

Grounds for War

The Evolution of Territorial Conflict

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The Badme region in the Horn of Africa is claimed by both Ethiopia and Eritrea. It contains few natural resources, and neither state considers it to have strategic value. As one local merchant put it, however, “It’s territory, you know. We’ll die for our country.”¹

Throughout history, humans have shown themselves willing to fight and die to seize or defend territory. For example, Chechnya’s long history of fighting off intruders—from the Iranian Alars (800–900), to the Golden Horde (1241), to the Turks and Persians (after 1300), and finally to the Russian empire (around 1800, and again in recent years)—imbued Chechen identity and culture with a folklore of fallen heroes who had died “for Chechnya” over the past millennium.²

Territory is central to some of the most vexing cases of conflict, especially where different groups lay claim to the same ground. Jerusalem, for example, has momentous significance for Christians, Jews, and Muslims alike. Each group is equally unwilling to yield control. The mere presence of Israeli Prime Minister Ariel Sharon at the Temple Mount in 2000 sparked the second intifada. Abkhaz and Georgians both view Abkhazia as their homeland, just as Serbs and Albanians see parts of Kosovo as theirs.³ In Northern Ireland’s pubs, discussions of the 1690 Battle of Boyne can still be heard “like it was last week’s hurling match,” with flags representing each side continuing to decorate and demarcate the different neighborhoods.⁴ Robert Pape has argued that the princi-

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1. Quoted in Ian Fisher, “Behind Eritrea-Ethiopia War, a ‘Knack for Stubbornness,’” *New York Times*, February 14, 1999.

2. Monica Duffy Toft, *The Geography of Ethnic Violence: Identity, Interests, and the Indivisibility of Territory* (Princeton, N.J.: Princeton University Press, 2003).

3. *Ibid.*

4. Dennis Pringle, “Separation and Integration: The Case of Ireland,” in Michael Chisholm and David M. Smith, eds., *Shared Space, Divided Space: Essays on Conflict and Territorial Organization* (London: Unwin Hyman, 1990), p. xxv.

pal impetus behind even transnational terrorist campaigns is localized territorial self-defense against foreign invaders and occupying powers.⁵ Osama bin Laden referenced the foreign occupation of “Muslim” territory as a primary basis for his holy war against the West.⁶ Although the role of territory in any specific case may be controversial, its powerful influence on conflict throughout history is beyond doubt.⁷ It can also be an important condition for cooperation. Nobel laureate Elinor Ostrom identified eight features critical for the effective management of common pool resources; “clearly defined boundaries” of the resources and the group authorized to use them appears first on the list.⁸

In many cases, competing claims over natural resources or where the territory itself is strategically located makes conflict over territory unsurprising. There is little consensus, however, on why territory in general remains such a sensitive flash point. As one recent study of how territorial borders are drawn observes, “The relative violence of territorial disputes is widely demonstrated empirically but is without a widely accepted explanation.”⁹ While material interests are often at stake, “symbolic” factors are also invoked as a powerful driver of war over territory, leading to conflict even over land “that for all practical purposes is devoid of value.”¹⁰ Why does territory carry such symbolic power for human beings? We propose that an evolutionary perspective offers important new insights.

Territorial behavior—or “territoriality”—is prevalent not only among humans, but across the animal kingdom. It has evolved independently across a

5. Robert A. Pape, “The Strategic Logic of Suicide Terrorism,” *American Political Science Review*, Vol. 97, No. 3 (August 2003), pp. 343–361. Pape’s argument has been challenged as well as supported by others. See Scott Atran, “The Moral Logic and Growth of Suicide Terrorism,” *Washington Quarterly*, Vol. 29, No. 2 (Spring 2006), pp. 127–147; and David Kilcullen, *The Accidental Guerrilla: Fighting Small Wars in the Midst of a Big One* (Oxford: Oxford University Press, 2009).

6. Steven Simon and Daniel Benjamin, “America and the New Terrorism,” *Survival*, Vol. 42, No. 1 (Spring 2000), pp. 59–75, 68.

7. John A. Vasquez, *The War Puzzle* (Cambridge: Cambridge University Press, 1993); John A. Vasquez, *The War Puzzle Revisited* (Cambridge: Cambridge University Press, 2009); and John A. Vasquez and Marie T. Henehan, *Territory, War, and Peace* (New York: Routledge, 2010).

8. Elinor Ostrom, *Governing the Commons: The Evolution of Institutions for Collective Action* (Cambridge: Cambridge University Press, 1990).

9. David B. Carter and H.E. Goemans, “The Making of the Territorial Order: New Borders and the Emergence of Interstate Conflict,” *International Organization*, Vol. 65, No. 2 (April 2011), pp. 275–309, at p. 306. Carter and Goemans’s own explanation is that the incidence of violent territorial disputes depends on whether borders are drawn along existing administrative boundaries or not. If they are, and thus encompass unified chunks of territory, then Carter and Goemans’s quantitative analysis suggests that both violent and nonviolent conflict is less likely to occur.

10. Vasquez, *The War Puzzle Revisited*, p. 157. See also Gary Goertz and Paul F. Diehl, *Territorial Changes and International Conflict* (London: Routledge, 1992); and Miles Kahler and Barbara F. Walter, *Territoriality and Conflict in an Era of Globalization* (Cambridge: Cambridge University Press, 2006).

wide range of taxonomic groups and ecological contexts, whether from the depths of the ocean to rainforest canopies, or from deserts to the Arctic tundra. This recurrence of territoriality suggests evolutionary “convergence” on a tried and tested strategic solution to a common environmental challenge. Organisms have tended to develop territoriality because it is an effective strategy for survival and maximizing “Darwinian fitness” (reproduction).

Territorial behavior facilitates effective competition for resources such as food, mates, shelter, breeding sites, and security from predators.¹¹ Territory per se—a particular patch of ground—is not necessarily intrinsically valuable. For example, you cannot eat land, but you can eat food that grows there. Territory is therefore a proxy through which organisms secure access to key resources and protect them from competitors. Across the animal kingdom, as well as in preindustrial human societies, access to and control over resources have been essential for survival and reproduction, and adaptations to acquire these via territorial behavior have been subject to strong selection pressure throughout evolutionary history.¹²

The idea that evolution helps to explain human territorial behavior is not new. Robert Ardrey’s popular book *The Territorial Imperative*, published in the 1960s, championed the role of territorial instincts in human conflict.¹³ This account, however, suffers from some now outdated views of evolution, for example, the idea that behaviors are “hard-wired,” or that they evolved because they helped the group or the species as a whole. More recently, a leading scholar of the role of territory in the causes of war, political scientist John Vasquez, argued in his landmark *The War Puzzle* that the field of international relations might benefit from exploring new work on the evolutionary and biological origins of territorial behavior.¹⁴ Vasquez predicted that “if this territori-

11. T.H. Kauffmann, “On the Definitions and Functions of Dominance and Territoriality,” *Biological Reviews*, Vol. 58, No. 1 (February 1983), pp. 1–20; and C.R. Maher and D.F. Lott, “Definitions of Territoriality Used in the Study of Variation in Vertebrate Spacing Systems,” *Animal Behaviour*, Vol. 49, No. 6 (June 1995), pp. 1581–1597.

12. J.L. Brown, “The Evolution of Diversity in Avian Territorial Systems,” *Wilson Bulletin*, Vol. 76, No. 2 (1964), pp. 160–169; Nicholas B. Davies, “Mating Systems,” in John R. Krebs and Nicholas B. Davies, eds., *Behavioural Ecology: An Evolutionary Approach* (Oxford: Blackwell Scientific, 1991), pp. 263–294; R. Dyson-Hudson and E.A. Smith, “Human Territoriality: An Ecological Reassessment,” *American Anthropologist*, Vol. 80, No. 1 (March 1978), pp. 21–41; Erik P. Willems, Barbara Hellriegel, and Carel P. van Schaik, “The Collective Action Problem in Primate Territory Economics,” *Proceedings of the Royal Society B: Biological Sciences*, Vol. 280, No. 1759 (2013), pp. 1–7; and John C. Mitani, David P. Watts, and Sylvia J. Amsler, “Lethal Intergroup Aggression Leads to Territorial Expansion in Wild Chimpanzees,” *Current Biology*, June 22, 2012, pp. 507–508.

13. Robert Ardrey, *The Territorial Imperative: A Personal Inquiry into the Animal Origins of Property and Nations* (New York: Kodansha America, 1997/1966).

14. Vasquez, *The War Puzzle*, chap. 4.

ality axiom were operating within the modern global political system,"¹⁵ then (1) states would divide the globe into territorial units by the use or threat of force; (2) states would be highly sensitive to threats to territory and prepared to meet them by force; (3) contiguous states of similar strength would establish boundaries through the use or threat of force at some point in their history; and (4) new states would threaten existing territories, increasing the use or threat of force. He concluded that the first two predictions "conform to some of the most obvious forms of behavior that have existed in world politics."¹⁶ Although the third and fourth predictions are harder to evaluate because they depend on other factors as well, such as population distribution and regime type, Vasquez nevertheless suggested that the "territoriality axiom" could account for four major phenomena in international relations, which represented a "testimony to its theoretical significance."¹⁷ Remarkably, however, scholars have not pursued this line of inquiry.

Humans are obviously different from other animals, but as with all biological organisms, natural selection has shaped our physiology and behavior. 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.¹⁸ Economics, political science, and other fields of academic inquiry are slowly adapting their theories to account for these empirical regularities.¹⁹ Territoriality is no exception and, viewed through the lens of evolutionary theory, offers a framework for understanding territorial behavior, in general, as well as sources of variation that help to explain the occurrence of

15. Vasquez, *The War Puzzle Revisited*, p. 155.

16. *Ibid.*

17. *Ibid.*, p. 159.

18. Jerome H. Barkow, *Missing the Revolution: Darwinism for Social Scientists* (Oxford: Oxford University Press, 2006); J. Cartwright, *Human Evolution and Behaviour* (Cambridge: Cambridge University Press, 2000); and Timothy D. Wilson, *Strangers to Ourselves: Discovering the Adaptive Unconscious* (Cambridge, Mass.: Belknap, 2004).

19. John M. Gowdy et al., "Economic Cosmology and the Evolutionary Challenge," *Journal of Economic Behavior and Organization*, Vol. 90, Supp. 1 (June 2013), pp. S11–S20; George A. Akerlof and Robert J. Shiller, *Animal Spirits: How Human Psychology Drives the Economy, and Why It Matters for Global Capitalism* (Princeton, N.J.: Princeton University Press, 2009); R.H. Frank, *The Darwin Economy: Liberty, Competition, and the Common Good* (Princeton, N.J.: Princeton University Press, 2011); Rose McDermott, James H. Fowler, and Oleg Smirnov, "On the Evolutionary Origin of Prospect Theory Preferences," *Journal of Politics*, Vol. 70, No. 2 (April 2008), pp. 335–350; James H. Fowler and Darren Schreiber, "Biology, Politics, and the Emerging Science of Human Nature," *Science*, November 7, 2008, pp. 912–914; and John R. Alford and John R. Hibbing, "The Origin of Politics: An Evolutionary Theory of Political Behavior," *Perspectives on Politics*, Vol. 2, No. 4 (December 2004), pp. 707–723.

territorial aggression in some cases but not others. As with many other human traits, territoriality might be loosely considered not as “hard-wired” but as “soft-wired”—a component of human nature but one that is responsive to prevailing conditions. Power, rational choice, domestic politics, institutions, and culture are of course important as well in explaining territorial conflict,²⁰ but evolutionary biology can provide additional explanatory power.²¹ As Vasquez notes, politics is a critical “intervening variable” even if a tendency toward territorial behavior “is deeply ingrained and is part of humanity’s collective genetic inheritance.”²²

With these earlier insights in mind, this article proceeds as follows. First, we review the powerful role of territory in international conflict. Second, we explore common patterns of territorial behavior across the animal kingdom. Third, we outline work in evolutionary game theory that deals with territorial behavior. Fourth, we set out novel predictions regarding the conditions under which one should expect to see higher or lower levels of territorial conflict. Fifth, we reexamine the decline in territorial conflict since the end of World War II—the so-called post-1945 anomaly—from an evolutionary perspective on territoriality. We conclude with a discussion of theoretical and practical implications of our argument for international politics.

Territorial Behavior in International Relations

The study of territorial behavior and international relations has focused on three broad topics: territory and interstate war; territory and intrastate war; and norms regulating the disposition of territory between states.

TERRITORY AND INTERSTATE WAR

Historically, the desire for territory has been a predominant cause of war. In a study of wars from 1648 to 1989, Kalevi Holsti found that 79 percent involved

20. John A. Vasquez, ed., *What Do We Know About War?* (Lanham, Md.: Rowman and Littlefield, 2012); D. Scott Bennett and Allan C. Stam, *The Behavioral Origins of War* (Ann Arbor: University of Michigan Press, 2004); and Jack S. Levy and William R. Thompson, *Causes of War* (Oxford: Wiley-Blackwell, 2010).

21. For previous efforts drawing on evolutionary approaches to understand war, see Stephen Peter Rosen, *War and Human Nature* (Princeton, N.J.: Princeton University Press, 2004); Bradley A. Thayer, “Bringing in Darwin: Evolutionary Theory, Realism, and International Politics,” *International Security*, Vol. 25, No. 2 (Fall 2000), pp. 124–151; Azar Gat, “So Why Do People Fight? Evolutionary Theory and the Causes of War,” *European Journal of International Relations*, Vol. 15, No. 4 (December 2009), pp. 571–599; and Azar Gat, *War in Human Civilization* (Oxford: Oxford University Press, 2006).

22. Vasquez, *The War Puzzle*, pp. 145, 139.

territorial issues.²³ In the more intensely studied period of 1816 to 2001, territorial issues have been found to represent 29 percent of wars in the Correlates of War (COW) dataset, around a quarter of events in the Militarized Interstate Dispute (MID) dataset, and around half of all those that developed into severe conflicts (i.e., those ending in fatalities or full-scale war).²⁴ A recent reanalysis of the COW data, focusing on what issues gave rise to the initial militarized dispute, rather than the purported aims of the war as a whole, suggests that of the seventy-nine interstate wars between 1816 and 1997, forty-three (54 percent) should be classified as territorial.²⁵ Several studies suggest that explicitly territorial issues are more likely to lead to war than other types of issues, more likely to lead to recurrent conflict, and more likely to result in high fatalities should war occur.²⁶ Other studies have found that, if territorial issues can be resolved, democratization and demilitarization are more likely to ensue.²⁷ Geographic contiguity is one of the best predictors of conflict escalation and interstate war,²⁸ but territorial conflict is not just a spurious correlation driven by the proximity or increased number of interactions among neighboring states. Territorial issues are significantly correlated with conflict in both contiguous and noncontiguous states.²⁹ In addition, there is something special about the notion of “homeland,” in particular. These homeland territories are imbued with historic significance, and their boundedness allows communities of individuals to maintain distinct identities and cultures. These unique properties mean that people and states behave differently in conflicts over home-

23. Kalevi J. Holsti, *Peace and War: Armed Conflicts and International Order, 1648–1989* (New York: Cambridge University Press, 1991); and Paul R. Hensel, “Territory: Geography, Contentious Issues, and World Politics,” in Vasquez, *What Do We Know About War?*, pp. 3–26.

24. Hensel, “Territory: Geography, Contentious Issues, and World Politics”; and Paul R. Hensel, “Territory: Theory and Evidence on Geography and Conflict,” in Vasquez, *What Do We Know About War?* pp. 57–84.

25. John A. Vasquez and Brandon Valeriano, “Classification of Interstate Wars,” *Journal of Politics*, Vol. 72, No. 2 (April 2010), pp. 292–309.

26. J. Vasquez and M.T. Henehan, “Territorial Disputes and the Probability of War, 1816–1992,” *Journal of Peace Research*, Vol. 38, No. 2 (March 2001), pp. 123–138; Vasquez, *The War Puzzle*; Hensel, “Territory: Theory and Evidence on Geography and Conflict”; Toft, *The Geography of Ethnic Violence*; Vasquez, *The War Puzzle Revisited*; Paul Domenic Senese and John A. Vasquez, *The Steps to War: An Empirical Study* (Princeton, N.J.: Princeton University Press, 2008); and Vasquez and Henehan, *Territory, War, and Peace*.

27. Douglas M. Gibler and Jaroslav Tir, “Settled Borders and Regime Type: Democratic Transitions as Consequences of Peaceful Territorial Transfers,” *American Journal of Political Science*, Vol. 54, No. 4 (October 2010), pp. 951–968.

28. Bennett and Stam, *The Behavioral Origins of War*; and Vasquez, *The War Puzzle*.

29. Hensel, “Territory: Theory and Evidence on Geography and Conflict.”

land territories.³⁰ For example, violence is more likely following exchanges of homeland than of colonial territory.³¹

If states were rational actors, options to resolve conflicts short of war should always be available. By enabling potential combatants to avoid the costs of fighting, such options would benefit both winners and losers.³² There are exceptions, of course. Even weaker states may sometimes rationally attack stronger opponents if they expect to prevail using superior strategies, or if they anticipate an improvement in their bargaining position, or a favorable intervention by third parties.³³ If military victory can deliver more than any negotiated solution could, other states may calculate that the benefits of war will exceed the costs.³⁴ Nevertheless, because wars do erupt even where such conditions are absent, they have to be explained in terms of imperfect processes that prevent rational actors from avoiding costly fights.

In "Rationalist Explanations for War," James Fearon highlighted three main obstacles to resolving conflicts short of violence: (1) private information (where actors go to war misperceiving the strengths of the other side); (2) commitment problems (where actors fight because they cannot credibly commit to maintaining a negotiated solution); and (3) indivisible issues, which we expand on here given their relevance to territorial conflict, in particular.³⁵ Indivisible issues arise when the object of contention cannot be divided without diminishing or destroying its value (a monarch cannot be cut in half, for example). Finding it impossible to arrive at a mutually acceptable division, actors turn to war as a rational strategy because the prize is all or nothing.³⁶ Al-

30. Toft, *The Geography of Ethnic Violence*; and Monica Duffy Toft, "Indivisible Territory, Geographic Concentration, and Ethnic War," *Security Studies*, Vol. 12, No. 2 (Winter 2002/03), pp. 82–119.

31. Goertz and Diehl, *Territorial Changes and International Conflict*.

32. James D. Fearon, "Rationalist Explanations for War," *International Organization*, Vol. 49, No. 3 (Summer 1995), pp. 379–414.

33. T.V. Paul, *Asymmetric Conflicts: War Initiation by Weaker Powers* (Cambridge: Cambridge University Press, 1994); John J. Mearsheimer, *The Tragedy of Great Power Politics* (New York: W.W. Norton, 2001); Jonathan D. Kirshner, "Rationalist Explanations for War?" *Security Studies*, Vol. 10, No. 1 (Autumn 2000), pp. 143–150; and Ivan Arreguín-Toft, *How the Weak Win Wars: A Theory of Asymmetric Conflict* (Cambridge: Cambridge University Press, 2005).

34. Mearsheimer, *The Tragedy of Great Power Politics*; Eric J. Labs, "Beyond Victory: Offensive Realism and the Expansion of War Aims," *Security Studies*, Vol. 6, No. 4 (Summer 1997), pp. 1–49; and Peter Liberman, *Does Conquest Pay? The Exploitation of Occupied Industrial Societies* (Princeton, N.J.: Princeton University Press, 1998).

35. Fearon, "Rationalist Explanations for War."

36. See also Monica Duffy Toft, "Issue Indivisibility and Time Horizons as Rationalist Explanations for War," *Security Studies*, Vol. 15, No. 1 (January/March 2006), pp. 34–69; Toft, *The Geography of Ethnic Violence*; and Ron E. Hassner, "The Path to Intractability: Time and the Entrenchment of

though issue indivisibility is acknowledged as theoretically possible, Fearon (and later Robert Powell) downplayed the notion that it accounts for much violence in the real world. The model Fearon developed assumes that the issue at stake can always be made divisible (e.g., through side payments).

In territorial disputes, however, both sides can often view the same location as indivisible; examples include Jerusalem's Temple Mount and al-Aqsa Mosque.³⁷ While critics—especially those favoring formal models as vehicles for illuminating political behavior—tend to argue that territory is intrinsically divisible, scholars of ethnic, national, and civil conflict generally reply that, even where divisibility may be possible in principle, most (if not all) territorial conflict is over land perceived as indivisible.³⁸ This argument reflects the constructivist insight that objects may not possess an obvious or universal meaning; rather, people bring meaning to objects.³⁹ Empirical studies have found, for example, that “otherwise mundane sociopolitical preferences may become sacred values, acquiring immunity to material incentives.”⁴⁰ This phenomenon makes indivisibility a major problem for any analysis of territorial conflict, even if it is a minor problem in other types of war. Rational choice explanations may be describing a world that many of those involved in territorial disputes would not recognize.

In sum, rationalist arguments tend to highlight the role of private information or commitment problems in the causes of wars. In wars over territory, however, the more common obstacle may be indivisibility—whether real or perceived. This is where an evolutionary approach offers an important explan-

Territorial Disputes,” *International Security*, Vol. 31, No. 3 (Winter 2006/07), pp. 107–138. Robert Powell argues that most previous research, following Fearon’s “Rationalist Explanations for War,” has given priority to private information as a cause of war, but that private information explanations fail to account for prolonged wars. Powell also argues that issue indivisibility obstacles should be reframed as commitment problems. See Powell, “War as a Commitment Problem,” *International Organization*, Vol. 60, No. 1 (January 2006), pp. 169–203.

37. Toft, “Issue Indivisibility and Time Horizons as Rationalist Explanations for War.”

38. Ron E. Hassner, “To Halve and to Hold: Conflicts over Sacred Space and the Problem of Indivisibility,” *Security Studies*, Vol. 12, No. 4 (Summer 2003), pp. 1–33; and Toft, “Issue Indivisibility and Time Horizons as Rationalist Explanations for War.” See also 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.

39. On this point, see Alexander Wendt, “Anarchy Is What States Make of It: The Social Construction of Power Politics,” *International Organization*, Vol. 46, No. 2 (Spring 1992), pp. 391–425.

40. Scott Atran and Jeremy Ginges, “Religious and Sacred Imperatives in Human Conflict,” *Science*, May 18, 2012, pp. 855–857, at p. 855; and Scott Atran, Robert Axelrod, and Richard Davis, “Sacred Barriers to Conflict Resolution,” *Science*, August 24, 2007, pp. 1039–1040.

atory role because, as we later argue, humans have a built-in propensity—one that is not wholly subject to standard conceptions of rational calculation—to privilege territory as all-important and indivisible. Although this argument suggests a lower bar for territorial conflict, it also predicts variation depending on local conditions.

TERRITORY AND INTRASTATE WAR

Territory is also an important driver of intrastate war. Civil wars often revolve around the control of material resources, such as oil and diamonds (e.g., Liberia and Sierra Leone).⁴¹ Territory, however, plays a major role in civil wars even where such material resources are not at issue. Modern nationalist movements are often tightly linked to concepts of territory, especially homeland, for a specific, often ethnic, group.⁴² From 1940 to 2000, 73 percent of all ethnic wars centered on the control of territory.⁴³

The topic of intrastate war offers an opportunity to highlight a common connection between territory and group identity. A number of scholars have isolated ethnic and national identity as a major factor in the causes of civil war.⁴⁴ Recall from the start that territoriality across the animal kingdom is not about space per se; rather it is about the defense of resources essential for survival and reproduction. We can draw the same distinction for humans. Apart from

41. James D. Fearon and David D. Laitin, "Ethnicity, Insurgency, and Civil War," *American Political Science Review*, Vol. 97, No. 1 (February 2003), pp. 75–90; Kristian Skrede Gleditsch, "Transnational Dimensions of Civil War," *Journal of Peace Research*, Vol. 44, No. 3 (May 2007), pp. 293–309; James C. Murdoch and Todd Sandler, "Economic Growth, Civil Wars, and Spatial Spillovers," *Journal of Conflict Resolution*, Vol. 46, No. 1 (February 2002), pp. 91–110; Michael Ross, "A Closer Look at Oil, Diamonds, and Civil War," *Annual Review of Political Science*, Vol. 9 (2006), pp. 265–300; Michael Ross, "What Do We Know about Natural Resources and Civil War?" *Journal of Peace Research*, Vol. 41, No. 3 (May 2004), pp. 337–356; Barbara F. Walter and Jack L. Snyder, *Civil Wars, Insecurity, and Intervention* (New York: Columbia University Press, 1999); and James Anderson, "Nationalist Ideology and Territory," in R.J. Johnston, David B. Knight, and Eleonore Kofman, eds., *Nationalism, Self-Determination, and Political Geography* (New York: Croom Helm, 1988), pp. 18–39.

42. A.D. Smith, *The Ethnic Origins of Nations* (Oxford: Blackwell, 1986); and Anderson, "Nationalist Ideology and Territory."

43. Anderson, "Nationalist Ideology and Territory"; Monica Duffy Toft, *Securing the Peace: The Durable Settlement of Civil Wars* (Princeton, N.J.: Princeton University Press, 2009); and Toft, "Issue Indivisibility and Time Horizons as Rationalist Explanations for War."

44. Roger D. Petersen, *Understanding Ethnic Violence: Fear, Hatred, and Resentment in Twentieth-Century Eastern Europe* (Cambridge: Cambridge University Press, 2002); Toft, *The Geography of Ethnic Violence*; and Lars-Erik Cederman, Nils B. Weidmann, and Kristian Skrede Gleditsch, "Horizontal Inequalities and Ethno-Nationalist Civil War: A Global Comparison," *American Political Science Review*, Vol. 105, No. 3 (August 2011), pp. 478–495.

obvious material resources such as water, food, and shelter, a key “resource” that makes territory worth fighting over is its human contents—the family, relatives, friends, allies, and ethnic group to which one belongs. Place of residency is fundamental to ethnic identity. After all, group names are defined by residency (e.g., Serbs in Serbia, Scots in Scotland).⁴⁵ This identity aspect of territoriality is powerfully reinforced by shared history and by in-group/out-group psychology.⁴⁶ Not only does group identity explain people’s attachment to their homeland, but it also constitutes a “nonmaterial” or symbolic factor, which can appear puzzling from a rational choice perspective. This critical interaction between identity and territory may help to explain disagreements in quantitative studies of intrastate war over whether ethnicity matters or not.⁴⁷

TERRITORY IN INTERNATIONAL RELATIONS

The special role of territory is also reflected in the norms that regulate the relations and borders between states. Consider the principle of sovereignty, which affords legitimate control over a given space. Without territory, there would be no sovereign states. As another example, just war theory explicitly cites the invasion of territory as one of the few justifications for war, while Chapter 7 of the United Nations Charter (though rarely invoked) provides for military action in the case of invasion of one country by another.⁴⁸ Conceptions of territory and homeland have also infused norms on human rights and migration.⁴⁹ These phenomena reflect the deep history of statehood and war being primar-

45. Smith, *The Ethnic Origins of Nations*.

46. Susan T. Fiske, “What We Know About Bias and Intergroup Conflict, Problem of the Century,” *Current Directions in Psychological Science*, Vol. 11, No. 4 (August 2002), pp. 123–128; and Henri Tajfel, “Social Identity and Intergroup Behaviour,” *Social Science Information*, Vol. 13, No. 2 (April 1974), pp. 65–93.

47. For studies highlighting the importance of ethnicity, see Cederman, Weidmann, and Gleditsch, “Horizontal Inequalities and Ethno-Nationalist Civil War”; and Toft, *The Geography of Ethnic Violence*. For studies highlighting the nonimportance of ethnicity, see Fearon and Laitin, “Ethnicity, Insurgency, and Civil War”; and Paul Collier, “Doing Well out of War: An Economic Perspective,” in Mats R. Berdal and David M. Malone, eds., *Greed and Grievance: Economic Agendas in Civil Wars* (Boulder, Colo.: Lynne Rienner, 2000), pp. 91–111.

48. Michael Walzer, *Just and Unjust Wars: A Moral Argument with Historical Illustrations* (New York: Basic Books, 2006).

49. Recognition of the degree to which individuals and ethnic and national groups attach identity to territory, and the potential of this attachment to serve as a *casus belli*, led over time to a shift in international law that privileged human attachment to territory. Since 1945, in particular, the forced expulsion or deportation of people from their land and homes has acquired the status of a crime against humanity (a grave breach of convention, equal in gravity to genocide). See, in partic-

ily about the ownership and defense of territory.⁵⁰ As Mark Zacher has argued, the preeminence of state boundaries became further ingrained by the “territorial integrity norm” that developed after the world wars.⁵¹ Scholars have considered this period an anomaly because states have almost ceased to extract territorial concessions after winning wars. The incidence of “state death”—a concept coined by Tanisha Fazal to explain the demise of states—has also declined.⁵² But although territorial conquest may have become rare in interstate wars (it continues unabated within states), the development of the territorial integrity norm itself suggests a strong human preoccupation with territorial borders and their maintenance. Of course, there are other factors at work as well, not least, as liberal theories emphasize, the roles of democracy, trade, and international institutions in the decline of war.⁵³

Whether in terms of interstate war, intrastate war, or the way international relations are organized as a whole, there is something special about territory. It influences individuals, groups, and states to risk an escalation in, and persist with, violence over land more often than over other issues.⁵⁴ We suggest that evolutionary theory offers an explanation for why wars are so tightly linked to territory, why they are especially linked to homeland, and why humans are so concerned with preserving territorial integrity. First, however, we need to understand the patterns and variation in territorial behavior in nature.

Territorial Behavior in Nature

Interest in the biology of territoriality dates to Aristotle and Pliny, both of whom were struck by the strict territorial behavior of birds. It has since

ular, Article 49 of the Fourth Geneva Convention (1949), and Article 7 of the Rome Statute of the International Criminal Court.

50. They also reflect the potential for perceptions of territory itself to affect politics, rather than the other way around. See Jordan Branch, “Mapping the Sovereign State: Technology, Authority, and Systemic Change,” *International Organization*, Vol. 65, No. 1 (January 2011), pp. 1–36.

51. Mark W. Zacher, “The Territorial Integrity Norm: International Boundaries and the Use of Force,” *International Organization*, Vol. 55, No. 2 (March 2001), pp. 215–250.

52. Tanisha M. Fazal, *State Death: The Politics and Geography of Conquest, Occupation, and Annexation* (Princeton, N.J.: Princeton University Press, 2007).

53. Steve Pinker, *The Better Angels of Our Nature: Why Violence Has Declined* (New York: Viking, 2011); John E. Mueller, *The Remnants of War* (Ithaca, N.Y.: Cornell University Press, 2004); and Joseph S. Nye, “Neorealism and Neoliberalism,” *World Politics*, Vol. 40, No. 2 (January 1988), pp. 235–251.

54. Vasquez and Henehan, *Territory, War, and Peace*; and Paul D. Senese, “Geographical Proximity

grown into a core area of research in the natural sciences.⁵⁵ Competition over territory pervades everyday life and activity for many species, with major consequences for survival and reproduction because of its effects on access to resources and mates, dominance hierarchies, subordination, displacement, migration, injury, and death.

Territoriality does not necessarily lead to violence. Indeed, biologists regard it as a mechanism that evolved to avoid violence.⁵⁶ By partitioning living space according to established behavioral conventions, animals can avoid the costs associated with constant fighting. Furthermore, although discussions of territorial behavior tend to focus on aggression, territorial behavior has two distinct components: attack and avoidance. Residents tend to attack in defense of their territory (fight), intruders tend to withdraw (flight). Biologists even note a “dear enemy” phenomenon in some settings, whereby animals recognize the territorial holdings of neighbors and do not fight them.⁵⁷ Most animals, most of the time, manage to resolve territorial conflicts through displays and threats short of fighting. The system is maintained by bouts of interaction that reestablish territorial configurations and ownership as individuals or groups wax or wane in power.

A classic definition of territoriality comes from E.O. Wilson: “an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defense or advertisement.”⁵⁸ Defense is often cited as the core feature, but the form of territorial behavior varies with ecological circumstances. In recent decades, the scientific literature has shifted from a focus on “territories” to “home ranges,” which emphasize frequently used space rather than exclusive areas that are “fenced off” to others. Many animals also use territorial borders to communicate and share information with others (e.g., through scent marking), rather than as defensive barriers to

and Issue Salience: Their Effects on the Escalation of Militarized Interstate Conflict,” *Conflict Management and Peace Science*, Vol. 15, No. 2 (Fall 1996), pp. 133–161.

55. E.O. Wilson, *Sociobiology: The New Synthesis* (Cambridge, Mass.: Belknap, 2000); John R. Krebs and Nicholas B. Davies, *An Introduction to Behavioural Ecology* (Oxford: Blackwell Scientific Publications, 1993); and David McFarland, *Animal Behaviour: Psychobiology, Ethology, and Evolution* (London: Longman, 1999).

56. Wilson, *Sociobiology*; and John Maynard Smith and George R. Price, “The Logic of Animal Conflict,” *Nature*, November 2, 1973, pp. 15–18.

57. Wilson, *Sociobiology*.

58. *Ibid.*, p. 256. For other definitions, see Maher and Lott, “Definitions of Territoriality Used in the Study of Variation in Vertebrate Spacing Systems”; and Kauffmann, “On the Definitions and Functions of Dominance and Territoriality.”

deter them.⁵⁹ Indeed, animals commonly breach territorial boundaries when seeking mates or resources, or when migrating or young animals are dispersing to find territories of their own.⁶⁰

VARIATION IN TERRITORIAL BEHAVIOR

Biology and “behavioral ecology” (a modern approach that compares variation in behavioral strategies across ecological contexts) stress that territoriality is not a universal strategy for all species, all populations of the same species, or even all individuals of the same population. Each may face widely differing ecologies, terrain, competitors, resource distributions, social organization, and life history strategies, and these variations lead to different risk sensitivities and strategies for “optimal foraging.”⁶¹ 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.⁶² Birds offer perhaps the clearest example of this variation. Some species are highly territorial during the breeding season, vigorously excluding rivals from their territory around the clock, only to abandon their territories in the winter—sometimes even leaving for another continent. Empirical studies also find variation over much shorter timescales depending on “economic defendability.”⁶³ For example, Hawaiian honeycreepers are territorial only when food levels are intermediate; they are not territorial when food is either abundant (and there is no need to defend it from others) or scarce (and it is not

59. Roger P. Johnson, “Scent Marking in Mammals,” *Animal Behaviour*, Vol. 21, No. 3 (August 1973), pp. 521–535.

60. Jean Clobert et al., eds., *Dispersal* (Oxford: Oxford, Oxford University Press, 2001).

61. David W. Stephens, Joel S. Brown, and Ronald C. Ydenberg, eds., *Foraging: Behavior and Ecology* (Chicago: University of Chicago Press, 2007); David W. Stephens and John R. Krebs, *Foraging Theory* (Princeton, N.J.: Princeton University Press, 1986); and McDermott, Fowler, and Smirnov, “On the Evolutionary Origin of Prospect Theory Preferences.”

62. Davies, “Mating Systems”; Dyson-Hudson and Smith, “Human Territoriality”; Judy Stamps, “Territorial Behavior: Testing the Assumptions,” *Advances in the Study of Behavior*, Vol. 23 (1994), pp. 173–232; and D.D.P. Johnson et al., “Does the Resource Dispersion Hypothesis Explain Group Living?” *Trends in Ecology and Evolution*, Vol. 17, No. 12 (December 2002), pp. 563–570. Although most territories serve the defense of resources, they may have other uses. Some male antelopes and birds, for example, defend “lek” sites: small territories with little resource value other than being a convenient spot for congregating to attract mates. Several males establish leks in the same area, so that passing females are lured to a “marketplace” of available males. An indirect value thus accrues to otherwise useless territory.

63. Brown, “The Evolution of Diversity in Avian Territorial Systems”; and Frank B. Gill and Larry L. Wolf, “Economics of Feeding Territoriality in the Golden-Winged Sunbird,” *Ecology*, Vol. 56, No. 2 (Early Spring 1975), pp. 333–345.

worth defending).⁶⁴ Studies of human territoriality in preindustrial small-scale societies have identified a similar pattern of ecological variation: human groups defend territories where or when it is economically efficient to do so, and not otherwise.⁶⁵ Some even establish or discard territory altogether with major seasonal changes in resources.

Variation also arises from differences among individuals—for example, in sex and status. Because of fundamental differences in sexual investment,⁶⁶ there are systematic patterns of sex roles in territorial behavior that transcend species (including humans) and time.⁶⁷ In general, males establish and defend territory; they are also more likely than females to fight over it. For example, male lions, which have a different reproductive biology from female lions, may fight to the death over territorial ownership. Male lions typically have only one chance for reproduction in their lifetimes (when they attain the status of alpha male of a pride). Females, by contrast, can reproduce throughout their lifetimes, regardless of who the alpha male is. From a genetic perspective, therefore, males have little to lose in incurring large costs in conflicts with intruders—it may be their last chance to reproduce.⁶⁸ Similar patterns exist across primate species, where territorial behavior is ever-present, but varies with a species' "operational" sex ratio and mating system.⁶⁹

64. F.L. Carpenter and R.E. MacMillen, "Threshold Model of Feeding Territoriality and Test with a Hawaiian Honeycreeper," *Science*, November 5, 1976, pp. 639–642.

65. Dyson-Hudson and Smith, "Human Territoriality"; Elizabeth Cashdan, "Territoriality among Human Foragers: Ecological Models and an Application to Four Bushman Groups," *Current Anthropology*, Vol. 24, No. 1 (February 1983), pp. 47–66; 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 Osborne and N. Parker Van Valkenburgh, eds., *Territoriality in Archaeology* (Washington, D.C.: Archaeological Papers of the American Anthropological Association, in press).

66. Robert L. Trivers, "Parental Investment and Sexual Selection," in Bernard G. Campbell, ed., *Sexual Selection and the Descent of Man* (Chicago: Aldine, 1972), pp. 136–179; and R.V. Short and E. Balaban, eds., *The Differences between the Sexes* (Cambridge: Cambridge University Press, 1994).

67. Richard W. Wrangham and Dale Peterson, *Demonic Males: Apes and the Origins of Human Violence* (London: Bloomsbury, 1996); John Archer, "Does Sexual Selection Explain Human Sex Differences in Aggression?" *Behavioral and Brain Sciences*, Vol. 32, Nos. 3–4 (August 2009), pp. 249–266; Malcolm Potts and Thomas Hayden, *Sex and War: How Biology Explains Warfare and Terrorism and Offers a Path to a Safer World* (Dallas, Tex.: Benbella, 2008); and Kingsley Browne, Co-Ed *Combat: The New Evidence That Women Shouldn't Fight the Nation's Wars* (New York: Sentinel [Penguin], 2007).

68. J. David Bygott, Brian C.R. Bertram, and Jeannette P. Hanby, "Male Lions in Large Coalitions Gain Reproductive Advantage," *Nature*, December 20, 1979, pp. 839–841.

69. Willems, Hellriegel, and Schaik, "The Collective Action Problem in Primate Territory Economics."

COMMON PATTERNS IN TERRITORIAL BEHAVIOR

Territoriality, then, is not uniform irrespective of circumstance—few traits in biology are. But despite considerable variation, the basic phenomenon of territorial behavior is widespread across the animal kingdom. As Wilson notes, nearly all vertebrates “conduct their lives according to precise rules of land tenure.”⁷⁰ Across animal species, territorial behavior has a number of common characteristics: (1) it is most developed in adult males; (2) it operates over a more or less clearly delimited area within which males signal displays of strength and agility to intruders (usually of the same species); (3) the resident male usually wins (or if not, it is the larger individual that does); (4) territorial displays are among the most elaborate of all behaviors in the species’ behavioral repertoire; (5) physical or auditory displays tend to make individuals appear larger and more dangerous; and (6) the competitive exchanges are mostly bluffing, and fighting does not usually result in injury or death.⁷¹

Wilson emphasizes that even where territorial aggression seems rare, territoriality is not absent. Rather, the absence of aggression indicates that rules governing space are not currently being challenged (a testament to their effectiveness). This observation has implications for the role of territoriality in international relations. Wars over territory are not raging all of the time, so one might think that territoriality is usually not an important factor in international politics. Territoriality, however, explains many aspects of peace as well—regulations over seas and airspace, international law, exploitation rights, border security, immigration controls, negotiations and treaties over territory that remain short of war and, not least, the very division of the globe into territorially bounded nation-states in the first place. The world map—even during times of peace—is a picture of human territoriality.

SOURCES OF VARIATION IN TERRITORIALITY IN NATURE

Evolution is useful in identifying common patterns, but its real utility is in explaining sources of variation: that is, it can predict when violence over territory is more or less likely. This allows us to derive novel predictions for international politics. The following sections outline three key mechanisms that explain the conditions under which territorial behavior leads to violence in nature: (1) “resource holding potential” (RHP), which can be equated with

70. Wilson, *Sociobiology*, p. 256.

71. *Ibid.*

military power in international relations; (2) “value asymmetry” (VA), which can be equated with the value that states attach to a given piece of territory; and (3) “economic defensibility” (ED), which can be equated with a rational cost-benefit analysis of the utility of fighting over territory.

RESOURCE HOLDING POTENTIAL: THE ROLE AND LIMITS OF POWER. According to Tacitus, “The gods are on the side of the stronger.” Across the animal world, it is also true that the larger and stronger opponent usually wins.⁷² Conflict outcomes are therefore typically determined by what biologists call “resource holding potential”: the phenotypic qualities that affect performance in a fight (e.g., size and strength).⁷³ Asymmetries are not always obvious at first, and animals often engage in escalated rituals to determine who is stronger, stopping short of actual conflict. They may resort to fighting, however, if neither backs down. Strength is not the only factor though. In contrast to Tacitus, Napoleon claimed that in war, morale is three times as important as physical strength. A smaller army may want to win more, and enjoy greater overall military effectiveness as a result.⁷⁴ The willingness to fight can be decisive in territorial conflicts among animals as well.⁷⁵ For example, when male elephants are in the reproductive state of “musth” (the Hindi word for madness), they have fifty times their normal level of testosterone. They become extremely aggressive and dangerous, systematically defeating much larger elephants.⁷⁶ In this physiological state, which allows them the opportunity to rise to temporary dominance and mate with available females, they are prepared to incur large costs of fighting while non-musth elephants are not. Because they are willing to invest greater energy and risk greater costs in a fight, their combat effectiveness can be higher than would be predicted by their size or strength alone. A similar (though usually less extreme) phenomenon appears across the animal kingdom—at certain times or in certain reproductive states, the cost-benefit ratio of conflict and thus the willingness to fight is not equal among competitors.

72. John Maynard Smith and Geoffrey A. Parker, “The Logic of Asymmetric Contests,” *Animal Behavior*, Vol. 24, No. 1 (February 1976), pp. 159–175.

73. Geoffrey A. Parker, “Assessment Strategy and the Evolution of Fighting Behaviour,” *Journal of Theoretical Biology*, Vol. 47, No. 1 (September 1974), pp. 223–243.

74. Arreguín-Toft, for example, shows that in most asymmetric conflicts (77 percent between 1800 and 2003), the bigger (stronger) actor won. He also argues that weaker actors are more likely to win asymmetric conflicts when they employ counterstrategies that make their material weakness less relevant to the fight. See Arreguín-Toft, *How the Weak Win Wars*.

75. Peter Hammerstein, “The Role of Asymmetries in Animal Contests,” *Animal Behaviour*, Vol. 29, No. 1 (February 1981), pp. 193–205.

76. Joyce H. Poole, “Announcing Intent: The Aggressive State of Musth in African Elephants,” *Animal Behaviour*, Vol. 37, No. 1 (January 1989), pp. 140–152.

This is important because, as we show in the next section, territory itself can affect an individual's willingness to fight, influencing outcomes over and above RHP. In the right circumstances, the weak can win.

VALUE ASYMMETRY: VESTED INTERESTS AND THE PRIMACY OF RESIDENCY. Across the animal kingdom, holders of territory (or "residents") tend to have a higher probability of winning contests, even against stronger intruders. Territoriality is thus heavily influenced by who was there first. This phenomenon has been found across a wide range of taxonomic groups and ecological contexts including butterflies,⁷⁷ damselflies,⁷⁸ spiders,⁷⁹ fish,⁸⁰ salamanders,⁸¹ and birds.⁸² Even in cases in which residents have been absent for an extended period, these residents are more likely to win fights to wrest their territories back from interlopers: one study found that returning male damselflies had a 90 percent chance of regaining their "home" territory from an intruder.⁸³

Value asymmetry proposes that the residents' advantage reflects the greater value (or greater future value) that owners attach to their territory, compared to intruders. Residents have more to lose: their 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. This familiarity helps to account for how residents with lower RHP are able to defeat intruders with higher RHP. Residents are fighting over higher stakes in defending territory they have discovered and held first, offsetting or leveling any power asymmetries. In international relations, the

77. Darrell J. Kemp and Christer Wiklund, "Fighting without Weaponry: A Review of Male-Male Contest Competition in Butterflies," *Behavioral Ecology and Sociobiology*, Vol. 49, No. 6 (May 2001), pp. 429–442; and Nicholas B. Davies, "Territorial Defense in the Speckled Wood Butterfly (*Pararge aegeria*): The Resident Always Wins," *Animal Behavior*, Vol. 26 (1978), pp. 138–147.

78. Jonathan K. Waage, "Confusion over Residency and the Escalation of Damselfly Territorial Disputes," *Animal Behavior*, Vol. 36, No. 2 (April 1988), pp. 586–595.

79. Margaret A. Hodge and George W. Uetz, "A Comparison of Agonistic Behavior of Colonial Web-Building Spiders from Desert and Tropical Habitats," *Animal Behavior*, Vol. 50, No. 4 (1995), pp. 963–972.

80. Jorgen I. Johnsson and Annica Forser, "Residence Duration Influences the Outcome of Territorial Conflicts in Brown Trout (*Salmo Trutta*)," *Behavioral Ecology and Sociobiology*, Vol. 51, No. 3 (February 2002), pp. 282–286.

81. Alicia Mathis, David W. Schmidt, and Kimberly A. Medley, "The Influence of Residency Status on Agonistic Behavior of Male and Female Ozark Zigzag Salamanders *Plethodon Angusticlavus*," *American Midland Naturalist*, Vol. 143, No. 1 (January 2000), pp. 245–249.

82. John R. Krebs, "Territorial Defense in the Great Tit (*Parus Major*): Do Residents Always Win?" *Behavioral Ecology and Sociobiology*, Vol. 11, No. 3 (1982), pp. 185–194; and J. Tobias, "Asymmetric Territorial Costs in the European Robin: The Role of Settlement Costs," *Animal Behavior*, Vol. 54, No. 1 (July 1997), pp. 9–21.

83. Robin R. Baker, "Insect Territoriality," *Annual Review of Entomology*, Vol. 28 (1983), pp. 65–89.

structure of this situation is analogous to Andrew Mack's idea of "interest asymmetry" in explaining why weaker, local insurgencies can defeat stronger, foreign opponents.⁸⁴

VA also has a capability component. Territories have particular terrain, vegetation, paths, dangers, and escape routes with which long-time residents are familiar, unlike interlopers. On home ground, therefore, residents may be more effective fighters than nonresidents beyond any difference in RHP or the stakes involved.

In sum, territorial incumbency and familiarity give residents important advantages over intruders. Natural selection may thus have encoded the strategic logic of value asymmetry into proximate mechanisms that spur an organism to fight harder or longer over home territory. The evolution of territorial behavior, in fact, offers a novel theoretical foundation for well-documented biases in human judgment and decisionmaking that value and maintain what we already have. These biases include "loss aversion" (the preference for avoiding losses over acquiring equivalent gains), the "endowment effect" (valuing the same item more than one would do otherwise simply because one owns it), the "status quo bias" (a preference to maintain what is already in place), and "prospect theory" itself (a tendency to be risk averse in the domain of gains, but risk prone in the domain of losses).⁸⁵ From an economic rational choice perspective, such biases are puzzling and tend to be attributed to errors or constraints of human cognition. But from an evolutionary perspective, they make perfect sense as design features with "ecological rationality," maximizing benefits over costs in the environment in which they evolved.⁸⁶ Although

84. Andrew J.R. Mack, "Why Big Nations Lose Small Wars: The Politics of Asymmetric Conflict," *World Politics*, Vol. 27, No. 2 (January 1975), pp. 175–200.

85. Daniel Kahneman and Amos Tversky, "Choices, Values, and Frames," *American Psychologist*, Vol. 39, No. 4 (April 1984), pp. 341–350; Daniel Kahneman and Amos Tversky, "Prospect Theory: An Analysis of Decisions under Risk," *Econometrica*, Vol. 47, No. 2 (March 1979), pp. 263–291; Richard H. Thaler, *The Winner's Curse* (Princeton, N.J.: Princeton University Press, 1992); William Samuelson and Richard Zeckhauser, "Status Quo Bias in Decision Making," *Journal of Risk and Uncertainty*, Vol. 1, No. 1 (March 1988), pp. 7–59; Rose McDermott, "Prospect Theory in Political Science: Gains and Losses from the First Decade," *Political Psychology*, Vol. 25, No. 2 (April 2004), pp. 289–312; and Rose McDermott, *Risk-Taking in International Politics: Prospect Theory in American Foreign Policy* (Ann Arbor: University of Michigan Press, 1998). These are powerful and deep-seated effects, such that people tend to value losses around twice as highly as gains of the same magnitude.

86. Leda Cosmides and John Tooby, "Better Than Rational: Evolutionary Psychology and the Invisible Hand," *American Economic Review*, Vol. 84, No. 2 (May 1994), pp. 327–332; McDermott, Fowler, and Smirnov, "On the Evolutionary Origin of Prospect Theory Preferences"; Gerd Gigerenzer, *Gut Feelings: The Intelligence of the Unconscious* (New York: Viking, 2007); and Wilson, *Strangers to Ourselves*.

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. A strong attachment to a "homeland," in particular, may exacerbate aggression against intruders, because residents are relatively insensitive to the (modern) costs of fighting or the possibility of losing.

ECONOMIC DEFENSIBILITY. Early work on territorial behavior in animals recognized that despite its benefits, territoriality can be costly in terms of time, energy, and the risk of injury.⁸⁷ Therefore, we should expect natural selection to favor territorial defense only where and when the benefits exceed the costs. This is the principle of "economic defensibility." Subsequent work has sought to identify sources of variation that alter defensibility—most important, the spatial and temporal distribution of resources.⁸⁸ Resources can be more effectively defended if they are close together and the patterns of their availability (e.g., timing and location) are predictable. In such settings, territoriality pays greater dividends. Critically, this is not just a predetermined given of the local environment. Different capabilities of the actors involved can affect the efficiency of resource exploitation and thus the economics of resource defense (in the case of humans, this may include variation in levels of cooperation, technology, or institutions).⁸⁹ Numerous experiments have demonstrated that economic defensibility underlies variation in territorial behavior in a range of animal species. The reason this simple but powerful idea is so important here is that it emphasizes that evolved territorial behavior can be flexible. Humans and animals have a baseline proclivity toward territoriality, but variable outcomes are still possible beyond this baseline given prevailing costs, benefits, and capabilities. As such, an evolutionary model of territoriality can explain variation in behavior across space and across time. Benjamin Chabot-Hanowell and Eric Alden Smith give a range of empirical examples of how human territorial behavior changed with shifting costs and benefits of resource defense, and changing capabilities to extract those resources from the land.⁹⁰ Evolution is less an alternative to economics than an example of it.⁹¹

87. Brown, "The Evolution of Diversity in Avian Territorial Systems"; Dyson-Hudson and Smith, "Human Territoriality"; and Nicholas B. Davies, John R. Krebs, and Stuart A. West, *An Introduction to Behavioural Ecology* (Chichester, U.K.: Wiley-Blackwell, 2012).

88. Dyson-Hudson and Smith, "Human Territoriality."

89. Chabot-Hanowell and Smith, "Territorial and Non-Territorial Routes to Power."

90. *Ibid.*

91. Geerat J. Vermeij, *Nature: An Economic History* (Princeton, N.J.: Princeton University Press, 2004).

So far we have introduced a number of mechanisms that explain the relationship between territoriality and conflict in humans and other species. The next step is to use this information to develop predictions for the onset of violence.

Territorial Behavior in Evolutionary Game Theory

John Maynard Smith pioneered the use of evolutionary game theory in the analysis of behavior, an approach now routinely used in biology, economics, and other disciplines.⁹² Standard game theory is static, examining the one-off or short-term behavior of agents under fixed conditions.⁹³ In contrast, evolutionary game theory allows for alternative strategies to compete with each other over multiple rounds of interaction, determining which strategies come to dominate in the population as a whole as a function of their relative success. Robert Axelrod used this method to great acclaim in his work on the evolution of cooperation.⁹⁴

What may be less well known is that some of the earliest (and best) work on evolutionary game theory derives from the study of territorial behavior among animals.⁹⁵ Curious about the empirical finding that territory residents tend to win fights, Maynard Smith developed the famous “hawk-dove game” to examine the relative costs and benefits of alternative territorial behaviors. As outlined in figure 1, players adopt one of two strategies: “hawks” attack and keep fighting until they win, or until they sustain significant injury; “doves” only display, and retreat if attacked.

92. John Maynard Smith, *Evolution and the Theory of Games* (Cambridge: Cambridge University Press, 1982); Jörgen W. Weibull, *Evolutionary Game Theory* (Cambridge, Mass.: MIT Press, 1995); and Martin A. Nowak, *Evolutionary Dynamics: Exploring the Equations of Life* (Cambridge, Mass.: Belknap, 2006).

93. Steven J. Brams, *Theory of Moves* (Cambridge: Cambridge University Press, 1993).

94. Robert Axelrod, *The Evolution of Cooperation* (London: Penguin, 1984). Many aspects of Axelrod’s approach have since come under scrutiny, but evolutionary game theory (along with empirical testing) remains a dominant methodological paradigm. See, for example, Weibull, *Evolutionary Game Theory*; Nowak, *Evolutionary Dynamics*; and Martin A. Nowak, “Five Rules for the Evolution of Cooperation,” *Science*, December 8, 2006, pp. 1560–1563.

95. Smith, *Evolution and the Theory of Games*; Smith and Parker, “The Logic of Asymmetric Contests”; and Smith and Price, “The Logic of Animal Conflict.” The literature on animal fighting prior to Smith’s work focused on two forms of “contest”: (1) signaling, and (2) actual fighting. This distinction drove the literature, because many animals rarely engage in lethal fighting, despite having lethal weapons. Smith’s original idea was to explore how animals could have evolved restraint via individual selection, in contrast to a then widely accepted, but naïve, group-selectionist view that the avoidance of fighting evolved “for the good of the species.”

Figure 1. Payoffs for Actors and Opponents in the Hawk-Dove Game

		opponent	
		hawk	dove
actor	hawk	$(V - D) / 2$	V
	dove	0	$V / 2$

SOURCES: John Maynard Smith, *Evolution and the Theory of Games* (Cambridge: Cambridge University Press, 1982); John Maynard Smith, and Geoffrey A. Parker, "The Logic of Asymmetric Contests," *Animal Behavior*, Vol. 24 (1976), pp. 159–175; and John Maynard Smith, and George R. Price, "The Logic of Animal Conflict," *Nature*, Vol. 246 (1973), pp. 15–18.

NOTE: The cells show the payoffs to the "actor" (row player), where V is the benefit of winning and D is cost of injury.

The results of the hawk-dove game are a little involved, but are worth working through, as they generate interesting predictions (summarized in table 1). As in figure 1, initial models assumed that payoffs are symmetric for each player. Under this assumption, if the benefits of winning exceed the costs of conflict ($V > D$), playing hawk is a pure "evolutionarily stable strategy" (ESS) and animals should always fight (an ESS refers to a strategy that cannot be outcompeted by any alternative strategy; in this case, doves cannot invade a population of hawks, but hawks can invade a population of doves, because doves always lose to hawks). If a significant fraction of lifetime reproductive success is at stake ($V \gg D$), animals should fight to the death—as occurs in some animals, including among mammals such as lions. If the costs of conflict exceed the benefits of winning ($D > V$), however, then doves can invade a population of hawks, but they do not eradicate them. Instead, what emerges is a mixed ESS to play hawk with probability p and dove with probability $1 - p$ (which can be manifested either by individuals playing hawk with a given probability p , or by the population being composed of p hawks).

Subsequent development of the hawk-dove game looked at asymmetric contests, where payoffs for alternative strategies differ for each player. Contests may be asymmetric because of "correlated asymmetries," in which asymmetries are related to the likelihood of winning (such as different strengths or val-

Table 1. Predictions for Territorial Aggression Derived from the Hawk-Dove Game in Evolutionary Game Theory

#	Conditions		Evolutionarily Stable Strategy	Predicted Behavior
1	$V > D$	symmetric or asymmetric payoffs	hawk	territorial aggression (all actors should fight)
2	$V \gg D$		hawk	lethal territorial aggression (all actors should fight to the death)
3	$D > V$	symmetric payoffs		some territorial aggression (actors may or may not fight)
4		asymmetric payoffs	correlated asymmetries	stronger actors play hawk; weaker actors play dove
5			uncorrelated asymmetries	territorial incumbents play hawk; intruders play dove

NOTE: V is the benefit of winning and D is the cost of conflict.

ues attached to the resource), or “uncorrelated asymmetries,” in which asymmetries ought not, on the face of it, to be related to the likelihood of winning (e.g., a difference in “role” such as resident vs. intruder).

In all such asymmetric contests, if $V > D$, animals should always play pure hawk, whatever asymmetries exist (the same outcome as in the symmetric game). If $D > V$, however, then the outcome depends on the type of asymmetry—whether it is a correlated or uncorrelated asymmetry.⁹⁶

Correlated asymmetries lead to two possible outcomes: (1) a “common-

96. Smith and Parker, “The Logic of Asymmetric Contests.”

sense" outcome (e.g., the bigger or hungrier animal wins), which is always an ESS irrespective of the magnitude of the asymmetry; or (2) a "paradoxical" outcome (e.g., the bigger or hungrier animal loses), which, as long as the asymmetry is small, can also be an ESS in theory (because although stronger animals lose some fights, all animals avoid the costs of conflict). Paradoxical outcomes are nevertheless thought to be rare in nature.

Uncorrelated asymmetries lead to a pure ESS, which Maynard Smith called the "bourgeois" strategy.⁹⁷ The bourgeois strategy is to behave like a hawk and defend aggressively if one is first into a territory (an incumbent), but to behave like a dove and withdraw if one is an invader. This results in a system in which the costs of fighting are avoided by a simple behavioral convention that favors incumbents, concordant with the widespread empirical observation that territory residents tend to win.⁹⁸

Maynard Smith and others agreed that in the real world most conflicts are likely to be asymmetric, at least to some small degree, and that the ESS in asymmetric contests will allow a cue of this asymmetry (e.g., strength, or resident vs. intruder status) to settle the contest without escalation.⁹⁹ Empirical studies support this conclusion: individuals usually identify and respect significant asymmetries, whereas escalation is much more likely when individuals are (or perceive themselves to be) equally matched, a finding most strikingly demonstrated in experiments with animals fighting their reflection in mirrors.¹⁰⁰

Subsequent literature shows that wherever fighting is costly, information exchange about payoff asymmetries should be favored by both parties. Contests should escalate gradually so that opponents can detect asymmetries before serious injuries are sustained.¹⁰¹ Other studies examine the effects of

97. Maynard Smith, *Evolution and the Theory of Games*. Reinhard Selten subsequently showed the general result that mixed ESSs cannot be evolutionarily stable in asymmetric settings. Instead there is a pure ESS in which only one strategy is played. See Selten, "A Note on Evolutionarily Stable Strategies in Asymmetrical Animal Conflicts," *Journal of Theoretical Biology*, Vol. 84, No. 1 (May 1980), pp. 93–101.

98. Peter Hammerstein examined what happens when there is more than one asymmetry at a time (e.g., different fighting ability and differing owner status). He showed that if $D > V$, conflicts can still be settled by payoff-irrelevant factors (e.g., territory ownership), even if there are differences in fighting ability. See Hammerstein, "The Role of Asymmetries in Animal Contests."

99. Smith and Parker, "The Logic of Asymmetric Contests"; and Parker, "Assessment Strategy and the Evolution of Fighting Behaviour."

100. Parker, "Assessment Strategy and the Evolution of Fighting Behaviour."

101. Magnus Enquist and Olof Leimar, "Evolution of Fighting Behaviour: Decision Rules and Assessment of Relative Strength," *Journal of Theoretical Biology*, Vol. 102, No. 3 (June 1983), pp. 387–410.

variation in resources and find that, as competition becomes more intense, the hawk strategy becomes increasingly dominant, resulting in more aggression and more lethal conflicts.¹⁰²

Despite these powerful insights, the Maynard Smith model did not explain why the rule should be that incumbents always win. The same model could result in a stable strategy in which invaders always win (the so-called anti-bourgeois strategy). Whichever “convention” is adopted, the costs of fighting are avoided. One solution to this problem is that, as we suggested in the value asymmetry section, territory holders enjoy an intrinsic combat advantage, such as familiarity with the terrain or relations with local kin or allies, that increases their probability of winning a fight upon it. This dynamic may be especially important in modern human conflict, because in many contexts there is an intrinsic defensive advantage in the offense-defense balance.¹⁰³ Evolutionary theorists, however, noted that such advantages were not always present in many empirical examples in nature, and thus renewed the search for a more general explanation. Economist Herbert Gintis made an important advance in his development of the hawk-dove game to explore the evolutionary origins of private property. Gintis expanded the game’s logic to show that as long as there is some (even minor) cost of transfer of territory ownership incurred by the intruder, then it is the incumbent strategy—where the resident always wins—that is the ESS.¹⁰⁴ His model identified three important conditions for a private property equilibrium (i.e., where ownership is not challenged and conflict is therefore avoided): (1) combatants are able to exact great harm; (2) migration costs are high; and (3) the issue at stake is not too valuable.

Despite its obvious simplification of reality, game theory distills strategic decisions down to their essence and generates predictions that international relations scholars can test. In addition, the models outlined have been heavily studied, scrutinized over several decades, and replicated in other disciplines. We can therefore be confident of their robustness.

102. Alasdair I. Houston and John M. McNamara, “Fighting for Food: A Dynamic Version of the Hawk-Dove Game,” *Evolutionary Ecology*, Vol. 2, No. 1 (January 1988), pp. 51–64. For further and more recent explorations of the hawk-dove game, see also Philip H. Crowley, “Hawks, Doves, and Mixed-Symmetry Games,” *Journal of Theoretical Biology*, Vol. 204, No. 4 (June 2000), pp. 543–563; and D.D.P. Johnson and James H. Fowler, “The Evolution of Overconfidence,” *Nature*, September 15, 2011, pp. 317–320.

103. Stephen Van Evera, “Offense, Defense, and the Causes of War,” *International Security*, Vol. 22, No. 4 (Spring 1998), pp. 5–43; and John J. Mearsheimer, “Assessing the Conventional Balance: The 3:1 Rule and Its Critics,” *International Security*, Vol. 13, No. 4 (Spring 1989), pp. 54–89.

104. Herb Gintis, “The Evolution of Private Property,” *Journal of Economic Behavior and Organization*, Vol. 64, No. 1 (2007), pp. 1–16.

New Predictions for Territorial Conflict in International Relations

We do not doubt that conventional explanations such as rational choice, misperceptions, or domestic politics may play a role in the causes of conflict, including wars over territory. We suggest, however, that a missing contributory factor is humans' evolutionary legacy of territoriality. Behavior that evolved under the prevailing costs and benefits of territoriality in our ancestral environment set a low bar for territorial aggression (we tend to defend territory aggressively), but it alters our territorial aggression beyond this baseline depending on perceived (not necessarily actual) costs and benefits. Territorial behavior is not a "fixed" or "hard-wired" response but, in line with a modern understanding of human biology, is more akin to a "soft-wiring" of behavior that permits flexibility with local conditions. This is important because, if territorial behavior never varied, it could not explain variation in peace and war. Rather, our evolutionary approach stresses that while territorial behavior is a universal trait, territorial aggression is contingent and depends on environmental conditions—namely, the prevailing cost-benefit ratios involved in fighting for territory.

As outlined above, evolutionary game theory has been useful in identifying general, qualitative predictions for which territorial strategies are likely to emerge under different conditions. There are reasons to believe that behaving as a "hawk" (behaving aggressively over territory) evolved as an adaptive strategy for territory holders. Wherever the prize at stake exceeds the costs of conflict ($V > D$), hawk is the evolutionarily stable strategy and cannot be trumped by any other strategy. This is the case whether payoffs are symmetric or asymmetric. More remarkably, however, even when the costs of conflict exceed the prize at stake ($D > V$), hawk still emerges as the dominant strategy under certain conditions—and these conditions are not restrictive. As Gintis shows, any minor costs associated with the transfer of territory make hawk the most effective strategy for territorial incumbents.¹⁰⁵ We make the additional argument that intrinsic combat advantages also make hawk a better strategy for territorial incumbents. In short, territorial aggression—hawk—is a strategy we should expect to have evolved even if (or perhaps because) fighting is costly.¹⁰⁶

105. *Ibid.*

106. This dominance of hawkishness appears to be remarkably mirrored in human cognition. Nobel laureate Daniel Kahneman remarked: "The bottom line is that all the biases in judgment that

Evolutionary game theory is general and simplified, but it is useful because it leads to straightforward predictions that can be tested in the real world. The main prediction is that agents who are (or perceive themselves to be) territory owners will act like hawks—a strategy that may have been generally adaptive in the past but is often counterproductive today, especially where perceptions of prior residency have been manipulated or blurred in history. Territory holders are therefore especially likely to adopt hawkish strategies, responding aggressively to threats, provocation, or incursion. Moreover, if this is an evolved strategy, territorial aggression may be triggered by proximate mechanisms irrespective of the value of the land, the costs of conflict, or the probability of victory. Where both sides perceive themselves to be the territory resident, the problem looms especially large because each side may expect to win and expect the other side to back down, somewhat regardless of size and strength. Manipulation experiments in biology show that when two individuals are tricked into believing a particular territory belongs to both of them, fighting can be especially intense.¹⁰⁷ Claims to land by more than one group are therefore expected to be more likely to lead to bloody and prolonged conflict. In such settings, the hawk-dove logic (a system that in equilibrium avoids the costs of fighting) breaks down and conflict can escalate despite rising costs, declining benefits, and likely defeat. This may help to explain enduring rivalries over such territories as Kashmir and Jerusalem.

We can derive finer-grained predictions from Gintis's work as well. The conditions for a private property equilibrium lead to the prediction that, even in a system in which territory ownership is generally accepted, territorial aggression is more likely when states (1) underestimate the costs of conflict (e.g., the false optimism often witnessed on the eve of war); (2) feel cornered or see alternatives as being worse (e.g., preventive/preemptive wars); or (3) contest sites of significant ethnic and cultural importance (e.g., conflicts over sacred land). This helps to explain why there can be a change in territorial aggression when the costs and benefits of the prevailing environment changes, or the perceptions of those costs and benefits change. These changes might occur within

have been identified in the last 15 years tend to bias decision-making toward the hawkish side." See Kahneman, quoted in Christopher Shea, "The Power of Positive Illusions," *Boston Globe*, September 26, 2004. Moreover, Kahneman and Jonathan Renshon suggest that leaders, whatever their own perceptions, tend to more readily accept the recommendations of hawkish rather than dovish advisers. See Kahneman and Renshon, "Why Hawks Win," *Foreign Policy*, December 27, 2006, pp. 34–38.

107. Davies, "Territorial Defense in the Speckled Wood Butterfly (*Pararge Aegeria*)."

a given dispute, or within the international system as a whole—an empirical phenomenon that we turn to in the next section.

The Post–World War II Anomaly: Why No More Conquest?

The so-called territorial integrity norm observed in international relations may seem to cast doubt on our thesis. At least since World War II, even when states are victorious in war, they appear to have largely decided not to annex others' territory.¹⁰⁸ States have also been much less likely to be subsumed by other states.¹⁰⁹ The reasons proposed for this norm, however—fear of sparking a major or nuclear war, interdependence and democracy (among developed nations), and military weakness and fear of internal disorder (among developing nations)—all constitute reasons why war in general has declined. An overall decline in war does not mean that human territoriality has vanished, or changed. On the contrary, the strong international concern to preserve existing state boundaries is itself evidence of a robust human penchant for territoriality. The development of international institutions and international law to protect these boundaries has benefited many states, locking in place their most important territorial possessions and reducing the threat of predation from other states.

Accepting this norm does not necessarily mean that states no longer “desire” territory, or that the costs of fighting wars to obtain it are too high, but rather that there are increasing costs of “owning” territory. The rise of nationalism in the last two centuries—itself a phenomenon in which groups of humans assert a strong attachment to a given territory to gain sovereignty over it—has made expansion into new territory militarily, economically, and politically costly.¹¹⁰ The advance of a new norm, in which national aspirations changed from facing down threats to monarchical power in multinational states, to a globalized principle of self-determination and legitimacy, meant that—all else equal—the costs of administration of conquered territories containing nationalist groups were bound to rise relative to the benefits one might have traditionally expected from conquest. Territoriality does not falter in the face of the territorial integrity norm; it helps to explain it. Furthermore, the scope, pace,

108. Zacher, “The Territorial Integrity Norm.”

109. Fazal, *State Death*. On how territorial conflict has changed over time, see also Gat, “So Why Do People Fight?”; and Gat, *War in Human Civilization*.

110. Robert Mandel, *The Meaning of Military Victory* (Boulder, Colo.: Lynne Rienner, 2006).

and success of decolonization following World War II is difficult to understand absent this attachment to territory. The territorial integrity norm is like a peaceful woodland in late spring, with birds already having established their territories and singing to advertise them. This equilibrium is hardly a denial of territorial behavior—it is a consequence of it. The game theoretical models introduced earlier specifically focused on how territoriality—when in equilibrium—serves to avoid conflict in the system as a whole, especially in a world where the costs of conflict can be high, such as with the advent of nuclear weapons after 1945.

Beyond war, territorial conflict can be seen at work in the post-1945 period in other areas in international relations, where it continues unabated: (1) within states (where rules of sovereignty do not apply); (2) in contested regions (where there is no accepted owner); and (3) in newly available territory (where equilibrium has not been reached). With respect to the first of these other domains, nearly all civil wars and ethnic conflicts raging within states around the world have territorial control as a central cause and goal of violence. Moreover, data suggest that lasting peace may depend on military conquest, as peaceful settlements often mean territorial disputes just linger and resurface later.¹¹¹ As for contested regions, the territorial integrity norm is largely a Western phenomenon. Elsewhere in the world, interstate conflict (if not war) over territory continues, from Kashmir and Israel/Palestine to the Falklands and the South China Sea. Third, while the “territorial integrity norm” appears to be suppressing territorial expansion among states (at least for now), territory remains central to international politics and trade. States (as well as other international entities) are engaged in new conflicts over political and commercial control and use of land, ownership of the Antarctic, the Arctic Ocean floor, outer space and near-Earth orbits, mobile phone frequency bands, undersea cables, and internet domains.¹¹² If territoriality is dying out in its literal form, we are seeing it reappear in others. These are not examples of “territory” in the traditional sense, but they may activate the same proximate mechanisms underlying the desire for control over spatially distributed resources, leading to similar patterns of behavior.

111. Toft, *Securing the Peace*; Edward N. Luttwak, *Strategy: The Logic of War and Peace* (Cambridge, Mass.: Belknap, 2001); and Monica Duffy Toft, “Ending Civil Wars: A Case for Rebel Victory?” *International Security*, Vol. 34, No. 4 (Spring 2010), pp. 7–36.

112. Fred Pearce, *The Landgrabbers: The New Fight over Who Owns the Earth* (Boston: Beacon, 2012); and “Antarctic Treaty Is Cold Comfort,” editorial, *Nature*, January 19, 2012, p. 237.

Conclusion

International relations theory offers a host of explanations for why states fight over territory that contains valuable resources (whether economic or strategic). Yet it fails to account for the recurrent and severe costs that individuals, groups, and states are prepared to accept in conflict over land, especially when such territory has little or no economic or strategic value. Evolutionary biology offers a novel and unique explanation for this behavior, and reveals that, first, territorial behavior is common across primates, mammals, and numerous other taxa, suggesting a convergent solution to a common strategic problem; second, territorial behavior reflects a dominant strategy in the hawk-dove game of evolutionary game theory (under certain well-defined conditions); and third, territorial behavior follows a strategic logic, but one calibrated to cost-benefit ratios that prevailed in humans' evolutionary past, not those of the present. What these insights also reveal is that human territorial behavior is universal while territorial aggression is contingent.

If an evolutionary history of competition for spatially distributed resources led humans to develop a tendency to pursue violent strategies over territory, these tendencies may persist today, even if such behavior no longer brings material payoffs. Such inertia is to be expected because human behavioral adaptations are millions of years old, whereas large, urbanized populations and nation-states are comparatively recent. "Mismatches" between evolved behavior and the evolutionarily recent physical, social, and political world in which we live today are commonplace and often lead to costly behaviors that are puzzling for approaches based on rational choice (such as addictions or bad diets).¹¹³ The eminent evolutionary biologist Theodosius Dobzhansky once declared, "Nothing in biology makes sense except in the light of evolution." Inasmuch as humans are biological organisms, an evolutionary perspective sheds considerable new light on human territorial aggression. It is not the whole story, of course, but it offers important and neglected insights.

In this article, we have stressed the variability of territorial behavior, which changes to maximize utility in different contexts. There is no guarantee, how-

113. Robert Wright, *The Moral Animal: Why We Are the Way We Are: The New Science of Evolutionary Psychology* (New York: Random House, 1994); Steven Pinker, *The Blank Slate: The Modern Denial of Human Nature* (New York: Penguin Putnam, 2002); and Terence C. Burnham, *Mean Markets and Lizard Brains: How to Profit from the New Science of Irrationality* (New York: John Wiley and Sons, 2005).

ever, that the cognitive mechanisms that evaluate this utility will be accurate. Moreover, they may be especially susceptible to misperceptions and cognitive constraints in the large-scale and complex context of international conflict. Even if human territorial behavior is adaptable, it may be a crude instrument in today's world. For this reason, when the cost-benefit ratio of territorial conflict exceeds that of the evolutionary environment in which human territorial behavior has evolved, territorial dispositions may compel humans to fight, even when conditions are unfavorable. When the cost-benefit ratio of territorial conflict falls below that of the evolutionary environment in which our territorial behavior evolved, territorial dispositions may make humans less aggressive and more vulnerable to exploitation. When the cost-benefit ratio is similar to that of our past, then territorial dispositions may continue to pay dividends. Who can deny that a strong attachment to homeland helped Vietnamese nationalists to persist and ultimately defeat both France and the United States, despite enormous costs and decades of commitment?¹¹⁴ Or helped poorly armed Afghan insurgents defeat the might of the Soviet Union? Or helped George Washington and his improvised army defeat Britain, the superpower of the day, in the War of Independence?

Although our evolutionary legacy suggests that humans may have a low bar for territorial aggression, we are not insensitive to changing costs and benefits. Indeed, as we have shown, flexibility in territorial behavior is common across the animal kingdom, and this flexibility is itself adaptive. Flexible territorial strategies would have outcompeted inflexible territorial strategies in the economic mill of natural selection. An evolutionary approach therefore also makes more specific predictions about the likelihood of territorial aggression and highlights that territorial aggression is not always the best strategy. The economic defensibility principle reflects the finding that territorial behavior is flexible among a variety of animals, as they adjust their behavior to changing costs and benefits of defending resources. Furthermore, evolutionary game theory shows that hawks tend to win in certain contexts but not in others. Hawks dominate wherever the benefits of winning exceed the costs ($V > D$). Where the costs of conflict exceed the benefits ($D > V$), an equilibrium occurs (i.e., ownership is not challenged), as long as (1) combatants are able to exact great harm; (2) migration costs are high; and (3) the issue at stake is not too valuable. These findings lead to predictions for the likelihood of war in the in-

114. See, for example, Walker Connor, "Nation-Building or Nation-Destroying?" *World Politics*, Vol. 24, No. 3 (April 1972), pp. 319–355.

ternational system as a whole. Territorial aggression should increase when there is an offensive advantage (e.g., novel weapons or military hegemony), unclaimed or disputed territory (e.g., Antarctica, space, Jerusalem, and Kashmir), and issues of extreme value (e.g., ethnic homeland or religious sites). By contrast, territorial aggression should decline when war is costly (e.g., when states have nuclear weapons), when territory elsewhere is already claimed (e.g., after colonization), and when territory has little intrinsic value (e.g., lacks natural resources or is costly to occupy).

The post–World War II “anomaly” is that states no longer appear to extract territorial concessions after war. This suggests a challenge for our theory. In the contemporary era, states have ceased seizing territory, meaning that territorial conquest is not only conspicuously absent (at least in interstate conflict), but also that it has changed over time (seizing territory in the past but not doing so today). In fact, an evolutionary account of human territoriality is perfectly consistent with both of these phenomena. Territoriality, like most human traits, is not a blind strategy that works irrespective of circumstances. Chimpanzees withdraw if they are outnumbered, and birds abandon territory if it becomes too costly to defend. It should therefore be no surprise that humans are less likely to claim territory if the political, military, or economic costs are (or seem) too high. The shift after World War II reflects a change in this strategic calculus. Human decisionmaking mechanisms need not have changed, but they are being fed new informational inputs on a changing cost-benefit ratio. The world before 1939 had all the ingredients for territorial war described above, at least among great powers: offensive advantages, unclaimed territory, and valuable resources to be seized. After 1945 the world has featured defensive advantages (especially with nuclear weapons), the gradual partitioning of the globe into self-determined territories, and resources that can no longer be easily seized, held, or exploited. The post–World War II anomaly is no more a challenge to the idea of evolved human territoriality than the changing distribution of flowers is for Hawaiian honeycreepers: just as honeycreepers engage contingent strategies, so too do humans.¹¹⁵

There is no shortage of examples from any era of history to show how easily periods of peace can succumb to the more vicious features of human behavior. As Robert Ardrey argued in *The Territorial Imperative*, “Civilization lacks nothing in its imitation of nature; what it lacks, and lacks only, is its recognition of

115. Carpenter and MacMillen, “Threshold Model of Feeding Territoriality and Test with a Hawaiian Honeycreeper.”

man as an animal.”¹¹⁶ What has changed since Ardrey’s time is our appreciation of significant behavioral variation as an integral aspect of animal, and human, nature. Natural selection favors behavior that is flexible and can adjust to the local ecology, leading to lax territorial concerns in some contexts but violent territorial aggression in others. The optimistic insight this offers is that human nature does not ineluctably lead to war, and if we can change the environment in the right ways, territorial aggression should decline. The sooner we begin to understand when and where humans are more likely to seek control over territory, the better we may be able to prevent people killing to achieve it.

116. Ardrey, *The Territorial Imperative*.