

UC Riverside

Cliodynamics

Title

Bringing “Geo” Back into Politics: Evolution, Territoriality and the Contest over Ukraine

Permalink

<https://escholarship.org/uc/item/59536683>

Journal

Cliodynamics, 5(1)

ISSN

2373-7530

Authors

Johnson, Dominic D. P.
Toft, Monica Duffy

Publication Date

2014-01-01

DOI

10.21237/C7clio5125317

Peer reviewed

SOCIAL EVOLUTION FORUM

Bringing “Geo” Back into Politics: Evolution, Territoriality and the Contest over Ukraine

Dominic D. P. Johnson and Monica Duffy Toft

University of Oxford

As the crisis continues to unfold in Ukraine, important questions are being asked about how we got here and what we should expect next. Political science sometimes gets a bad rap for a poor ability to make predictions in a world of complex events, but building on some foundational principles, broad predictions are possible. In a 2008 *Foreign Policy* article, Toft expressed particular concern about Russia’s maneuvering in the region; she indicated that as the crisis in Georgia over South Ossetia winds down, we should next turn our attention to Crimea and Transdnestria. The premise of that piece was that Russia had been working for some time to ensure its influence throughout the region by way of old-fashioned empire-building. But the key question is, why certain places over others? Why Crimea and eastern Ukraine, for instance, and not elsewhere?

In a recent *International Security* article, “Grounds for War” (Johnson and Toft 2014), we outlined how evolutionary science might provide some foundational principles to help us to understand these dynamics. A critical factor is the qualities that inhere in territory—geographic spaces—and how people as individuals and groups relate to particular parcels of territory. Crimea and eastern Ukraine each continue to hold special import to both Russians and Ukrainians, which means that contests for their control are both vestiges of the past and, at the same time, are overlain with contemporary trends and interests.

Just consider the Crimea crisis, where factors deeper than economics or politics are at work. While researching her Ph.D. dissertation in Ukraine in 1992, just one year after independence from the Soviet Union, Monica passed by the Parliament building in the capital city of Kyiv (to Ukrainians, Kiev to Russians). Parliament was in session and various people were lingering about, trying to get their concerns heard. One was a Cossack—a huge man in full Cossack regalia (it was August). In his arms was a basket filled with small, clear plastic bags. The bags were sealed with a golden cord and affixed with a

Corresponding author’s e-mail: dominic.johnson@politics.ox.ac.uk

Citation: Johnson, Dominic and Monica Duffy Toft. 2014. Bringing “Geo” Back into Politics: Evolution, Territoriality and the Contest over Ukraine (with comment). *Cliodynamics* 5: 87–122.

waxed seal that contained a trident—a symbol of Ukraine. It was not the seal or cord or the bag that mattered most, but the contents. Inside each bag was about two ounces of what to any outsider would have been, well, dirt. But for the Cossack and his peers, these were precious; these were bags of Cossack *land—homeland*. He and his fellows had gone to great lengths to conceive of, design, and distribute this physical representation of Cossack territory. Cossacks believe it is their mission to defend Russian Orthodoxy. They claim Crimean Tatars as enemies; accusing them of wanting to steal land and build an independent Tatar state on the peninsula. As this particular Cossack understood, the root cause of the crisis then and today was not ideas or ideology, but territory.

Although United States Secretary of State John Kerry declared Russia's behavior as reminiscent of the 19th century and therefore puzzling in the modern era, such behavior is far from puzzling—and far from unique to Russia—when examined in the context in which it evolved and continues today. From the perspective of evolutionary science, conflicts over territory show consistent patterns across the animal kingdom. Territorial behavior—what we term “territoriality”—has evolved independently across a wide range of ecologies and species, from the depths of oceans to desolate deserts, and from arctic tundra to tropical rain forests. This recurrence of territoriality suggests a convergence of solutions to a common strategic problem: how to obtain and maintain access to the land in order to survive and thrive. Humans are but one of many organisms that have developed territoriality as an effective strategy for maximizing “Darwinian fitness.” Understanding this basic compulsion towards territoriality shifts the focus of the questions away from *whether* to *why* people fight over territory at some times and not others.

From a broader evolutionary perspective, territoriality exhibits three properties:

1. It is widespread across the animal kingdom, indicating a convergent solution to a common strategic problem;
2. It is a dominant strategy in the “hawk-dove” game of evolutionary game theory (under certain but common conditions). What this means is that no other strategy can trump it, and even more remarkably, this holds even when the costs of conflict exceed the prize at stake; and
3. It follows a strategic logic, but one that is calibrated to cost-benefit ratios that prevailed in humans' evolutionary past, not those of the present.

Taken together, what we find is that humans share a common propensity with other species when it comes to territoriality. Territory is usually worth fighting for, and invaders can usually be defeated. This is important because in the field of international relations, there are few fundamental principles or laws. The world map, however, highlights at least one iron law of global politics: human territoriality. Almost every inch of the globe is partitioned into

exclusive and bounded spaces that are claimed by specific groups of humans. Furthermore, territory has led to recurrent and some of the most severe conflicts. These fights include those over land of little material worth or “strategic” importance, which remains a puzzle for many scholars of international relations. This propensity also helps to explain a number of empirical findings about wars over territory: for example, why they tend to last longer, are more difficult to resolve, and are more likely to lead to intractable conflicts than wars fought over other issues.

In “Grounds for War,” we highlight several behaviors likely favored by evolution in conflicts over territory, depending on the circumstances. Over time, there are multiple returns to investing in sustained occupancy; for example, residents will tend to fight harder to maintain their control of a territory (incumbency adds value; see examples in our original article, p. 23). Following early work in game theory, we contend that defense of territorial control will likely escalate to violence because it is in the interests of incumbents to protect what they have: a “hawkish” strategy referred to as *Bourgeois*. This terminology is derived from the French *bourgeois*, delineating the property-owning middle class from the landless, lower working class. By contrast, organisms prospecting or intruding into a territory, even one with manifest advantages in terms of food or shelter endowments, are likely to withdraw when threatened by the territory owner. We identify this behavior as “dove” behavior because an initially hostile or aggressive display is very likely to be followed by a de-escalation and departure. This “convention”—common across nature—serves to avoid conflict. Hawkish territory owners and dovish intruders are following the optimal strategy, as long as (1) combatants can cause great harm; (2) the costs of finding alternative territory are high; and (3) the benefits at stake are not too valuable. If these conditions are broken (cheap conflict, unclaimed land, or priceless stakes), fighting can escalate—in such cases, natural selection may even favor the evolution of lethal conflict.

But fighting can escalate for another reason: misperceptions. Because judgments about duration of habitation or the costs of conflict can be complex (and suffer from misinformation or rival interpretations), what we observe across most species is often a mix of behaviors: sometimes both organisms play hawk, and sometimes both play dove, or each may display combination of the two. In an unusual, novel, or fast-moving setting, even a well-adapted organism can make a mistake—deploying the wrong strategy for the situation. Again, humans are only one of many organisms who exhibit these shared characteristics regarding territory, but we are particularly susceptible to misjudgments and misperceptions because of our complex, global, historical communities.

In the example at hand, it is not just Crimea that is a cause for concern. In that case, the Ukrainians played “dove” in line with predictions of evolutionary game theory—if the polls are to be believed, ethnic Russians were the territory

owners. Russia did have a good (that is, longer) claim to the territory: after having occupied and controlled Crimea for centuries, it was ceded to the Ukrainian republic only in 1954. For many Russians in Crimea and beyond, the sovereignty of Kyiv over Crimea is just as suspect and illegitimate as the sovereignty of Moscow over the Baltic states was to the peoples of Latvia, Lithuania, and Estonia. Eastern Ukraine's position, however, is more precarious in that both Ukrainians and Russians see it as their own. There are two perceived territory owners, and two hawks facing each other down. However, because settlement patterns after Stalin's ascent to power favored ethnic Russians, the strong concentration of ethnic Russians in Ukraine's east (the Donbass in particular) as compared to ethnic Ukrainians causes us to predict that the Ukrainians are again likely to play "dove" (either through government action or popular alignment). The truly risky part of Ukraine in terms of war is its western territories, where, due to both to ethnic settlement patterns and duration of habitation, we would expect Ukrainians to act as "hawks." Unfortunately, even in western Ukraine, many ethnic Russians (and for reasons of state, Moscow) see large parts of the territory as part of an historic homeland. If there is a region of Ukraine that could spark a fully-fledged war, it is there.

However, saying this does not mean that war over this western bit of territory is inevitable. Rather, the nature of the territory and the different claims to it only suggest that the risk of war is highest there. Other factors are involved, but the logic of territorial behavior increases the risk of war. We can state the risks somewhat lexically for analytical clarity as follows: (1) humans tend to fight over territory, and those fights tend to escalate to violence (hawks) when multiple communities perceive that control of territory is important to their survival or prosperity; (2) ethnic Russians and Ukrainians will tend to back down (doves) when either their communities have been settled more recently than the incumbent group or when their demographic distribution is sparse; but (3) contemporary strategic, material, and political interests overlay the previous two by altering the relative costs of acquiring, maintaining, or ceding control of territory. It is not only a matter of perceived ownership, but a matter of power to enforce it.

In sum, our contribution is adding the first layer, which helps resolve the puzzle over why so many conflicts over *territory* escalate to violence as opposed to conflicts over other important issues affecting a given community's survival, prosperity, and security. Crimea is a flashpoint not because Russia is throwing down the gauntlet to the west, but because it is throwing down the gauntlet on what it considers home territory. Moreover, an evolutionary understanding of the importance of territory and the mechanisms by which species come to value it (via duration and distribution of ethnic kin, for example), help predict whether a given community is more or less apt to escalate its interests to violence over territory. In short, for humans and for the

family, ethnic, national, and state groupings in which they find themselves today, territory matters in a visceral way. As Scarlet O’Hara’s father Gerald reminds her in David O. Selznick’s film adaptation of Margaret Mitchell’s *Gone with the Wind*, territory, *land*, is special: “Why, land is the only thing in this world worth working for, worth dying for—because it’s the only thing that *lasts*.”

References

- Dominic D.P. Johnson and Monica Duffy Toft. 2014. “Grounds for War: The Evolution of Territorial Conflict,” *International Security*, Winter 2013/2104. http://www.mitpressjournals.org/doi/abs/10.1162/ISEC_a_00149#.Uoftn9wuxZw
- Dominic D.P. Johnson and Monica Duffy Toft. 2014. “”Grounds for Hope: The Evolutionary Science behind Territorial Conflict” Policy Brief, Belfer Center for Science and International Affairs, Harvard Kennedy School, *March*.
http://belfercenter.hks.harvard.edu/publication/24074/grounds_for_hope.html
- Monica Duffy Toft, 2008. “Russia’s Recipe for Empire,” *Foreign Policy*, September 2. http://www.foreignpolicy.com/articles/2008/09/01/russias_recipe_for_empire
- Monica Duffy Toft, 2003. *The Geography of Ethnic Violence*, Princeton University Press.

Commentaries

Peter Turchin. ‘*Devoted Realism*’: a Commentary on Johnson and Toft

University of Connecticut

Corresponding author’s email: peter.turchin@uconn.edu

Dominic Johnson and Monica Duffy Toft wrote a very interesting article. I applaud the explicitly evolutionary approach that they bring to political science. I also agree with their emphasis on territory: “It’s the only thing that *lasts*.”

Nevertheless, I don't agree with everything they say. Johnson and Toft employ insights from game theory to understand why states, the principal actors on the international arena, pursue different courses of action in different circumstances (again, an approach with which I heartily agree). However, they suggest that under some circumstances, international actors play the 'dove' strategy, whereas they could play a 'hawkish' or 'bourgeois' strategies in other circumstances. I think this approach muddies the theoretical waters.

My alternative proposal is that all modern states play essentially the same strategy, which I will call 'Devoted Realism' for reasons given below. What differs between players is the relative amount of geopolitical power possessed and the nature of the resource (territory) in conflict. As does any theoretical model, Devoted Realism oversimplifies the situation. States are not really unitary agents, they are composed of various interest groups that may cooperate, or be in conflict with each other. The configuration of the international arena also plays a role. There are many other factors that could affect the behavior of the players, but let's keep things simple and explore the implications of the basic model.

My Devoted Realism model is simply an elaboration of the Offensive Realism of John Mearsheimer (2001) that incorporate the importance of Sacred Values in influencing the behavior of individuals, interest groups, and whole polities (Atran 2010). In Atran's terminology, agents motivated by Sacred Values are called 'Devoted Actors' (thus, 'Devoted Realism').

As in Offensive Realism, I postulate that states are involved in a single-minded pursuit of geopolitical power. The principle resource they vie for is territory, for reasons explained by Johnson and Toft. Different pieces of land, however, vary in their value. The value of territory is affected by its ability to generate taxes for the state treasury and recruits for the state army, its mineral and natural endowments, and its role in the economic division of labor (for example, containing industries that provide some key products for the rest of economy). Other benefits include the ability to project geopolitical power, or to deny this ability to potential rivals.

Territories also impose costs. They may have restive populations or even separatist groups that need to be suppressed. They may be located far away from the center, imposing a significant logistical burden on the state. And possessing them may be costly or dangerous because of other actors on the international arena (e.g., the sanctions imposed by the US and the EU on Russia following its annexation of Crimea).

So far, we are solidly within Offensive Realism. In deciding whether to grab or let go a piece of territory, states weigh the territory's utility (benefits minus costs) and its own power relative to that of its opponents. 'Power' here means not only material factors (army size, armaments, the state of the treasury), but also the degree of political unity and the willingness of the elites and

population to spend treasure and blood for the sake of obtaining (or keeping) the territory.

All we need to do now is to realize that the ‘utility function’ of territory includes not only its material advantages—natural, economic, and geopolitical endowments—but also its Sacred Value. Sacred Value can vary from zero to some intermediate values (so that overwhelming material costs may trump it) to essentially infinity (when it trumps any considerations of material advantage).

How does land become Sacred? Partly it is a result of mere possession—incumbency. States are very reluctant to give up any territory that they already possess, no matter how worthless and costly to defend. Giving up land suggests to other actors that the state lacks commitment to defend its own. The importance of possession is illuminated by the hawk-dove game discussed by Johnson and Toft, where the dominant strategy is ‘bourgeois,’ in which incumbents fight to keep their property, but don’t attempt to take the property of others.

Incidentally, I dislike the term ‘bourgeois,’ which confuses rather than illuminates the theoretical issues (because a true bourgeois would never fight to the death over any issue). Furthermore, the bourgeois strategy is an overly simplistic description of the strategy that real states pursue, for two reasons. First, as Offensive Realism shows, states will grab territory that they don’t own if the balance of benefits versus costs is favorable. As an example, when Mexico became devastated by internal fighting and persistent Comanche raids in the 1840s, the United States went to war with it and acquired New Mexico and California. The disappearance of the Soviet Union in 1991 left a similar ‘geopolitical black hole’ into which the NATO expanded. As Offensive Realists, including Mearsheimer, pointed out at the time, there was very little geopolitical advantage to be gained from this expansion (and it broke the explicit promises made to Gorbachev as a condition of his approving the German Reunification). Nevertheless, this expansion proceeded because its costs were minimal; during the 1990s, Russia was powerless to prevent it.

Second, possession is not all-or-nothing. Two or more states can claim the same territory and at the same time assign very different value to it. This is why we need a continuous variable that measures the non-materialistic aspects of territory’s value.

Clearly, the length of possession increases the Sacred Value of a territory to the state. For example, Taiwan has been owned by the Chinese Empire since the seventeenth century, and just by virtue of extended ownership, it has become a Sacred Value for the Chinese, who explicitly justify their insistence that eventually Taiwan must be re-unified with the mainland China by referring to it as their Sacred Land.

Other factors, however, can be even more important in making territory Sacred than the length of possession. I have explored such factors in the case of

Crimea in Turchin (2014). A general rule, which I have called the “coevolution of geopolitics and Sacred Values,” is that geopolitically important areas tend to be defended more fiercely—initially, because of their geopolitical value. But with time, such lands also acquire a Sacred value, because they are sites of numerous wars, battles, and sieges resulting in ‘heroic deeds’ that are deposited into the collective memory.

Because Sacred Values are a cultural phenomenon, locations also gain “Sacredness” by being associated with writers, composers, political statesmen, and military heroes. Thus, birth places and burial sites (e.g., mausoleums) of various notables are definitely part of the Sacred Landscape.

Most of this commentary has been devoted to theoretical issues—extending the Offensive Realism model by adding a Sacred Value dimension to it. But the theory has practical applications. In the context of the Ukrainian crisis, for example, the Devoted Realism model suggests that there is a big difference between Crimea and eastern Ukraine when considered from the point of view of Russia.

Crimea is of immeasurably higher geopolitical and cultural significance to Russia than the Donetsk and Lugansk regions (see Turchin 2014 for details). Crimean annexation brought two ‘Hero Cities’ into the Russian fold: Sevastopol, the third most Sacred city for the Russians (after Moscow and St. Petersburg), and Kerch. Eastern Ukraine has no Hero Cities. Until recent events, most Russians would be hard pressed to locate Lugansk on a contour map.

The Crimean population was staunchly in favor of unification with Russia. Characteristically, the Russian President, Putin, admitted that they ran secret polls in Crimea on this question before committing to the referendum and annexation. In eastern Ukraine, as best as we can tell from the polls, while rejecting the “illegitimate” Kiev authority, the majority of the population is probably not going to support entering Russia.

Geographically, Crimea is essentially an island, which is easy to defend. It’s an unsinkable aircraft carrier that allows Russia to project power into the Black Sea and the eastern Mediterranean. On the other hand, there is no defensible boundary between eastern Ukraine and the rest of Ukraine. Absorbing Crimea into Russia is already going to be very costly economically, but the cost of doing the same for Donbass in eastern Ukraine is clearly prohibitive.

Finally, annexing Donbass is sure to trigger much more severe sanctions from the United States and the European Union, and create a rift with other BRICS countries, which have refrained from criticizing Russian actions so far.

In short, the balance of costs and benefits (including its low Sacred Value) is such that annexation of eastern Ukraine is simply not a rational strategy. There are a number of indicators that the Russian leadership understands this calculus very well. For example, the Donbass activists, to whom the Western

Press usually refers to as “separatists,” are called “supporters of federalization” by the official Moscow. This is a clear sign that Moscow has currently no desire to enter into the quagmire of eastern Ukraine. And, I would argue, the reason why it is so different from Crimea can be seen by considering the Sacred Landscape of Russia.

References

- Atran, S. 2010. *Talking to the Enemy: Faith, Brotherhood, and the (Un)making of Terrorist*. Harper Collins, New York.
- Mearscheimer, J. J. 2001. *The Tragedy of Great Power Politics*. Norton, New York.
- Turchin, 2014. “Why national honour trumps rationality.” *Aeon*. 3 April 2014. <http://aeon.co/magazine/society/why-national-honour-trumps-rationality>

Scott Atran,¹ Jeremy Ginges,² and Rumen Iliev.³ *Devoted Actors, Devoted Realism, and the Territorial Imperative: A Commentary on Johnson and Toft.*

¹National Center for Scientific Research, France; ²New School for Social Research; ³University of Michigan
Corresponding author's email: satran@umich.edu

What is the other commonwealth that remains standing now that the mundane commonwealth, embodied in the Roman Empire, has fallen?

Saint Augustine, The City of God (De Civitate Dei), on what survived and thrived after the Visigoths sacked Rome in 410 AD

Peter Turchin's Devoted Realism proposal is a laudable attempt to incorporate the sacred values and social cohesion of “devoted actors” (Atran, Axelrod & Davis, 2007) into a utility model that integrates the material and moral bases for political behavior. As Turchin rightly implies, the intractable character of many longstanding intergroup conflicts reside in the sacred value attached to territories in dispute – a site of heroic deeds and cultural achievements, providing continuity with ancestors and future generations – and defies diplomatic solution (Ginges & Atran, 2011). It is only when territory becomes “Sacred Land” that it truly becomes indivisible and non-negotiable (Fearon,

1995). There are, however, two objections to this approach. First, as with Johnson and Toft (2013/2014), there is an assumption that the logic of territorial behavior is the main driver of political developments in history and cultural evolution, and the chief reason for enduring and intractable inter-group conflicts, when territory is only one pillar of many that characterizes the ethos of a conflict (Atran, Wilson, Davis & Sheikh, 2014). Second, the utility calculus assumes that sacred values can vary continuously, or at least over graduated intervals, but two separate sacred values may have arbitrary—and flexible—values relative to one another.

On the first point: Grant that territory, like kinship, is a touchstone in the historical and cultural developments of our species. Nevertheless, as human societies have progressed from bands to chiefdoms, states, and transnational movements, territory, like kinship, has often become subordinated to more abstract ideas and causes “to which no creature but man is subject,” as Thomas Hobbes put it in *Leviathan*. Indeed, the rise of universal religions were associated first, in Christianity, with explicit subordination of territorial ambitions to proselytization via charity and other social works, and, in Islam, with explicit submission (*islam*) of kin-based loyalties to the larger community (*ummah*) of mostly anonymous strangers. Of course, competition for territory and kin-based maneuvering has been recurrent and strong in the development of Christianity and Islam, for each ultimately has sought the ingathering and loyalty of all humanity, a concept that universal religion created. This is also true of the political history and cultural evolution of the great secular, salvational ‘-isms’ that have dominated world politics since the French Revolution (liberalism, anarchism, communism, fascism, socialism, etc.). Nevertheless, issues that become the source of intractable conflicts needn’t involve kinship or territory in direct ways (e.g., rights to worship and intermarry freely), although they often do have psychological connection to our *sense* of kinship (e.g., pro-life vs. pro-choice, gay marriage) and territory (e.g., Iran’s nuclear program or Palestinian Right of Return as a sacred principle, Dehghani et al., 2010; Ginges et al., 2007). Often, the issues that keep longstanding disputes alive between states, although initially rooted in territorial conflict, later acquire stronger association with sacralized sentiments of (lack of) recognition and respect.

Even if the focus is on territorial claims and ambitions, historical precedents blur the picture. Take the Crimea, which Vladimir Putin claims “is sacred to us” (cited in Englund, 2014) and which very well may be for many Russians (Turchin, 2014). Yet, in the past, the same territory has been Scythian, Greek, Tatar, and Ukrainian. How people in a country decide what is just, and what is worth fighting for, cannot be merely a primacy effect based on past possession (Israel as ancient Judea) or enduring entrenchment (Palestine since the Romans). For example, Hawaii was the last territory incorporated into the USA, but many Americans across the country would probably consider

it sacred. Generally, when countries start guiding their foreign policy based on historical claims it's a red light for disaster. Thus, Poles were most happy to get back historic lands from Czechoslovakia when Germany annexed the Sudetenland in 1938, but most unhappy just one year later when Germany claimed its historic lands in Poland.

For modern states, the resource at stake may not be so much territory, as human minds. Take Putin's appeals in favor of annexing the Crimea: this played out as much in the virtual reality of media and internet as on the ground. It might be interesting to compare game theory models based on territory, where causality is based on some kind of spatial grid, with models based on minds and hearts. In the "territory as a resource" case, the state of a cell might change based only on the state of the neighboring cells (with few exceptions, like airborne or seaborne assaults). Here, actors always lose territory gradually, and it is more or less clear what the current state is. A Hearts and Mind game would aim at capturing population rather than territory *per se*. In the "population as a resource" model, the causal connections will have different dimensionality based on social networks, media or other widespread sources of information: players might suddenly lose all resources were a message convincing enough.

On the second point: Although a graduated notion of "sacred value" can also be applied to "social goods" that needn't involve territory (Bowles & Polania-Reyes, 2012), we find in our research that Devoted Actors follow a rule-bound logic (Berns, et al. 2012), motivated by sacred values embedded in fused social groups (Atran, 2010). Adherence to those values is inviolable and inalienable (intrinsic to "who I am," and "who we are," Atran & Ginges, 2012), and fusion with the primary reference group is complete and irrevocable (Swann et al., 2014). In terms of impact on human decision-making, sacred values may be defined as values for which people refuse material trade-offs and resist normative social influence. Nothing in the proposed incorporation of sacred values into a utility function predicts the "backfire effect," where states and individuals reject material tradeoffs and even seek out costly sacrifices in the face of sincere offers of compromise or negotiated settlement of disputes. Indeed, the backfire effect is sometimes associated with demonstrable willingness to ratchet up commitment to defend sacred values against all odds and unto death, sacrificing the totality of self-interests. Moreover, sacred values are often associated with radical skewing of functions for temporal or spatial discounting: psychological attachment to distant events and places linked with the sacred can be much more powerful than attachment to closer mundane events and places (Sheikh, Ginges & Atran, 2013).

Nevertheless, sacred values may themselves be ranked and prioritized in different ways, at different times. For example, Abraham Lincoln and many who he represented held as sacred values both preservation of the Union and abolition of slavery. At the beginning of the Civil War, he prioritized

preservation of the Union over abolition. But towards the end of the war, he reversed priorities and prolonged the war for several costly and bloody months, claiming that preservation of the Union and its territory was meaningless unless the Union stood for sacred, moral principles that necessarily included abolition of slavery. Nothing in a proposed utility function accounts for the ranking and prioritization of sacred values relative to each other, but they are distinct in their lack of relation to material trade-offs.

The goal of adequately describing, and ultimately explaining, the interaction of material interests and sacred values in motivating human behavior, whether for individuals or groups, is almost entirely absent from current theorizing. “Devoted Realism” is a step in the right direction, but perhaps still too tethered to the material side of things in general, and as with Johnson and Toft, particularly to the struggle over territory. The territorial imperative, however important or even sacralized, did not alone or even primarily move us out of the caves, drive civilizations forward, create the concept of humanity, or produce globalization, along with most of the ensuing geopolitical ramifications.

References

- Atran, S. (2010). Talking to the enemy: Violent extremism, sacred values, and what it means to be human. London: Penguin.
- Atran, S., Axelrod, R. & Davis, R. (2007). Sacred barriers to conflict resolution. *Science*, 317, 1039–1040.
- Atran, S. & Ginges, J. (2012). Religious and sacred imperatives in human conflict. *Science*, 366, 855–857.
- Atran, S., Wilson, L., Davis, R. & Sheikh, H. (2014) Devoted actors, sacred values, and willingness to fight: Preliminary studies with ISIL volunteers and Kurdish frontline fighters. Report presented in conjunction with the U.S. Dept. of Defense Minerva Initiative to the Strategic Multilayer Assessment of ISIL in support of SOCCNET, November–December, Washington DC, http://artisresearch.com/wp-content/uploads/2014/11/Atran_Soccnnet_MINERVA_ISIS.pdf
- Berns, G., Bell, E., Capra, C.M., Prietula, M., Moore, S., Anderson, B., Ginges, J. & Atran S. (2012). The price of your soul: Neural evidence for the non-utilitarian representation of sacred values. *Philosophical Transactions of the Royal Society–B*, 367, 754–762.
- Bowles, S. & Polania-Reyes, S. (2012). Economic incentives and social preferences: Substitutes or complements? *Journal of Economic Literature*, 50, 368–425.
- Dehghani, M., Atran, S. Iliev, Sachdeva, R., Ginges J. & Medin, D. (2010). Sacred values and conflict over Iran’s nuclear program. *Judgment and Decision Making*, 5, 540–546.

- Englund, W. (2014). Kremlin says Crimea is now officially part of Russia after signing, Putin speech. Washington Post, May 18.
- Fearon, J. (1995). Rationalist explanations for war. *International Organization*, 49, 379–414.
- Ginges, J. & Atran, S. (2011). War as a moral imperative (not practical politics by other means). *Proceedings of the Royal Society–B*, 27, 2930–2938.
- Ginges, J., Atran, S., Medin, D. & Shikaki, K. (2007). Sacred bounds on the rational resolution of violent political conflict. *Proceedings of the National Academy of Sciences, USA*, 104, 7357–7360.
- Johnson, D. & Toft, M. (2013/2014, Winter). Grounds for war: The evolution of territorial conflict. *International Security*, 38, 7–38.
- Sheikh, H, Ginges, J. & Atran, S. (2013) Sacred values in intergroup conflict: Resistance to social influence, temporal discounting, and exit strategies. *Annals of the New York Academy of Sciences*, 1299, 11–24.
- Swann, W., Gomez, A., Buhrmester, M., Lopez-Rodriguez, L., Jiménez, J. & Vazquez, A. (2014). What makes a group worth dying for? Identity fusion fosters perception of familial ties, promoting self-sacrifice. *Journal of Personality and Social Psychology*, 106, 912–926.
- Turchin, P. (2014). Russia's sacred land. *Aeon*, <http://aeon.co/magazine/living-together/why-national-honour-trumps-rationality/>

Radek Szulga. *Territoriality and Conflict: an Economist's View. A Commentary on Johnson and Toft*

Grinnell College

Corresponding author's email address: szulgara@grinnell.edu

Dominic Johnson and Monica Duffy Toft analyze the importance of territoriality in their Special Feature article, “Bringing ‘Geo’ Back into Politics,” as well as in the related piece in *International Security*, “Grounds for War” (2013/14). Peter Turchin also stresses the importance of territory for understanding conflict in his response article (see also Turchin, 2014). Atran, Ginges, and Iliev do not abandon this approach entirely, but do depart from the focus on territory to some extent.

From a strictly economic point of view, territory matters because it is an asset. It provides a stream of resources which can be used for consumption, acquisition of geopolitical power, or evolutionary success. In aggregate, it is in

fixed supply. This suggests that conflicts over territory are likely to be negative-sum contests. Therefore, narrowly focused, economic approaches have limitations because rational actors should be able to avoid conflicts which destroy net value. Regardless of who happens to be in possession of the territory at a given moment, if side payments are possible, a peaceful settlement which benefits both parties should be reached. Some elements of a particular situation—asymmetric information, negotiation costs, indivisibilities, imperfect commitment—might make it more difficult to arrive at a resolution. However, as has been recognized for quite some time, and as Johnson and Toft note, the frequency of territorial conflicts necessitates an explanation which goes beyond simple pecuniary cost/benefit calculations even with these standard modifications.

The authors provide that extension by invoking evolutionary pressures which make actors more aggressive—territorial—when they are already in a possession of a territory. Peter Turchin incorporates the notion of Sacred Land in the context of the Devoted Realism strategy. Evolutionary theory certainly adds to our understanding of present day social phenomenon, and indeed it is complementary to the economic analysis of conflict. As the authors aptly put it, “Evolution is less an alternative to economics than an example of it” (Johnson and Duffy Toft, 2013/14). However, its application to economics is by no means straight forward. The difficulties are both theoretical and applied.

On the theoretical side, there actually isn't really anything special about territory in the Hawk/Dove/Bourgeois (henceforth H/D/B) game. Yes, the story woven around this game-theoretic model is a narrative about individuals defending territory they own more aggressively than territory they seek to acquire. And yes, the Bourgeois strategy has an evolutionary advantage. But the source of that advantage is not possession of territory per se; the model assumes that the payoffs to ownership are symmetric. Rather, it is the ability of species or actors to correlate their strategies based on an external event that gives Bourgeois the edge. But this event could really be anything. One could construct a different narrative to argue, for example, that conflicts are more likely to occur when it rains than when it is sunny. An individual plays Hawk if it's raining and Dove if the sun is out. This will also be an evolutionary stable strategy (ESS), and could be used as an argument for making weather a candidate for explaining observed human conflicts. Another often-cited anomalous example is the “Encroachment” strategy, which involves the incumbent playing Dove and the intruder playing Hawk and which has the same exact payoff as the territorial Bourgeois strategy.

Of course, weather is a pretty poor predictor of conflicts. Likewise, the existence of the so-called *endowment effect*—the fact that we tend to value something more, simply because we already possess it—has been well-documented in the literature (but see below). The theory is in need of other features which will make territory central. In “Grounds for War,” the authors

discuss associated issues in much more depth, but here, space limitations constrain the ability to comment upon them fully. In particular, they invoke Herbert Gintis' (2006) work on the existence of what he refers to as private property equilibrium, which corresponds to the Bourgeois strategy. The authors cite a result from the paper which shows that if there is a (small) cost of transferring the territory, then the Bourgeois strategy is the only ESS. However, Gintis also extends his model in the other direction, where the Encroachment strategy is the only viable one. Hence, the territorial narrative of the H/D/B model is constructed ad-hoc to make it fit facts which we already suspect to be true, but this narrative itself is neither a prediction of the model nor is it in any way a necessary component.

The second difficulty lies in the application of evolutionary theory to modern social phenomenon. We can take states as the relevant actors, although it is not immediately obvious that this is the appropriate mapping. Regardless, states-as-actors requires that we follow through with the logic of the underlying model; it is the current possession of territory by a particular state at the outset of a conflict that matters. This is where the application of the model to the Crimean dispute runs into problems. If we take the H/D/B model literally, then we should have predicted that the Ukrainian state aggressively defended what was their territory at the outset. Of course, the opposite happened. To make the situation fit the predictions of the model, the authors are forced to stretch the definition of "ownership" in order to place it on the Russian side. But the fact that historically, Russia was in possession of Crimea for longer should not matter; past ownership is not part of the model. Likewise, the ethnic composition of the peninsula's population, or a moral right to the territory, should not play a role, either.

There are some complicating factors. The presence of Russian naval bases in Crimea suggests that true ownership was actually split. But that, too, is a different model. The purpose here is to point out the pitfalls of trying to map evolutionary theory into modern social interactions.

Peter Turchin's concept has evolutionary logic behind it, with the initial possession of land replaced by the Sacred designation. Putting aside the theoretical drawbacks of the H/D/B approach discussed above, the idea of Sacred Land appears to be a macro version of some findings in recent research on the *endowment effect*, which link its presence to identity formation.

The original postulate of the endowment effect goes back to Richard Thaler's 1980 paper, itself based on earlier work by Kahneman and Tversky (1979) (see also Kahneman, Knetsch and Thaler, 1990 and 1991). It is important to note that the endowment effect's existence, source, and generality are not universally agreed upon. In a recent *American Economic Review* article, Apicella et al. (2014) show that the endowment effect is present among hunter-gatherers who have had contact with modern society, but not among those who have been relatively isolated from it. Maddux et al. (2010) present

evidence that it is stronger for Western subjects than those from East Asia. Thus, the endowment effect might be a product of sociocultural evolution rather than something inherited from our distant evolutionary past. More directly related to economics, the endowment effect has been, unsurprisingly, of interest to marketing researchers. The main finding is that endowment matters because possession is linked to identity formation (Loughran Dommer and Swaminathan, 2013). We attach extra value to something we already possess when it becomes part of our identity. This finding is probably not surprising to anyone who has had a favorite shirt, toy, blanket, or hang-out spot (territory!).

This is a similar phenomenon to that of Sacred Land, although it occurs at the level of individuals and particular goods rather than territory and peoples. Its synthesis is probably the same. Land becomes sacred when it is inhabited, worked and possessed, and in so doing, becomes part of a people's identity. While it is common for land to be named after a people, sometimes peoples are named after their lands (Prussians or... Americans), reflecting the process of land-based identity formation. Although the development of Sacred Land may have a primarily historical and cultural basis that varies between peoples, that does not invalidate its importance.

The application of the idea of Sacred Land to Crimea is self-evident. Still, although incorporating Sacred Land into models of conflict can potentially increase their explanatory power, the analysis inherits all the limitations of the basic economic model discussed at the beginning of this essay. Economists understand the importance of non-pecuniary incentives and do not confuse value with price. If economic theory can be summarized by a single, simple postulate, it is that "the demand curve slopes downward"—the more costly something is, the less of it you will do. That "something" is open-ended. The claim is only that if the cost of fighting over territory is high, actors will be less likely to fight if the "Sacredness" of the land is held constant. This means, however, if the degree of relative Sacredness is known to the parties involved, the situation with Sacred Land isn't conceptually distinct from the set up where monetary value of a piece of land is higher to one party. And the big question—the frequency of conflict over territory—is still on the table.

Recalling that indivisibility is one of the things which can impede a peaceful resolution, I tend to sympathize with Atran, Ginges, and Illiev's argument that Sacredness may very well be an all-or-nothing variable in the relevant utility functions. This may actually be an advantage of the concept, although it may also make its quantitative application more difficult.

My own preferred explanation of conflict and territoriality is some form of modified standard economic approach, although the unspecified model I have in mind involves equilibria which are very sensitive to parameter specification, initial conditions, and maybe are non-unique. Many disputes do get resolved peacefully, but because violence is more tantalizing, as social scientists and

historians, we tend to focus on the “interesting” cases which make for dramatic stories. Many disputes appear to linger in a kind of a limbo (for example, Cyprus or Taiwan) where a kind of steady state is achieved. This persists until some exogenous shock alters the parameters (game theoretic models are notorious for their sensitivity to specification and applications of evolutionary theory to modern social phenomenon tend to inherit this “over-abundance of riches”) and opens up a window of opportunity, as well as a period of adjustment. Either conflict results or the dispute is resolved. An example of the latter could be the finalization of the German-Polish border in the treaty of 1990, motivated by the shock “fall of communism” and German desire for reunification. The present situation in Ukraine, where an internal shock, the overthrow of Yanukovich, altered the cost-benefit calculus of international geopolitics, is an obvious example of the former.

I admit that from the perspective of a social scientist interested in developing frameworks which have predictive power, this view of the world is somewhat pessimistic since these kinds of theoretical non-robustness imply that “all kinds of things can happen.” Although cautious, I do believe that it is worthwhile to chip away at the problem and the approaches discussed here contribute towards that end.

References

- Apicella, C.L., Azevado, E.M., Fowler, J.H. and Christakis, N.A. *In press*. Evolutionary Origins of the Endowment Effect: Evidence from Hunter-Gatherers. *American Economic Review*, 104: 1793–1805.
- Gintis, H. (2007). The Evolution of Private Property. *Journal of Economic Behavior and Organization*, 64(1), 1–16.
- Johnson, D.D.P. and Duffy Toft, M. (2013/14). *International Security*. 38(3), 7–38.
- Kahneman, D. and Tversky, A. (1979). Prospect Theory: An Analysis of Decision Under Risk. *Econometrica*, 47(2), 263–291.
- Kahneman, D., Knetsch, J.L. and Thaler, R.H. (1990). Experimental Tests of the Endowment Effect and the Coase Theorem. *Journal of Political Economy*, 98(6), 1325–1348.
- Kahneman, D., Knetsch, J.L. and Thaler R.H. (1991). Anomalies: The Endowment Effect, Loss Aversion and Status Quo Bias. *Journal of Economic Perspectives*, 5(1), 193–206.
- Loughran Dommer, S. and Swaminathan, V. (2013). Explaining the Endowment Effect through Ownership. The Role of Identity, Gender, and Self-Threat. *Journal of Consumer Research*, 39(5), 1034–1050.
- Maddux, W.W., Yang, H., Falk, C., Hajo A., Adaur, W., Endo, Y., Carmon, Z. and Heine, S.J. (2010). For Whom Is Parting With Possessions More

Painful? Cultural Differences in the Endowment Effect. *Psychological Science*, 21(12), 1910–1917.

Thaler, R.H. (1980). Towards a Positive Theory of Consumer Choice. *Journal of Economic Behavior and Organization*, 1(1), 1–16.

Turchin, P. (2014). Russia's Sacred Land. *Aeon Magazine*. April 3.

Anthony C. Lopez. *Adaptations for Territoriality and the False Residency Problem. A Commentary on Johnson and Toft*

Washington State University (Vancouver)

Corresponding author's email address: anthony.c.lopez@wsu.edu

Johnson and Toft (2014) argue that humans possess an evolved psychology of territoriality that generates a range of adaptively conditional behavior. Although the conditional logic embedded within this territorial psychology is posited to be a human universal, the resulting motivations and behavior are varied as a consequence of adaptively relevant variation in the socio-ecological environment. Thus, in contrast to Audrey's "territorial imperative" (1966), humans seem imbued with a "territorial conditionality."

But just what do we mean by "territoriality"? Two questions are often conflated when considering the existence and design of putative psychological adaptations: What is the adaptive problem or set of problems that "territoriality" is designed to solve? What is the design of adaptations that were sculpted to solve them? There are a number of ways to proceed from these questions in the case of territoriality.

The simplest way is to assume that no special adaptationist argument is necessary; in this case, territory is like any other asset and it poses no adaptive problem. As with any other asset, humans may fight to defend their territory. In this scenario, we need only interrogate the operation of known adaptations *for aggression* (not territoriality, per se) and ask how this particular asset is likely to alter (if at all) the expression of our evolved calculus for violence. This seems to be Szulga's preferred approach. Another way to proceed is to assume that territory is *not* like any other resource, and that it may have posed a unique adaptive problem. Thus, Johnson and Toft argue that territory has a unique cost-benefit ecological profile about which humans are designed to reason adaptively. Yet another possibility is that territory may become special when (and only when?) adaptations for imputing sacred value assign special value to territory (Atran, Axelrod, and Davis 2007; Atran and Ginges 2012).

Absent the imputation of sacred value, territory may operate in the mind's eye just like any other asset. Explanations in this domain require us to understand psychological design for the generation of sacred value, not territoriality, *per se*.

I don't believe that the evidence as of yet allows us to differentiate successfully among these alternative explanations for the observed phenomenon of "territoriality." At least—and I may be mistaken—I have not yet seen hypotheses derived and tested that can adjudicate directly among the competing models of territoriality-as-asset, territoriality-as-adaptation, and territoriality-as-by-product (i.e., a by-product of sacred value systems). The first suggests little more than the straightforward operation of adaptations for aggression; the second, the operation of a unique psychology of territoriality; the third, the operation of sacred value mechanisms that generate the appearance of "territoriality" as a by-product.

Because I believe the weight of evidence supports Johnson and Toft, let me proceed here for the sake of argument by agreeing with them that there are indeed unique adaptations for territoriality. I will refer to "territoriality" as the collection of psychological adaptations designed to respond to adaptive problems relating to the acquisition, maintenance and defense of territory. This would include everything from psychological design for finding certain landscapes more "instinctively" appealing (S. Kaplan 1987; R. Kaplan, Kaplan, and Brown 1989), to psychological decision rules that regulate the use of violence to acquire or defend territory. In consideration of the latter, the asymmetric war of attrition (Maynard Smith and Price 1973; Maynard Smith and Parker 1976) is often modeled to represent agonistic contests between "residents" and "intruders," in which the former prevails, on average, in contests against the latter. In these situations, the convention "if resident, attack; if intruder, retreat" can arise and become stable. In the language of international relations theory, we would say that this environment is "defense dominant" because it is easier to defend than to attack (Jervis 1978).

As Johnson and Toft point out, the possibility of territorial conflict is intensified when both actors view themselves as "resident" and thus are both motivated to attack and expel the other (as may be the case in western Ukraine). Assuming that no two actors can correctly and simultaneously both claim to be residents (an assumption that can be violated), one simple explanation for this dynamic is that for some individuals in some circumstances, it may have been adaptive to "bluff" one's way into residency—i.e., to behave as "resident" despite being "intruder." The operation of this "illusion of residency" (viewing yourself as resident when you are intruder) would likely be facilitated by self-deception (Trivers 2011), in much the same way as overconfidence, or positive illusions (Johnson and Fowler 2011).

What conditions might facilitate such an illusion? As Johnson and Toft rightly point out, our evolved psychology is designed to be adaptive in

ancestral environments, not modern ones. One very dramatic difference between ancestral and modern environments is nomadism. Notwithstanding the epic territorial shifts and grabs that characterized the Age of Empire (e.g., the “Scramble for Africa”), the modern international system is characterized by a relatively stable and fixed distribution of territorial nation states. This simple fact has many implications that can deeply affect the costs and benefits of territory and its defense: “running” or “hiding” from attack is increasingly implausible; today’s neighbors are tomorrow’s neighbors, etc. Alen Grafen (1987) has argued that a very different situation arises when “the winner of a fight is likely to retain the territory for a long time.” Where ownership or residency is relatively stable and new patches of land are few and far between, the Bourgeois strategy may, in fact, break down (i.e., fail to be an ESS) and it may pay both actors to play Hawk. It is in this environment that positive illusions would be particularly beneficial. This qualification to the asymmetric war of attrition seems to fit the modern international system remarkably well. Although space limits further development here, future research should consider ways to test hypotheses that can adjudicate among explanations for this false residency problem.

Lastly, many have worried that the application of the hawk-dove game in international relations is problematic because it applies a micro-framework to macro-dynamics. This is a valid concern; but again, the need is for clearer questions and testable hypotheses. When do groups behave as individuals (and when don’t they)? How does our unique coalitional psychology interact with the incentive structures provided by modern institutions? This is an exciting new frontier of research (e.g. see Boyer and Petersen 2011; Alexander and Christia 2011), and the sensible caution against deriving macro trends from micro principles should not lead us to falsely conclude that macro dynamics are not built upon micro foundations.

References

- Alexander, Marcus, and Fotini Christia. 2011. “Context Modularity of Human Altruism.” *Science* 334 (6061): 1392–94.
- Ardrey, Robert. 1966. *The Territorial Imperative: A Personal Inquiry into the Animal Origins of Property and Nations*. BCE edition. Atheneum: New York.
- Atran, Scott, Robert Axelrod, and Richard Davis. 2007. “Sacred Barriers to Conflict Resolution.” *Science* 317 (5841): 1039–40.
- Atran, Scott, and Jeremy Ginges. 2012. “Religious and Sacred Imperatives in Human Conflict.” *Science* 336 (6083): 855–57.
- Boyer, Pascal, and Michael Bang Petersen. 2011. “The Naturalness of (many) Social Institutions: Evolved Cognition as Their Foundation.” *Journal of Institutional Economics* 8 (1): 1–25.

- Grafen, Alan. 1987. "The Logic of Divisively Asymmetric Contests: Respect for Ownership and the Desperado Effect." *Animal Behaviour* 35 (2): 462–67.
- Jervis, Robert. 1978. "Cooperation under Security Dilemma." *World Politics* 30 (2): 167–214.
- Johnson, Dominic D. P., and James H. Fowler. 2011. "The Evolution of Overconfidence." *Nature* 477 (7364): 317–20.
- Johnson, Dominic D.P., and Monica Duffy Toft. 2014. "Grounds for War: The Evolution of Territorial Conflict." *International Security* 38 (3): 7–38.
- Kaplan, Rachel, Stephen Kaplan, and Terry Brown. 1989. "Environmental Preference: A Comparison of Four Domains of Predictors." *Environment and Behavior* 21 (5): 509–30.
- Kaplan, Stephen. 1987. "Aesthetics, Affect, and Cognition Environmental Preference from an Evolutionary Perspective." *Environment and Behavior* 19 (1): 3–32.
- Smith, J. Maynard, and G. R. Price. 1973. "The Logic of Animal Conflict." *Nature* 246 (5427): 15–18.
- Smith, John Maynard, and G. A. Parker. 1976. "The Logic of Asymmetric Contests." *Animal Behaviour* 24 (1): 159–75.
- Trivers, Robert. 2011. *The Folly of Fools: The Logic of Deceit and Self-Deception in Human Life*. Basic Books: New York.

Peter J. Richerson. *Was Territoriality Important in the Pleistocene? A Commentary on Johnson and Toft*
University of California (Davis)
Corresponding author's email address: pjrigherson@ucdavis.edu

I'm quite skeptical of the idea that territoriality is a part of our genetically evolved social psychology. Rada Dyson-Hudson and Eric Alden Smith wrote a classic paper in 1978 on territoriality in humans in which they pointed out that at least some hunter-gathers who live in sparse or variable environments do not find it worthwhile to defend territories. The Western Great Basin Shoshone, for example, did not even defend piñon groves, the nuts of which were their main winter staple, because the nut yield of groves fluctuated dramatically and unpredictably from year to year. Territoriality was much more marked in the more humid, more densely settled Aboriginal California compared to the Great Basin.

If we imagine that our innate social psychology evolved in the Pleistocene, we have to infer what Pleistocene environments were like and ask whether they were likely to favor territoriality. Paleoclimatologists have produced a reasonably high resolution picture of last glacial cycle climates (125,000 to 11,500 years ago), paleoecologists can tell us something about the animal populations and plant communities, and archaeologists know a lot about western Eurasia and increasingly about Africa (Hofreiter and Stewart 2009). Geneticists can roughly reconstruct the demography of the period. The deeper Pleistocene record is more poorly known but the best high resolution cores cover 4–8 glacial cycles. Pleistocene climates, particularly glacial climates, were highly variable and apparently became increasingly variable at millennial and submillennial scales over the last four–eight 100,000 y glacial–interglacial cycles (Richerson and Boyd, 2013). Genetic evidence suggests that populations of Europe and Africa were on the order of tens of thousands during most of the last glacial after 50,000 ya (Atkinson, et al. 2008), though South and South-East Asia seems to have been roughly ten times as populous. Before 50,000 ya, human populations in Africa either went through a bottleneck with numbers on the order of a few thousand at the minimum or hominin populations were chronically rare. The genetic estimates agree roughly with guesstimates that archaeologists have made for Europe in the last glacial cycle (Bocquet-Appel et al. 2005). Neandertals seem to have been even rarer than Upper Paleolithic Anatomically Modern people, whereas approximately 200,000 hunter-gatherers lived in California at the eve of European conquest. Late Pleistocene humans seem to have been big game hunting specialists, whereas Holocene hunter-gatherers seem to have become progressively more adapted to use plant resources even when they did not evolve agriculture. The frequently territorial hunter-gatherers of the ethnographic record may be very misleading as regards the Pleistocene situation.

Low-density populations can experience what ecologists call the “Allee Effect” named after Warder C. Allee, an American ecologist active in the first half of the 20th Century (Courchamp, Clutton-Brock, & Grenfell 1999). At low enough densities, the usual competitive effects of density on population growth rates will change sign. Mates become hard to find, the protection against predators afforded by herds or troops fails, and so forth. Humans specialize in cooperation and in using culturally transmitted technology and social institutions that might have been difficult to sustain at very low densities (Kline and Boyd 2011). The switch from simpler Middle Paleolithic to more complex Upper Paleolithic may have resulted from the increased density and/or better connectedness of populations after 50,000 ya (Powell, Shennan, & Thomas 2009). One possibility is that the uptick of high frequency, high amplitude climate variation that also occurred about 50,000 ya helped humans better compete in the crowded top carnivore guild filled with the big cats, hyenas, dogs, wolves, and bears of the time. Human adaptation by

cultural means is swifter than adaptation by genetic changes (Richerson and Boyd 2013). The onset of especially high frequency, high amplitude climate changes may have been analogous to Br'er Fox throwing Br'er Rabbit into the briar patch.

One possible scenario is, thus, that humans experienced the Allee Effect until after the Last Glacial Maximum around 20,000 ya. Small parties of hominins pursued ephemeral patches rich in game and other resources in an environment that was often highly dynamic. Plant and animal distributions might seldom be in equilibrium with the current climate. Other human groups would be an important resource more than competition. From them, a group could acquire mates, swap information about distant regions, cooperate in drive hunting projects, acquire the latest technology, and trade for resources like marine shells and high quality toolstone. This situation would be somewhat analogous to the one facing the Western Shoshone. Territoriality would not have been adaptive.

Some scraps of data, besides the population size estimates above, support this scenario. Neandertals acquired raw materials quite locally compared to Upper Paleolithic people (Klein 2009) and one well-sequenced Neandertal genome was highly inbred (Prufer et al. 2014). Archaic hominins might often have lived in small and isolated family groups. The population increases of Anatomical Moderns after 50,000 ya may still have been insufficient to bring them into the range of population sizes experiencing negative density dependence. The two major stylistic traditions of the west Eurasian Upper Paleolithic, the Aurignacian and the Gravettian, were similar over very large areas, as if they were one ethnic group with free circulation of bands from the Atlantic to the Urals and from the glacial margin to the Mediterranean (Klein 2009:Fig 7.25), something like the Western Shoshone on a continental rather than regional scale. Holocene hunter-gatherers, who were often territorial, have symbolic differences marking ethnicity on a much smaller scale. Dale Guthrie (2005), a Pleistocene paleoecologist with an artistic bent, analyzed a very large corpus of Pleistocene cave art and compared it to the ethnographically known parietal art of South Africa and Australia. The Pleistocene art is remarkably free of depictions of collective violence and defensive weapons relative to ethnographically known traditions in the Holocene. Many of the cruder images in Pleistocene caves seem to have been the work of adolescent boys. Hunting and sexual themes, but not warrior themes, are present in it. The graffiti of contemporary adolescents is rich in depictions of war. Guthrie finds it hard to imagine that UP adolescents were warriors-in-training to defend territories and yet did not depict warrior themes in their graffiti.

Conceivably, genetic predispositions for territoriality could have evolved in the latest Pleistocene and Holocene. Increased population densities and an increasing reliance on plant-rich diets seem to have led to a wave of genetic

evolution at this time (Hawks et al. 2007). However, the facility with which people can culturally evolve social institutions suggests that cultural adaptations for territoriality would be the dominant process.

I hope I have sufficiently stressed here how uncertain our reconstructions of hominin evolution in the Pleistocene still are. Progress over the last two decades has been impressive, beginning with high resolution ice and ocean cores showing the dramatic variation in last glacial climates. In the last few years, genomic data from fossils and living humans is beginning to give us glimpses into Pleistocene demography and evolution. Archaeological work in Africa has begun to reveal how Anatomically Modern people evolved many modern behaviors before our increase in population and range expansion out of Africa 50,000 years ago. Long term studies of the few remaining hunter-gatherer societies have yielded important new insights. Over the next two decades, we can look forward to a much higher resolution record. Today's hypotheses, if our current rank speculations deserve that sobriquet, are liable to seem naïve in retrospect. In the meantime, we can hope that they help alert us to what to look for in the evidence as it emerges.

References

- Atkinson, Q. D., Gray, R. D., & Drummond, A. J. (2008). mtDNA variation predicts population size in humans and reveals a major southern Asian chapter in human prehistory. *Molecular Biology and Evolution*, 25(2), 468–474.
- Bocquet-Appel, J.-P., Demars, P.-Y., Noiret, L., & Dobrowsky, D. (2005). Estimates of Upper Paleolithic meta-population size in Europe from archaeological data. *Journal of Archaeological Science*, 32(1656–1668).
- Courchamp, F., Clutton-Brock, T., & Grenfell, B. (1999). Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution*, 14(10), 405–410. doi: [http://dx.doi.org/10.1016/S0169-5347\(99\)01683-3](http://dx.doi.org/10.1016/S0169-5347(99)01683-3).
- Dyson-Hudson, R., & Smith, E. A. (1978). Human territoriality: An ecological reassessment *American Anthropologist* 80:21–41.
- Guthrie, R. D. (2005). *The Nature of Paleolithic Art*. Chicago: Chicago University Press.
- Hawks, J., Wang, E. T., Cochran, G. M., Harpending, H. C., & Woyzis, R. K. (2007). Recent acceleration of human adaptive evolution. *Proceedings of the National Academy of Sciences USA*, 104(52), 20753–20758.
- Hofreiter, M., & Stewart, J. (2009). Ecological change, range fluctuations and population dynamics during the Pleistocene. *Current Biology*, 19(14), R584–R594. doi: <http://dx.doi.org/10.1016/j.cub.2009.06.030>
- Klein, R. G. (2009). *The Human Career: Human Biological and Cultural Origins* (3rd ed.). Chicago: University of Chicago Press.

- Kline, M. A., & Boyd, R. (2010). Population size predicts technological complexity in Oceania. *Proceedings of the Royal Society B*, 277, 2559–2564. doi: 10.1098/rspb.2010.0452.
- Powell, A., Shennan, S., & Thomas, M. G. (2009). Late Pleistocene demography and the appearance of modern human behavior. *Science*, 324, 1298–1301.
- Prufer, K., et al. (2014). The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature*, 505(7481), 43–49. doi: 10.1038/nature12886
- Richerson, P. J., & Boyd, R. (2013). Rethinking paleoanthropology: A world queerer than we supposed. . In G. Hatfield & H. Pittman (Eds.), *Evolution of Mind, Brain, and Culture* (pp. 263–302). Philadelphia: University of Pennsylvania Museum of Archaeology and Anthropology.

Dominic Johnson and Monica Duffy Toft. *Reply: Common Ground? Critiques and Consensus on Human Territoriality*

International crises often spur debate among scholars. The Ukrainian crisis is important and instructive, but it can also distract us from the bigger picture—the patterns that underlie general theories of conflict. Ukraine tends to make people talk about the unique circumstances of regional history and politics. Territoriality tends to makes people talk about theories, and that is what we focus on here. Theories should be judged by many cases, not just one.

Four factors compelled us to write our original article on territorial conflict: (1) empirically, it is frequent, severe, and recurrent; (2) existing explanations fail to account for it; (3) it is not unique to humans, but a recurrent phenomenon in nature across a vast range of species and taxonomic groups; and (4) it is a contingent behavior in that it is manifested in relation to shifting costs and benefits.

Ours was, therefore, a humble aim, an invitation of sorts. We sought to illustrate to social scientists that what they take to be a puzzle has long been addressed by natural scientists with well-developed theories and data that account for territorial behavior among all organisms. We sought to start a potentially fruitful dialogue across previously isolated literatures, and with this exchange, we believe we have succeeded at least on this score.

All respondents agree there is something important to explain here, in the high levels of conflict and violence over territory, and that human behavior seems to have something to do with it (Table 1). The question is: what? Before engaging with the responses directly, we start by highlighting three important

themes that emerge across all of them, and are therefore worth stressing at the outset:

1. **Conditionality:** We argued that territorial behavior is contingent, whether as an evolved mechanism or as predictions of game theory. Nearly all respondents focused on the “bourgeois” strategy, where it is only territory owners that play hawk. However, this is a small subset of possible outcomes of the hawk-dove game (Johnson & Toft, 2014, p.28; Maynard Smith, 1982). If the benefits of victory (V) outweigh the costs of conflict (D), that is, where $V > D$, and even in various scenarios of the reverse ($D > V$), hawk is a universal or common strategy. We need to keep this broader picture in mind.
2. **Perceptions:** All of the issues discussed are important for understanding the conditions leading to territorial behavior. However, the importance (and complexity) of such conditions are often magnified because they can be *misperceived* as well as real. Because people act on what they believe to be true, whether it is true or not, perceptions can matter more than reality. Perceptions about territory loom especially large for human beings.
3. **Agency:** Some see an evolutionary approach to territoriality as too reductionist, questioning how much individual behavior really affects the behavior of ethnic groups or nation states, or whether there is any legacy of evolution on human behavior at all. However, only part of the argument is about *psychology*—it is about the emergence of effective *strategies*, which may occur by many means (natural selection, learning, imitation, calculation). Even for a creationist, the hawk-dove game can still lead to useful insights about the behavior of any agent, whether an individual, robot, group, or state.

Are We Devoted to Offensive Realism?

Turchin argues that rather than states playing contingent strategies, they all play the *same* strategy (Devoted Realism). Here, material interests are supplemented by “sacred values” attached to territory (as advanced by Atran *et al.*). Not only do we think this is a fruitful approach, but is in principle compatible with ours. *In a given strategic environment* (that is, with certain prevailing costs and benefits), states may indeed play the same strategy (e.g. residents play hawk, intruders play dove). Strategies only change if prevailing conditions change. But, having said this, we believe there are at least three challenges to Turchin’s formulation.

First, the theory of offensive realism itself is highly contested in international relations (IR). Since the 1990s, IR scholars have debated whether it is the case that states really want as much territory and power as they can get (Offensive Realism), such that they cannot help but fill any vacuums in their

way. Or, is it the case that states seek to preserve the status quo (Defensive Realism), in recognition that sometimes the costs to filling power vacuums might be high or higher than the expected benefits. Much evidence seems to support the latter (Mearsheimer, 2001; Walt, 1998; Waltz, 1979). So, not only does support for an Offensive Realist argument face a high burden of evidence, but most IR scholars support Defensive Realism (they may be wrong, of course).

Second, the Devoted Realism model combines theoretically conflicting themes at different levels of analysis: Offensive Realism is derived from a conception of the international system of states as anarchical in nature irrespective of states' internal features, whereas sacred values are characteristics of a states' internal composition as derived from their leaders, populations, and cultures (and they may therefore vary among states). Building a parsimonious theory that invokes international anarchy but tacking on domestic-level factors poses complex theoretical issues, including a serious reduction in parsimony.

Table 1. Key positions and differences among approaches

Author	Discipline	Key Cause	Additional factor	"Sacredness" binary
Johnson & Toft	Biology/ Political Science	Rational choice	Evolved psychology	—
Turchin	Ecology	Offensive Realism	Sacred land	No
Atran, Ginges & Iliev	Anthropology/ Psychology	Groups, identity	Sacred values	Yes
Turner	Sociology	History, society	Emotions	—
Szulga	Economics	Rational choice	Chance; external events	Maybe
Lopez	Biology/ Political Science	Rational choice	Evolved psychology	—
Richerson	Anthropology	Rational choice?	Ecology	—

Third, Offensive Realism implies that war is cheap (in contrast to Defensive Realism); hence we are in the domain of the Hawk-Dove game in which territorial conflict is expected among all players ($V > C$). If this is the case, then

why do we need to add on “sacred values” if the resulting prediction is the same?

Despite these three challenges, if we accept the role of sacred values, there are ways to integrate our two perspectives. One way to present our argument is to see natural selection itself as having encoded “sacred values”, precisely because they serve as proximate mechanisms to promote effective territorial behavior (e.g. vigorous defense of territory when *homeland* is threatened). Such a mechanism can still be flexible, as it is likely to be at least partially influenced by material cost/benefit calculations (e.g. avoiding impossible odds). Combining these features thus returns us to an evolved “contingent territoriality”, which is what we outlined. Sometimes, territory is important enough for organisms to treat it as if it is sacred.

Devoted Realism seems to imply that sunk costs and cultural factors tend to make fighting for sacred land non-rational, ineffective, or too costly in that sacred value can trump material factors. We would agree with the emphasis on emotional attachment, but suggest that this is not necessarily irrational, but precisely part of the adaptive mechanism, with past ties serving as (imperfect) signals of land that is genuinely valuable to continued survival. Whether, today, such a strategy continues to bring net material gains or incurs net losses is not fixed, however. It depends on the degree of mismatch between the evolved mechanism and the prevailing costs and benefits. Today is very different from the past, but sometimes key underlying variables are broadly similar.

Sacred Social Institutions or Scars of Evolution?

Atran, Ginges and Iliev stress that “sacred values” take us beyond the relevance of territory *per se*, to the motivating aspects of more abstract human concepts such as identity. Again we find complementarity and continuity here rather than differences. We agree that abstraction, symbolism, and identity is greater among humans than other animals (although note that territoriality itself can be astonishingly strong in both animals and humans), and indeed we stressed in our article that territory, in itself, is not necessarily intrinsically valuable. Rather, it is a proxy by which organisms secure access to key resources—including other members of their species. Territory may therefore be an important adaptation for group cohesion and, in the case of humans, identity. This raises the possibility that even suicide terrorism can be explained by psychological mechanisms arising from kin selection (even or especially if and where groups are *perceived or misperceived* as kin—exactly as occurs in the “identity fusion” that Atran *et al.* cite) (Orbell & Morikawa, 2011). In short, even if territorial conflict is “about” identity, we think evolution may have encoded this at least partly via land: a secure hold of land helps to safeguard and perpetuate the individual and their inclusive fitness in the group.

More generally, Atran *et al.* suggest that there is an absence of theorizing on “the interaction of material interests and sacred values in motivating human behavior”. While true in relation to the use of that particular terminology, we suggest that evolutionary psychology has been doing precisely this to some extent, in that “sacred values” are the proximate mechanisms for adaptive behaviors (as we noted above), and that these are designed to achieve adaptive, material ends (as Szulga notes in his response, sacred values can just be part of the utility function). Therefore, defense of sacred land may be one of evolution’s ways to help secure our kin, group, or way of life. Today, of course, such evolved mechanisms may vary in their effectiveness—a problem of mismatch again, which we believe is critical to understanding why (and when) violence and war still occur.

Given this, the key questions become: Under what conditions do sacred values help or hurt us? And, what perceptual lenses or forms of social organization make these conditions more or less likely?

History or Political Science?

Turner stresses that history and politics are complicated, and that we might need to generate one evolutionary theory for past territoriality (genetic evolution) and a different evolutionary theory for modern territoriality (cultural evolution). There’s no denying that cultural evolution plays an important role. However, because the adaptive logic is the same irrespective of the mechanism of selection (i.e., facing the same essential payoff matrix, the game theory leads to the same conclusions whether the actors are individuals, cultural ideas, or states) we would argue that the core evolutionary logic holds regardless.

There is also the problem that, however complex politics can look in its diversity of social, cultural and political manifestations, underlying it all—especially at the level of the international system—is a basic desire for resources to sustain life (Gat, 2009). Gat points out that much of IR theory simply glides over the question of the ultimate drivers of conflict, and assumes the utility of power without questioning its character or why humans want it.

We need to distinguish two approaches, which we outline in the article. The first is the ultimate causes of why humans groups come into conflict with each other, to which evolutionary theory (among others) brings important insights. The second is the proximate causes of war, for which history and politics become crucial to understanding any one particular case. While historians are able and eager to accommodate a range of multiple factors, the goal of political science (and evolutionary biology) is to identify patterns across cases and broader trends over time, influenced by a limited set of key variables, to identify general principles from a mass of apparently unique events. Our goal was the latter, to identify general patterns, those that not only transcend any

given case (such as Ukraine), but actually transcend all of human history and all species. We identified a general principle of behavioral ecology that applies across numerous taxonomic groups and has evolved independently many times. Humans could be an exception to this widespread pattern, but despite some good reasons for recognizing humans as different in many ways, the notion that we stand entirely outside of such core biological logic is unlikely (by Occam's Razor).

The Forgotten Hawks

Radek Szulga's economists' perspective is very interesting, aligning precisely with our baseline as adapted from James Fearon's article "Rationalist Explanations for War." Admirably Szulga is nevertheless willing to accept that something else is going on, since the rational choice approach does not seem to account for the severity of territorial conflict we witness.

However, Szulga points out there is nothing inherent about territory, *per se*, in the hawk/dove game: the game itself can apply to anything (with that particular payoff matrix). However, while true, Maynard-Smith's explicit motivation was to explain empirical phenomena related to territorial behavior, notably why animals with dangerous weapons sometimes do not use them to fight, and why residents tend to win. His approach was not divorced from the biological literature on territoriality that fed into it (and later scrutinized and developed the hawk-dove game in great detail). Moreover, other authors have explicitly found the model useful in predicting aspects of human private property and territoriality (DeScioli & Wilson, 2011; Gintis, 2007; Stake, 2004). The Hawk-Dove game could have been framed around some other problem, but the reasons it has become attached to territory are not coincidental. They are well reasoned and have come to be shaped by intense analytical interaction between field data and theory.

Szulga also critiques the Bourgeois strategy for being arbitrary (an ESS can just as easily arise whereby residents *lose*, or whether it is sunny or rainy). However, as noted in other cases above, this focuses only on the limited case where costs exceed benefits ($D > V$). Where benefits exceed costs ($V > D$) there is no ambiguity and the ESS is always Hawk (and if the imbalance is strong, $V \gg D$, opponents "should" fight to the death). Second, even within the $D > V$ domain, territorial incumbency can be the dominant strategy if there are (perfectly realistically) costs of transferring territory ownership (Gintis, 2007), or if residents have intrinsic combat advantages (e.g. familiarity with terrain, or the presence of local kin and allies) that increase their probability of defeating intruders (Johnson & Toft, 2014, p.30). Both make Hawk the favorite even in the Bourgeois scenario. So while Szulga is right that territoriality and Hawk are not a *necessary* outcome of the model, they are nevertheless a

recurrent and common outcome of it, as we have stressed, and there are well-specified conditions for when this will be the case.

As for Ukraine, it can indeed be seen in different ways. Is the “incumbent” Ukrainians or Russians? That partly depends on *when* you look. We defend our designation of Crimea and Eastern Ukraine as candidates to be viewed as on the Russian side (in applying the Hawk-Dove model, at least) because of contemporary population distributions (not national boundaries). As we stressed above, we think territory matters not least for the people and identities they contain, and thus the relevant agents here are population clusters, and who identifies with whom.

Also, perceptions can matter more than reality. Whatever the real distribution of ethnicities or power, if people *perceive* themselves to be incumbents, hawk may appear the best strategy whether or not that is the case. Here, evolution can be useful for making predictions about people’s preferences and behavior regardless of what the game theory suggests is the “correct” strategy today.

Szulga’s closing emphasis is on social scientists’ overly heavy focus on wars—times when things go wrong and bargaining breaks down. Many states are in a kind of *status quo* state, and only get studied when chance events or external shocks alter the parameters of the system (and the underlying game theory). But this suggests we should look closer at these models rather than reject them. Our *leitmotif* is contingency: under what conditions does playing hawk pay? The game theory suggests several overarching conditions that make the strategy good or bad. The payoffs, and even the game itself, may change. Moreover, evolved mechanisms themselves can also lead to behavioral change if there is a shift in the informational inputs (prevailing conditions change, or perceptions of those conditions change). It is a theory of change rather than stasis that we are searching for, and formulating the problem in game theoretical terms can help us understand when or how change may come, as well as the apparently static equilibria within the model.

Sorting Through the Alternatives

Anthony Lopez’s response is helpful in clarifying what exactly is being proposed (see Table 2). He also brings clarity in focusing on what kind of evidence we would need to identify behavioral adaptations such as territoriality (what problem were they designed to address, and what are their design features?). This highlights several important questions that have not yet been properly explored, including some simple ones in need of empirical investigation: what are the characteristics of human preferences, attitudes, and behavior towards territory? He suggests that the *null hypothesis* (Hypothesis 1) is that territory is not special, and will just be fought over (or not) in line with more general contingent adaptations for aggression. This can be

counterpoised against the hypothesis that territorial behavior is a specific adaptation in humans (Hypothesis 1; as we suggested), or that territory only becomes important when imbued with sacred value (Hypothesis 2; Atran *et al.*). Our original paper (and several respondents' models here too) contains elements of both, seeing material conditions as making aggression over territory a more or less rational strategy (H1), but that this is also influenced by evolved mechanisms specific to territory (H2). Nevertheless, Lopez suggests that while the evidence remains equivocal (and we need more research), the weight of evidence at present does indeed lie with territory as an adaptation (H2).

Table 2. Emerging hypotheses

	Territory special?	Principle Supporters*						
		J&T	T	AGI	T	S	L	R
Territoriality-as-asset	No	*	*			*		?
Territoriality-as-adaptation	Yes	*					*	
Territoriality-as-by-product	Depends		*	*	?			

*Initials of authors

If so, then we need to consider when such an adaptation is more or less likely to lead to war. Lopez emphasizes the problem of two sides both seeing themselves as resident (in which case both play hawk, even if prevailing conditions would recommend against it for one or both of them). He introduces the interesting idea that the “illusion of residency” might itself be a strategy to *bluff* the appearance and perception of one’s residency to others, if doing so serves to increase the probability of obtaining or retaining it. What, then, might encourage such illusions? Lopez notes that one key shift from our (more) nomadic ancestors into today’s world is our “relatively stable and fixed distribution of territorial nation states”, with many implications for the actual costs and benefits of territorial aggression. He cites Alan Grafen’s work showing that if territory tends to become occupied for long periods of time (by winners), then the Bourgeois strategy breaks down and both actors are better off playing hawk. This parallels findings that other circumstances, relevant to our contemporary world, including Ukraine, but also Israel and Jerusalem, can influence expectations of behavior. For example, when populations reach high density, hawk takes over even if it was rare before (Houston & McNamara, 1988). And finally, we note again that hawk is an ESS wherever $V > D$ and common even where $D > V$. Which world are we living in? And do we (and the “others”) perceive it that way?

How Far Do We Go Back?

Pete Richerson raises the important and compelling problem of how territorial humans actually were in our evolution—what is *our* natural history of territoriality? He is skeptical of territoriality as an evolved characteristic because anthropological studies have found that while some human societies are territorial, others are not. However, these studies do not logically challenge our hypothesis. In fact they support it.

Our article stressed that prevailing costs and benefits should make territoriality advantageous in one area and not in another. For that you need a contingent adaptation, and contingent adaptations are very common (e.g. we can be aggressive or cooperative, but are not all the time). We expect, therefore, that territoriality will be expressed in some human groups but not others, and this indeed appears to depend on local resources (e.g. Cashdan, 1983; Chabot-Hanowell & Smith, In Press; Dyson-Hudson & Smith, 1978). Moreover, we have direct evidence of this across species. As we pointed out in our article, 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 worth defending) (Carpenter & MacMillen, 1976). If birds can alter their territorial behavior, so can we. That hardly rules it out as an evolved trait.

Nevertheless, we know that the character of territoriality varies and that human societies differ enormously along a number of dimensions. Despite this, anthropologists Lee and Daly note that there are at least four characteristics that are shared by small-scale hunter-gatherers worldwide (our likely analogue for the kinds of societies among which we evolved). One of these four recurrent characteristics is that *land itself* is controlled by kinship groups. And that even within this practice of territorial control, ecological variation is managed with rules of reciprocal access that allow individuals to access resources in others' territories when permitted (Lee & Daly, 2004, p.4). In short, territories and territoriality persist even when individuals need to forage beyond them.

But, whatever the degree or importance of territoriality in the Pleistocene, even that window of reference (from c.2 million to c.10 thousand years ago) may be too narrow. One of our key points is that territoriality predates humans by millions of years, and is common across a stunning diversity of taxonomic groups (and from oceans to deserts). These bigger, phylogenetic and pan-ecological patterns reflecting the adaptive logic of territorial behavior may be more important in identifying broad trends than the small subset (and more speculative nature) of the human past. We did ourselves argue that we must look at humans' *own* evolutionary history, as well as phylogeny, since what is important is understanding adaptation to the environment in which a given

species evolved—that is indeed important. Nevertheless, the cross species patterns are also remarkable and not to be overlooked.

A final, critical point Richerson raises is that population sizes of ancestral humans may have been very low, and that human groups evidently traded far and wide, both conditions perhaps making territoriality unnecessary or counter-productive. We agree these conditions existed, but would argue that although human populations may have been low in size, they still clustered geographically and were therefore competitive in productive regions (not least because of the very Allee effects Richerson mentions—people need at least some other people around to reproduce effectively). What matters therefore is not population *size*, but population *density within a given area*. Studies trying to control for this problem have found that population pressure (population density controlled for available resources) correlates with the level of warfare (Kelly, 2013). While there may have been few humans to compete over unproductive deserts or mountains, there may have been many striving for choice territories in productive valleys or along shorelines. As for trade, the exchange of goods in no way precludes territoriality, and may even facilitate it (since one is less likely to be able to get all one needs in a system of exclusive territories). Examples from today and the past suggest that even rivals can trade—China and the US being one such example.

Box 1. Key research questions for future investigation

- What is the natural history of territoriality among human societies?
 - What are the characteristics of human territorial behavior?
 - What are the conditions that alter territorial behavior among humans?
 - Can territory *per se* acquire “sacred” value (like other objects do)?
 - Does territory become especially “sacred” *when* it is fought over?
- When are people more likely to perceive territory as their own (the false residency problem)?
 - Are there ways of operationalizing these hypotheses to test with empirical data (on small-scale or modern societies and war)?
 - Can these hypotheses be tested experimentally in the lab?

Conclusion

To summarize, territoriality remains an intractable problem for humans in the 21st century. But, from an evolutionary perspective it is unsurprising. Territorial conflict has been around for many millions of years. Therefore, we might want to look beyond the blinkers of our own recorded history if we are to identify broader patterns that may be at work. Territoriality among humans and other animals reveal a range of striking empirical similarities, many of which are captured by game theoretical models. While unique aspects of

human history, politics, intelligence, and values no doubt play a role, we would be ill advised to ignore the role that natural selection is likely to have played as humans distributed themselves across the globe—and not infrequently via bloody conflict. The range of responses to this suggestion have usefully widened the debate, introduced additional factors, and clarified the alternatives, but all at least seem to agree that we have an important problem to solve. Now would a good time to explore how far these interdisciplinary insights might help us—and to begin to test them with data.

References

- Carpenter, F. & MacMillen, R. (1976). Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. *Science*, 194, 639–42.
- Cashdan, E. (1983). Territoriality among human foragers: ecological models and an application to four bushman groups. *Current Anthropology*, 24, 47–66.
- Chabot-Hanowell, B. & Smith, E. A. (In Press). Territorial and non-territorial routes to power: reconciling evolutionary ecological, social agency, and historicist approaches. In J. Osborne & N. P. V. Valkenburgh (Eds.), *Territoriality in Archaeology*. Washington, D.C.: Archaeological Papers of the American Anthropological Association.
- DeScioli, P. & Wilson, B. J. (2011). The territorial foundations of human property. *Evolution and Human Behavior*, 32, 297–304.
- Dyson-Hudson, R. & Smith, E. A. (1978). Human territoriality: An ecological reassessment. *American Anthropologist*, 80, 21–41.
- Gat, A. (2009). So why do people fight? Evolutionary theory and the causes of war. *European Journal of International Relations*, 15, 571–599.
- Gintis, H. (2007). The Evolution of Private Property. *Journal of Economic Behavior and Organization*, 64, 1–16.
- Houston, A. I. & McNamara, J. M. (1988). Fighting for food: a dynamic version of the Hawk-Dove game. *Evolutionary Ecology*, 2, 51–64.
- Johnson, D. D. P. & Toft, M. D. (2014). Grounds for war: the evolution of territorial conflict. *International Security*, 38, 7–38.
- Kelly, R. L. (2013). From the peaceful to the warlike: Ethnographic and archeological insights into hunter-gatherer warfare and homicide. In D. P. Fry (Eds.), *War, Peace, and Human Nature: The Convergence of Evolutionary and Cultural Views* (pp. 151–167). New York: Oxford University Press.
- Lee, R. B. & Daly, R. (ed.) (2004). *The Cambridge Encyclopedia of Hunters and Gatherers*. Cambridge: Cambridge University Press.
- Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

Johnson and Toft: Social Evolution Forum. Cliodynamics 5:1 (2014)

- Mearsheimer, J. J. (2001). *The Tragedy of Great Power Politics*. New York: Norton.
- Orbell, J. & Morikawa, T. (2011). An Evolutionary Account of Suicide Attacks: The Kamikaze Case. *Political Psychology*, 32, 297–322.
- Stake, J. E. (2004). The property "instinct". *Philosophical Transactions of the Royal Society of London, Series B*, 359, 1763–1744.
- Walt, S. M. (1998). International relations: One world, many theories. *Foreign Policy*, 29–46.
- Waltz, K. N. (1979). *Theory of International Politics*. New York: McGraw-Hill.