Proceedings of the National Academy of Sciences* 83 (19): 7340–43.
Sanderson, Stephen K. 2001. *The evolution of human sociality: A Darwinian conflict perspective*. Lanham, MD: Rowman and Littlefield.
Selten, Reinhard. 1999. Response to Shepsle and Laitin. In *Competition and cooperation: Conversations with Nobelists about economics and political science,* ed. James E. Alt, Margaret Levi, and Elinor Ostrom, 303–8. New York: Russell Sage.
Sherif, Muzafer, O. J. Harvey, B. J. White, W. E. Hood, and C. W. Sherif. 1961. *Intergroup conflict and cooperation: The robber's cave experiment*. Norman, OK: University of Oklahoma Press.
Simon, Herbert A. 1957. *Models of man*. New York: John Wiley.
———. 1985. Human nature in politics: The dialogue of psychology with political science. *American Political Science Review* 79 (2): 293–304.
———. 1997. Bounded rationality. In *Models of bounded rationality*. Vol. 3, *Empirically grounded economic reason,* ed. Herbert A. Simon, 291–94. Cambridge: MIT Press.
Smith, Vernon L. 2000. *Bargaining and market behavior: Essays in experimental economics*. New York: Cambridge University Press.
Sober, Elliott, and David Sloan Wilson. 1998. *Unto others: The evolution and psychology of unselfish behavior*. Cambridge: Harvard University Press.
Somit, Albert, and Steven A. Peterson. 1996. *Research in biopolitics.* Vol. 4. Greenwich, CT: JAI Press.
———. 1999. Rational choice and biopolitics. *PS* 32 (1): 39–44.
Strate, John. 1983. Political systems and defense. *Politics and the Life Sciences* 1 (2): 150–51.
———. 1985. The role of war in the evolution of political systems. *Humboldt Journal of Social Relations* 12 (2): 87–114.
Sullivan, Dennis G., and Roger D. Masters. 1988. Happy warriors: Leaders facial displays, viewers' emotions, and political support. *American Journal of Political Science* 32 (2): 345–68.
Tedin, Kent L. 1974. The influence of parents on the political attitudes of adolescents. *American Political Science Review* 68 (4): 1579–92.
Thaler, Richard H. 1992. *The winner's curse: Paradoxes and anomalies of economic life*. Princeton: Princeton University Press.
Thompson, Leigh, Laura J. Kray, and E. Allan Lind. 1998. Cohesion and respect: An examination of group decision making. *Journal of Experimental Social Psychology* 34 (3): 289–311.
Tooby, John, and Leda Cosmides. 1992. The psychological foundations of culture. In *The adapted mind: Evolutionary psychology and the development of culture*, ed. Jerome H. Barkow, Leda Cosmides, and John Tooby, 19–136. New York: Oxford University Press.
Van Dijk, Eric, and Riel Vermunt. 2000. Strategy and fairness in social decision making: Sometimes it pays to be powerless. *Journal of Experimental Social Psychology* 36 (1): 1–25.
Varshney, Ashutosh. 2003. Nationalism, ethnic conflict, and rationality. *Perspectives on Politics* 1 (1): 85–99.
Wahlke, John C. 1979. Pre-behavioralism in political science. *American Political Science Review* 73 (1): 9–31.
Waltz, Kenneth N. 2001. *Man, the state and war: A theoretical analysis*. New York: Columbia University Press.
Wedekind, Claus, and Manfred Milinski. 1996. Human cooperation in the simultaneous and alternating prisoner's dilemma: Pavlov versus generous tit-for-tat. *Proceedings of the National Academy of Sciences* 93 (7): 2686–89.
Wilson, David Sloan, and Elliott Sober. 1994. Reintroducing group selection to the human behavioral sciences. *Behavioral and Brain Sciences* 17 (4): 585–654.
Wilson, Edward O. 1975. *Sociobiology*. Cambridge: Harvard University Press.
Wrangham, Richard W. 1999. The evolution of coalitionary killing. *Yearbook of Physical Anthropology* 42 (1): 1–30.
Wynne-Edwards, Vero C. 1962. *Animal dispersion in relation to social behavior*. London: Oliver and Boyd.