Correspondence

Evolution and Territorial Conflict

Raymond Kuo
Dominic D.P. Johnson and
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To the Editors (Raymond Kuo writes):

For decades, evolutionary psychologists have offered explanations for complex human behaviors. These efforts are typically plagued by methodological problems, including unfalsifiability, reasoning by analogy, and endogeneity. Dominic Johnson and Monica Duffy Toft's evolutionary explanation for the unique place of territory in human conflict stumbles on these same grounds.[1] Johnson and Toft argue that humans—perhaps all vertebrates—have evolved a propensity for territoriality, incurring higher costs and fighting harder for land as compared with other sources of conflict. Their claims suffer from four problems, however. First, their understanding of evolution is imprecise and problematic, employing what is known as the "adaptationist fallacy" in lieu of clearly specifying a causal, biological mechanism. Second, they fail to sharply distinguish their account from plausible nonbiological alternatives. Third, they invite significant endogeneity problems by crossing the species barrier and traversing multiple levels of analysis. Fourth, they neglect cutting-edge research pointing to the limits of biological inheritance and evolutionary effects on behavior. Ultimately, their approach adds little to scholars' understanding of territoriality.

Johnson and Toft suggest that territoriality is "'soft-wired'—a component of human nature but one that is responsive to prevailing conditions" (p. 11). As such, vertebrate organisms have evolved both a predisposition toward territorial aggression and, critically, "assessment," the ability to evaluate the relative value, resources, and defensibility of a piece of land; the costs of aggression; and an opponent's capabilities.[2] Based on these two assumptions, Johnson and Toft identify three conditions—value asymmetry, economic defensibility, and resource holding potential—that they maintain leads to variation in the willingness of creatures to fight or posture over terrain.

There are four problems with Johnson and Toft's claims. First, they rest on a shaky conception of evolution, because the authors assume that physical traits and even

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1. Dominic D.P. Johnson and Monica Duffy Toft, "Grounds for War: The Evolution of Territorial Conflict," *International Security*, Vol. 38, No. 3 (Winter 2013/14), pp. 7–38. Subsequent citations to this article appear parenthetically in the text.
2. Geoffrey A. Parker, "Assessment Strategy and the Evolution of Fighting Behaviour," *Journal of Theoretical Biology*, Vol. 47, No. 1 (September 1974), pp. 223–243; and Geoffrey A. Parker and D.I. Rubenstein, "Role Assessment, Reserve Strategy, and Acquisition of Information in Asymmetric Animal Conflicts," *Animal Behavior*, Vol. 29, No. 1 (February 1981), pp. 221–240.

International Security, Vol. 39, No. 3 (Winter 2014/15), pp. 190–201, doi:10.1162/ISEC_c_00180

behaviors are optimal adaptations to some natural or sexual selective pressure in the past.[3] Selection is only one of several possible evolutionary pathways, however. The others—mutation, migration, and genetic drift—do not imply that territorial behavior fulfills some specific function. Neutral theories of molecular evolution posit that these other processes account for most evolutionary change as well as a greater share of human genetic differences than selection.[4] In addition, territoriality could emerge from biological, but non-evolutionary, processes. Stephen Jay Gould and Richard Lewontin raise the issue of "spandrels," physical features that are simply the by-product of other dynamics and do not serve an adaptive purpose.[5] Alternatively, territoriality could be a syndrome, part of a suite of generic aggressive responses not tied specifically to land.[6] If this is the case, such a mechanism rules out a specifically biological explanation for why humans are uniquely aggressive about terrain.

Most important, territoriality could be an exaptation: an evolved trait that has been co-opted to serve some new function. Indeed, Johnson and Toft identify this possibility: "Although attachment to territory may have been an adaptive disposition in humans' evolutionary past, in an environment of vast nation-states, modern weapons, and massive armies, it can contribute to disastrous losses or Pyrrhic victories" (p. 25). Exaptation is a challenge to their approach, however, not evidence for it. How can one be certain that humans have not continued to evolve, and that territoriality is indeed a result of past adaptation instead of more recent biological or immediate social incentives? Why should a particular behavior resist new selective pressures, when it previously emerged in response to that same process? Recent studies suggest that human evolution has sped up over the past 40,000 years, calling into question Johnson and Toft's assumption of a stable biological proclivity toward territoriality.[7]

Second, Johnson and Toft do not specify a testable selection mechanism or devise sharp hypotheses distinguishing their argument from existing material or social expla-

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3. George C. Williams, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought* (Princeton, N.J.: Princeton University Press, 1966); Stephen Jay Gould and Richard C. Lewontin, "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme," *Proceedings of the Royal Society of London B 205*, September 1979, pp. 581–598; Richard C. Lewontin, "Sociobiology as an Adaptationist Program," *Behavioral Science*, Vol. 24, No. 1 (January 1979), pp. 5–14; and Richard C. Lewontin, *Biology as Ideology: The Doctrine of DNA* (New York: Harper Collins, 1993).

4. Motoo Kimura, *The Neutral Theory of Molecular Evolution* (Cambridge: Cambridge University Press, 1983). T. Hofer et al., "Large Allele Frequency Differences between Human Continental Groups Are More Likely to Have Occurred by Drift during Range Expansions than by Selection," *Annals of Human Genetics*, Vol. 73, No. 1 (2008), pp. 95–108.

5. Gould and Lewontin, "The Spandrels of San Marco and the Panglossian Paradigm."

6. Andrew Sih, Alison Bell, and J. Chadwick Johnson, "Behavioral Syndromes: An Ecological and Evolutionary Overview," *Trends in Ecology and Evolution*, Vol. 19, No. 7 (July 2004), pp. 372–378.

7. John Hawks et al., "Recent Acceleration of Human Adaptive Evolution," *Proceedings of the National Academy of Sciences of the United States of America*, December 26, 2007, pp. 20753–20758; Gregory Cochran and Henry Harpending, *The 10,000 Year Explosion: How Civilization Accelerated Human Evolution* (New York: Basic Books, 2009); Wenqing Fu et al., "Analysis of 6,515 Exomes Reveals the Recent Origin of Most Human Protein-Coding Variants," *Nature,* January 10, 2013, pp. 216–220; and Peter J. Richerson, Robert Boyd, and Joseph Henrich, "Gene-Culture Coevolution in the Age of Genomics," *Proceedings of the National Academy of Sciences of the United States of America*, May 11, 2010, suppl. 2, pp. 8985–8992.

nations. Instead, they adopt an expansive definition of the biological, such that it is impossible to distinguish the in-born from the external. Of their principal theoretical components—a propensity for territorial behavior and assessment ability—the former is effectively a constant. They write, "Humans and animals have a baseline proclivity toward territoriality, but variable outcomes are still possible beyond this baseline given prevailing costs, benefits, and capabilities" (ibid.). This variation—and the theory's explanatory power—is driven by assessment, the capacity for evaluation, analysis, and decisionmaking. But while assessment has a biological component, it is deeply and clearly influenced by social, political, and environmental factors, resulting in contingent and plastic human (and nonhuman) behavior.[8]

The assumption that assessment is fundamentally biological overreaches by erasing all distinction between the biological and nonbiological. Johnson and Toft's three conditions explaining variation in territoriality particularly suffer from this conceptual imprecision. On economic defensibility, Johnson and Toft argue, "We should expect natural selection to favor territorial defense only where and when the benefits exceed the costs." They highlight resource distribution as affecting the ease of defensibility. This is a feature of the terrain, however, not something inherent to the organism. The value asymmetry concept is similarly problematic: "the territory itself can affect an individual's willingness to fight," including such variables as knowledge of the terrain (p. 23). As Johnson and Toft contend, a resident's "familiarity with the area and its contents confers significant survival and reproductive advantages compared to an interloper who is only prospecting and can move on to look for other territories instead" (ibid.). Knowledge of specific territory, however, is acquired through direct learning or social teaching, not passed down through a selective process.

The resource holding potential condition (RHP) also fails to distinguish itself from social explanations. Johnson and Toft define RHP as "the phenotypic qualities that affect performance in a fight (e.g., size and strength)," and argue that those organisms possessing higher RHP display greater territoriality (p. 22). As in military studies, however, performance capability is fundamentally a relative and relational variable. Physical qualities and potential are partially derived from evolution, but their distribution, assessment of value, and the strategies chosen to account for them are influenced by so-

8. Parker, "Assessment Strategy and the Evolution of Fighting Behaviour"; and Parker and Rubenstein, "Role Assessment, Reserve Strategy, and Acquisition of Information in Asymmetric Animal Conflicts"; Theodore Garland Jr. and Scott A. Kelly, "Phenotypic Plasticity and Experimental Evolution," *Journal of Experimental Biology*, Vol. 209, No. 12 (June 2006), pp. 2344–2361; John H. Flavell, *Cognitive Development* (Englewood Cliffs, N.J.: Prentice-Hall, 1985), pp. 114–115; Aleksandr R. Luria, *Cognitive Development: Its Cultural and Social Foundations* (Cambridge, Mass.: Harvard University Press, 1976); Albert Bandura, "Social Cognitive Theory: An Agentic Perspective," *Annual Review of Psychology*, Vol. 52 (2001), pp. 1–26; and Keith Trigwell and Michael Prosser, "Improving the Quality of Student Learning: The Influence of Learning Context and Student Approach to Learning on Learning Outcomes," *Higher Education*, Vol. 22, No. 3 (October 1991), pp. 251–266. As Evan Charney defines it, plasticity refers to "the ability of an organism to modify development trajectories and change phenotypic state or activity in response to variations in environmental conditions." See Charney and William English, "Genopolitics and the Science of Genetics," *American Political Science Review*, Vol. 107, No. 2 (May 2013), pp. 382–395, at p. 392.

cial, environmental, and developmental factors. Indeed, the elaborate "ritualization" of contests among birds, horned mammals, and even insects reinforces this character. Consequently, labeling RHP an inherently biological condition is problematic. Moreover, this concept's predictions are unsurprising: stronger states or parties win more often. Johnson and Toft contend that their approach highlights the role of strength, morale, and costly demonstrations of intent. These issues, however, are well known and have been well studied.[9]

Third, Johnson and Toft invite significant endogeneity challenges by crossing multiple levels of analysis, as well as the species barrier. Phenotype (i.e., an organism's observable characteristics or behaviors) does not emerge directly from genotype (i.e., an organism's genetic makeup). Traversing the levels of analysis from genetic and evolutionary to international introduces an escalating host of intermediating variables. Developmental conditions, the presence of genetic drift, access to basic sanitation and nutrition, political regimes, international institutions, economic conditions, the presence of conflict, educational opportunities, family structures and dynamics, and religious precepts: these and many other factors confound a clear, causal, and evolutionary link between genotype and phenotype. Previous evolutionary psychology approaches addressed this problem through reductionism, the claim that alternative levels of analysis have no effects independent of the one in question (usually genetic).[10] But as discussed previously, Johnson and Toft's soft-wiring framework explicitly allows for direct environmental effects on human decisions through assessment.[11] Their expansive definition of biology compounds these issues, as they must isolate the effects of competing biological, social, and material variables at and across each level of analysis.

The RHP condition also leads to concerns about crossing the species barrier. Assessing phenotype is difficult even when dealing with observable and relatively stable physiological changes across generations. The challenge is compounded, however, when examining behavior, which is subject to interpretation, unstable definitions, and issues of comparability. Outwardly similar activity among multiple species could indicate common biological origins, as Johnson and Toft claim. Alternatively, it could be driven by species-specific factors, rendering the similarities superficial.[12] Or, it might be a response to similar environmental conditions, such as common levels of resource

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9. Randolph M. Siverson and Joel King, "Attributes of National Alliance Membership and War Participation, 1815–1965," *American Journal of Political Science*, Vol. 24, No. 1 (February 1980), pp. 1–15; Robert Powell, *In the Shadow of Power: States and Strategies in International Politics* (Princeton, N.J.: Princeton University Press, 1999); and David B. Carter, "The Strategy of Territorial Conflict," *American Journal of Political Science*, Vol. 54, No. 4 (October 2010), pp. 969–987.

10. Richard Dawkins, *The Selfish Gene* (Oxford: Oxford University Press, 1976); Richard Dawkins, *The Extended Phenotype: The Gene as the Unit of Selection* (Oxford: Oxford University Press, 1982); and Matt Ridley, *The Red Queen: Sex and the Evolution of Human Nature* (New York: Harper Perennial, 1994).

11. In fact, they allow for environmental effects both in a multi-generational evolutionary time frame and in the assessment of immediate conditions. Had they allowed only for the first, their genetic explanation for environmental influence might remain viable. Their claims, however, are also predicated on the organisms' assessments of the availability of nearby resources, terrain advantages in combat, or other local conditions.

12. Henry Tobin and A.W. Logue, "Self-Control across Species (*Columba livia, Homo sapiens*,

constraints relative to need. Gibbons, for example, were once thought to form exclusive, long-lasting pair-bonds across sexes, analogous to strict monogamy in humans. Matt Ridley contended that the genetic and taxonomic connections between this species and humans meant that a common biological source drove similar mating patterns.[13] Ryne Palombit and others, however, discovered that gibbons frequently "cheat" on their mates, conditional upon the availability of nearby resources and opportunities.[14] Jennifer Williams et al. argue that female chimpanzee ranging behavior—where and how widely they travel to acquire resources—is highly variable and conditioned upon feeding competition and social benefits.[15] Moving to (somewhat) analogous human studies, Elizabeth Cashdan finds that primitive communities fight not when resources are abundant and concentrated, but when they are dispersed and scarce. As she states, "Competition results not simply from scarcity of resources in any absolute sense, but from scarcity relative to population density."[16] Taken together, these studies suggest that primate behavior is highly responsive to variable environmental and resource conditions, and comparisons across species must account for these factors. This observation lends additional support to a nonbiological explanation for territoriality.

Fourth and finally, Johnson and Toft's approach fails to address for cutting-edge research on heritability rates, epigenetics, and multifactorialism that place limits on the importance of heritability in animal behavior. First, the heritable component of propensities such as aggression can be as low as 10 percent, using controlled, selective breeding laboratory experiments on traits that can be quantitatively measured.[17] Second, epigenetics focuses on heritable change derived from biochemical processes that regulate and activate genetic transcription. These processes respond directly to environmental conditions, and recent studies highlight their role in human brain and behavioral development.[18] One study finds that posttraumatic stress disorder among expectant mothers stemming from the September 11, 2001, attacks resulted in lower cortisol levels that were passed on to their children.[19] Another study found that mice will avoid a par-

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and *Rattus norvegicus*)," *Journal of Comparative Psychology*, Vol. 108, No. 2 (June 1994), pp. 126–133, http://psycnet.apa.org/journals/com/108/2/126/.

13. Ridley, *The Red Queen*.

14. Ryne Palombit, "Dynamic Pair Bonds in Hylobatids: Implications Regarding Monogamous Social Systems," *Behaviour*, Vol. 128, Nos. 1–2 (February 1994), pp. 65–101; Pascal Gagneux, Christophe Boesch, and David Woodruff, "Female Reproductive Strategies, Paternity, and Community Structure in Wild West African Chimpanzees," *Animal Behaviour*, Vol. 57, No. 1 (January 1999), pp. 19–32; and Warren Y. Brockelman et al., *Behavioral Ecology and Sociobiology*, Vol. 42 (1998), pp. 329–339.

15. Jennifer M. Williams et al., "Female Competition and Male Territorial Behaviour Influence Female Chimpanzees' Ranging Patterns," *Animal Behavior*, Vol. 63, No. 2 (February 2002), pp. 347–360.

16. Elizabeth Cashdan, "Territoriality among Human Foragers: Ecological Models and an Application to Four Bushman Groups," *Current Anthropology*, Vol. 24, No. 1 (February 1983), p. 48.

17. Liesbeth Zwarts et al., "Complex Genetic Architecture of Drosophila Aggressive Behavior," *Proceedings of the National Academy of Sciences of the United States of America*, October 11, 2011, pp. 17070–17075.

18. See Evan Charney, "Behavior Genetics and Postgenomics," *Behavioral and Brain Sciences*, Vol. 35, No. 5 (October 2012) pp. 331–410.

19. Rachel Yehuda et al., "Transgenerational Effects of Posttraumatic Stress Disorder in Babies of

ticular smell if it is coupled with a negative shock. Interestingly, their offspring displayed the same adverse reaction despite the lack of a selective mechanism.[20] By ignoring epigenetics, Johnson and Toft neglect a critical method by which ecological and social stimuli affect genetic expression and evolutionarily derived behavior, including territoriality. Third, the genetic component of complex human behaviors is undoubtedly polygenic, meaning that multiple genes interact to express a single phenotype. Human height, for example, is linked to 180 genes, many of which are pleiotropic (i.e., the proteins the genes encode for are involved in multiple physiological processes).[21] An adaptationist view of human behavior, based on the assumption of stable genetic codings and behavioral proclivities, is likely too simple to encompass the multiple and highly complex interactions occurring between and among genes. In light of low heritability, any individual gene explains only a small amount of variation in behavior. Coupled with epigenetics, each gene provides multiple points of influence for social and environmental factors. Thus, the simple assumption that territory is driven by evolution masks a wide range of complex, causal pathways and interactions, each generating different behavioral implications and theoretical conclusions.[22]

Ultimately, Johnson and Toft's claim that territoriality is grounded in evolution is flawed. These problems validate Evan Charney and William English's point that "genopolitics" is likely a misguided undertaking.[23] Natural and social scientists may yet arrive at "consilience," a fusion of both areas' knowledge into a common framework.[24] First, however, scholars must have a clear understanding of evolution's complexity, as well as a rigorous accounting of the challenging methodological obstacles inherent to solid social inquiry.

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Mothers Exposed to the World Trade Center Attacks during Pregnancy," *Journal of Clinical Endocrinology and Metabolism*, Vol. 90, No. 7 (July 2005), pp. 4115–4118.

20. Brian G. Dias and Kerry J. Ressler, "Parental Olfactory Experience Influences Behavior and Neural Structure in Subsequent Generations," *Nature Neuroscience*, Vol. 17 (2014), pp. 89–96.

21. Hana Lango Allen et al., "Hundreds of Variants Clustered in Genomic Loci and Biological Pathways Affect Human Height," *Nature*, October 14, 2010, pp. 832–38.

22. A comparison might help to highlight this inadequacy. James H. Fowler and Dawes T. Christopher identify two genes that they claim predict voter turnout, specifically polymorphism of the MAOA and 5HTT genes. These genes are associated with serotonin output and antisocial personality disorders. Fowler and Christopher carefully distinguish between the effects of these two genes and those of environmental conditions; for instance, they find that religious attendance also moderates voter turnout. See Fowler and Christopher, "Two Genes Predict Voter Turnout," *Journal of Politics*, Vol. 70, No. 3 (July 2008), pp. 579–594. Charney and English, however, rightly point to a number of problems with both Fowler and Christopher's handling of statistics and their understanding of genetics. These problems include result replication, population stratification, omitted variable bias, and overinflated claims of effect resulting from small quantities of interest and polygenicity. See Charney and English, "Genopolitics and the Science of Genetics." Fowler and Christopher do, however, suggest a clear, genetic causal pathway, unlike Johnson and Toft.

23. Charney and English, "Genopolitics and the Science of Genetics."

24. Edward O. Wilson, *Consilience: The Unity of Knowledge* (New York: Vintage, 1998).

Dominic D.P. Johnson and Monica Duffy Toft Reply:

We thank Raymond Kuo for his letter in response to our article, "Grounds for War: The Evolution of Territorial Conflict."[1] The article argues that evolutionary theory helps to explain the empirical puzzle of why human beings seem prone to territorial conflict. As we and other scholars before us have highlighted, existing theories fail to explain the frequency or severity of territorial aggression. We investigated whether an evolutionary perspective might offer new insights, predictions about conducive conditions, and fundamental patterns that transcend species, space, and time.[2]

We begin our reply to Kuo by noting two important overarching issues. First, Kuo critiques the extent to which evolutionary legacy affects human behavior in general. His letter therefore amounts to a critique of any evolutionary theory of human behavior (e.g., of aggression or mate preferences), and therefore does not engage with our specific argument about territory. Second, Kuo critiques the importance of adaptation in evolution. His letter therefore also amounts to a critique of the role of evolution in the behavior of animals as well as humans. His arguments imply that territoriality (or any other behavior) is unlikely to be an adaptation among any species, which fundamentally contradicts Darwin and subsequent literature.

Thus, rather than debate the issue of territory and war, Kuo engages in a general debate about (1) the role of evolution in human behavior, and (2) the role of evolution in animal behavior. These issues have been extensively examined and debated before,[3] including in this journal.[4]

Kuo appears to have arrived at these general critiques because of several fundamental misunderstandings about evolution, which we correct here. Evolutionary theory does not threaten a wholesale destruction of existing theories, as many social scientists seem to fear, to be replaced by a deterministic, biological theory of social behavior. Like all theories, evolutionary theory plays a contributory role to understanding and explaining human behavior. Are biological influences on behavior limited? Of course. Does that make for a reason to discount it? Of course not. Does biology present complexities in theory development? Of course. Does that make our theory of territoriality

1. Dominic D.P. Johnson and Monica Duffy Toft, "Grounds for War: The Evolution of Territorial Conflict," *International Security*, Vol. 38, No. 3 (Winter 2013/14), pp. 7–38. Subsequent citations to this article appear parenthetically in the text.
2. For a more recent article making this argument, see Dominic D.P. Johnson and Monica Duffy Toft, "Bringing 'Geo' Back into Politics: Evolution, Territoriality, and the Contest over Ukraine (with Commentaries)," *Cliodynamics: The Journal of Quantitative History and Cultural Evolution*, Vol. 5, No. 1 (2015), pp. 87–122.
3. For some general reviews, see Steven Pinker, *The Blank Slate: The Modern Denial of Human Nature* (New York: Penguin Putnam, 2002); Jerome H. Barkow, *Missing the Revolution: Darwinism for Social Scientists* (Oxford: Oxford University Press, 2006); Robert Wright, *The Moral Animal: Why We Are the Way We Are—The New Science of Evolutionary Psychology* (New York: Random House, 1994); Richard Dawkins, *The Selfish Gene* (Oxford: Oxford University Press, 1976); and D.D.P. Johnson, "Survival of the Disciplines: Is International Relations Fit for the New Millenium?" *Millennium: Journal of International Studies*, forthcoming.
4. See, for example, Duncan S.A. Bell and Paul K. MacDonald, "Correspondence: Start the Evolution without Us," *International Security*, Vol. 26, No. 1 (Summer 2001), pp. 187–194.

fundamentally different from other theories or undermine Darwin's theory of evolution? Of course not.

The crucial question, then, is not whether biology influences human behavior, but how much.[5] Kuo appears to acknowledge that biology exerts some influence on human behavior. His criticism is therefore limited to an argument about its extent—is it a little or a lot?

A more profound problem with Kuo's response is his misunderstanding of evolution itself. In what follows, we discuss his misunderstandings in each of his four topic areas: (1) adaptation; (2) mechanisms and alternatives; (3) levels of analysis; and (4) biological barriers.

ADAPTATION

Drawing on the non-mainstream views of Stephen Jay Gould and Richard Lewontin dating from the 1970s,[6] Kuo suggests that adaptation is a "shaky conception of evolution." He points instead to the role of "mutation, migration, and genetic drift" as accounting "for most evolutionary change." There are at least four problems with this claim.

First, adaptation is key to evolution, not an exception to it. If genetic drift were dominant, organisms would fail to adapt to their environment, and Darwin would never have developed his theory of adaptation by natural selection. Second, mutation is an essential part of adaptation. It is not an alternative. Third, arguing that some biological traits might be accidents of evolution ("spandrels") is a weak argument. As biologists have stressed, to advocate a trait as being a spandrel is an even more onerous task than demonstrating it to be an adaptation.[7] Before invoking more complicated alternatives, the biological approach is to explore hypotheses for how traits may be adaptive.[8] In the case of territoriality, the argument for adaptation is already strong. Fourth, Kuo points to molecular biological findings suggesting that processes such as drift "account for a greater share of human genetic differences than does selection." This comparison is wrong. Genetic differences among populations as a whole reveal nothing about adaptations: consider, for example, that although humans clearly differ from chimpanzees we share up to 99 percent of the same DNA. Some genes are more important than others in explaining differences among species, populations, and individuals. Why? Because traits coded for by some genes are under strong selection pressure (and thus represent adaptations), whereas others are under no selection pressure (and are thus allowed to drift).

Kuo's list of reasons for why traits might not be adaptations reflects fundamental

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5. Azar Gat, "So Why Do People Fight? Evolutionary Theory and the Causes of War," *European Journal of International Relations*, Vol. 15, No. 4 (Decmber 2009), pp. 571–599.
6. For a critique of Gould and Lewontin, see Paul W. Andrews, Steven W. Gangestad, and Dan Matthews, "Adaptationism: How to Carry Out an Exaptationist Program," *Behavioral and Brain Sciences*, Vol. 25 (2002), pp. 489–553; Janet R. Richards, *Human Nature after Darwin: A Philosophical Introduction* (London: Routledge, 2000); and Pinker, *The Blank Slate*.
7. Andrews, Gangestad, and Matthews, "Adaptationism."
8. George C. Williams, *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought* (Princeton, N.J.: Princeton University Press, 1966).

misunderstandings about evolution and certainly does not challenge evolutionary theory and adaptation by natural selection. After all, if adaptation is as unlikely as Kuo argues, then how does one explain the many physiological and behavioral traits among animals, plants, and other organisms? Kuo is taking on the logic of evolutionary adaptation rather than us. If he is right, then Darwin is wrong, leaving us with an easy choice of allegiance.

mechanisms and alternatives

Kuo's second critique is that we do not identify proximate mechanisms underlying territorial behavior or distinguish our explanation from nonbiological alternatives.

Earlier versions of our article included a section on proximate mechanisms, but we removed it in response to the request of a reviewer, who viewed the subject as a separate line of argumentation. There were in fact plenty of candidate proximate mechanisms, including the endowment effect, loss aversion, emotional attachment to homeland, sacralizing land, and the "first owner bias"—an empirical tendency to assume that individuals who possess something first are the true owners.[9]

As for alternative theories, we focused on rational choice (see pp. 13–15). We argued that from an evolutionary perspective, territorial aggression can be perfectly "rational," depending on the prevailing costs and benefits. As we wrote, "Territoriality may be beneficial in one place and costly in another, and it is an effective strategy only where and when the benefits outweigh the costs, just as a rational choice approach would predict" (p. 19). There is nothing inherently contradictory about evolution and rational choice—both aim to maximize returns on investment. The distinguishing feature of an evolutionary theory, however, is that human beings may be endowed with a utility function that is (at least partly) at odds with the costs and benefits of contemporary war. We explicitly framed our article around empirical work suggesting that territorial conflict is more frequent, more costly, and more likely to recur than expected by existing rational cost/benefit analyses. It is these very anomalies that led us to investigate the conditions under which territorial behavior might be more or less effective, and to discern whether new insights from evolutionary biology—both theoretical and empirical—might account for them.

Kuo argues that the explanatory power of our theory is "driven by assessment, the capacity for evaluation, analysis, and decisionmaking" and is "deeply and clearly influenced by social, political, and environmental factors." That should be obvious, and there is nothing in our article that contradicts this claim (we explicitly state that human

9. Jefferey Evans Stake, "The Property 'Instinct,'" *Philosophical Transactions of the Royal Society of London, Series B*, Vol. 359 (2004), pp. 1763–1744; Herb Gintis, "The Evolution of Private Property," *Journal of Economic Behavior and Organization*, Vol. 64, No. 1 (September 2007), pp. 1–16; Richard Sosis, "Why Sacred Lands Are Not Indivisible: The Cognitive Foundations of Sacralizing Land," *Journal of Terrorism Research*, Vol. 2, No. 1 (June 2011), pp. 17–44; Peter DeScioli and Bart J. Wilson, "The Territorial Foundations of Human Property," *Evolution and Human Behavior*, Vol. 32, No. 5 (September 2011), pp. 297–304; Peter R. Blake and Paul L. Harris, "Children's Understanding of Ownership Transfers," *Cognitive Development*, Vol. 24, No. 2 (April/June 2009), pp. 133–145; and Ori Friedman and Karen R. Neary, "Determining Who Owns What: Do Children Infer Ownership from First Possession?" *Cognition*, Vol. 107, No. 3 (June 2008), pp. 829–849.

intelligence and reasoning contribute to decisionmaking). The puzzle is why social scientists sometimes think that biological theories imply that only biology matters. No biologist would make such a strong, deterministic claim. Why would anyone else?

A key source of Kuo's misunderstanding appears to come from a lack of appreciation of how biological mechanisms can interact with the environment. As biologists have established, biological mechanisms themselves have environmental inputs (e.g., sunflowers turn toward the sun), so there is no reason to artificially separate evolved mechanisms from social or environmental aspects of decisionmaking. Indeed, they are inextricably (and adaptively) linked. For this reason, biology can explain a lot more behavioral variation than Kuo seems to realize (the same trait can be manifested differently under different conditions). Indeed, in the specific area of human territoriality, there has been a long tradition showing how evolutionary models interact with ecological variation to account for differences in human territorial behavior over space and time.[10] It is this interaction that offers novel predictions for territorial behavior today and in the future.

Kuo misses this vital point because he depicts our argument as deterministic, with an "assumption that assessment is fundamentally biological" and that this "erases all distinctions between the biological and nonbiological." This, however, is the opposite of what we say. As we state, "Although human intelligence and cultural factors complicate any reductionist understanding of human behavior, a core insight of evolutionary theory is that much of our behavior, even if broadly rational in many settings, is also influenced by evolved physiological and psychological mechanisms that we cannot switch on or off at will" (p. 10). This distinction between biological and rational assessment underpins Kuo's most fundamental misunderstanding. He sees key sources of environmental variation (economic defensibility and value asymmetry) as problematic for evolutionary theory, writing: "Knowledge of a specific territory, however, is acquired through direct learning or social teaching, not passed down through a selection process." This should be obvious, and hardly means that biological mechanisms cannot react to changing circumstances. As we noted, even birds alter their territorial behavior depending on the availability of food (pp. 19–20). Is this because birds are carrying out a conscious process of rational deliberation? No.

This assumption that adaptations are unable to generate differential outcomes in different environmental contexts fails to appreciate how biological mechanisms work. Adaptive traits receive real-time informational inputs from the world around them, and they are designed to respond accordingly (inflexible strategies would be inferior or lethal, and quickly selected out). Although perhaps hard to grasp in the case of humans, the mental block fades when applied to other species: birds migrate only when the seasons change, moths fly toward a light source, and so on. The environment can

10. Rada Dyson-Hudson and Eric Alden Smith, "Human Territoriality: An Ecological Reassessment," *American Anthropologist*, Vol. 80, No. 1 (March 1978), pp. 21–41; and Benjamin Chabot-Hanowell and Eric Alden Smith, "Territorial and Non-Territorial Routes to Power: Reconciling Evolutionary Ecological, Social Agency, and Historicist Approaches," in James F. Osborne and Parker Van Valkenburgh, eds., "Territoriality in Archaeology," special issue, *Archaeological Papers of the American Anthropological Association*, Vol. 22, No. 1 (2013), pp. 72–86.

alter our evolved behavioral mechanisms just as it can alter our conscious decision-making process.

LEVELS OF ANALYSIS

Kuo then turns to a critique of our argument on the basis of "traversing the levels of analysis from genetic and evolutionary to international," thereby introducing "an escalating host of intermediating variables." This criticism can be leveled at any argument that individual human beings influence politics (whether made by a historian, a psychologist, or an evolutionary biologist). This is not the venue to engage in a debate about whether individuals matter. The point is that, to whatever extent individuals do matter, then so do influences on those individuals. The selective pressures that shaped the structure and function of human brains is one such important influence.

Citing Richard Dawkins and Matt Ridley, Kuo suggests that "previous" evolutionary approaches addressed the levels of analysis problem by arguing that "alternative levels of analysis have no effects" independent of genes. This statement miscasts their work. Dawkins and Ridley themselves offer numerous examples of how genes interact with the environment (including with other individuals and among groups) to create outcomes at higher levels (e.g., see their discussions of the evolution of cooperation).[11] Evolution has been influencing behavior across multiple levels of analysis for millions of years, and social groups and intergroup relations are just one of many increments in the so-called major transitions of life in which genes have come to affect ever larger collections of entities (cells, organs, individuals, groups).[12] It is genes that are selected or not selected—a simple process with far-reaching effects.

BIOLOGICAL BARRIERS

Kuo's fourth critique concerns "crossing the species barrier." Kuo writes, "Outwardly similar activity among multiple species could indicate common biological origins. . . . Alternatively, it could be driven by species-specific factors, rendering similarities superficial." This statement reveals another of Kuo's misunderstandings of evolution. Common descent may explain similar traits, but traits may also be similar as a result of similar selection pressures. This process, called "convergent evolution," is common in nature. For example, wings have evolved independently in birds, mammals, and insects—but the ability to fly was not inherited across these taxonomic groups; rather it represents a convergent response to a similar adaptive challenge in the environment. The same is true for territoriality, which has evolved independently many times.

Finally, Kuo is concerned that traits can be influenced by multiple genes and suggests that "the adaptationist view of human behavior, based on the assumption of stable genetic codings and behavioral proclivities, is likely too simple to encompass the multiple and highly complex interactions occurring between genes." This is wrong,

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11. Richard Dawkins, *The Extended Phenotype: The Long Reach of the Gene* (Oxford: Oxford University Press, 1982); and Matt Ridley, *The Origins of Virtue: Human Instincts and the Origins of Cooperation* (London: Penguin, 1996).
12. John Maynard Smith and Eörs Szathmàry, *The Major Transitions of Evolution* (Oxford: W.H. Freeman, 1995).

again arising from a fundamental misunderstanding of evolution. The fact that traits can be influenced by multiple genes changes nothing about the logic of adaptation. Natural selection operates on the differential fitness effects of a trait, regardless of its recipe (the collection and interdependence of the genes that give rise to the trait). Traits can be selected for, evolve, and adapt whether they arise from one or a thousand genes. Here we can use Kuo's own example: he cites evidence that human height is influenced by 180 genes. Does this mean that height is immune from natural selection as an adaptation? Of course not.

CONCLUSION

Kuo's critique of our article displays a fundamental disconnect between the weight Kuo gives to the intricacies of human biology and genetics and the issue of whether human behaviors—indeed the behavioral traits of all organisms—are adaptations. It is important to remember that Darwin developed his theory of natural selection before the existence of genes was even known. Critics often get bogged down in (and confused by) the technicalities of genetics and molecular biology, but the logic of evolutionary theory and adaptation by natural selection remains the same. Scholars need to know biology, but equally important is a proper, well-informed, and up-to-date understanding of evolution. It is the interaction between the two that is key, and yet so commonly misunderstood.

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