



Calhoun: The NPS Institutional Archive

Faculty and Researcher Publications

Faculty and Researcher Publications Collection

2012

The Peacock's Tale: Lessons from evolution for effective signaling in international politics

Blumstein, Daniel T.

Blumstein, Daniel T., et al. 2012. The Peacock's Tale: Lessons from evolution for effective signaling in international politics (with comment). *Clodynamics: Journal of Theoretical and Mathematical History*, v. 3, iss. 1, pp. 191-214.



Calhoun is a project of the Dudley Knox Library at NPS, furthering the precepts and goals of open government and government transparency. All information contained herein has been approved for release by the NPS Public Affairs Officer.

Dudley Knox Library / Naval Postgraduate School
411 Dyer Road / 1 University Circle
Monterey, California USA 93943

<http://www.nps.edu/library>

SOCIAL EVOLUTION FORUM

The Peacock's Tale

Lessons from Evolution for Effective Signaling in International Politics

Daniel T. Blumstein (1), Scott Atran (2), Scott Field (3), Michael E. Hochberg (4), Dominic D. P. Johnson (5), Raphael Sagarin (6), Richard Sosis (7), and Bradley Thayer (8)

1) *Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA.* 2) *CNRS, Institut Jean Nicod-Ecole Normale Supérieure, 29 rue d'Ulm, 75005 Paris, France.* 3) *National Security Affairs Department, Naval Postgraduate School, 1411 Cunningham Rd., Monterey, CA 93943, USA.* 4) *Institut des Sciences de l'Évolution, Université Montpellier II, CNRS, Place Eugène Bataillon, 34095 Montpellier, France.* 5) *Politics and International Relations, University of Edinburgh, 15a George Square, Edinburgh, EH6 6LG, UK.* 6) *Institute of the Environment, University of Arizona, Tucson, Arizona 85716, USA.* 7) *Department of Anthropology, University of Connecticut, Storrs, Connecticut 06269-2176, USA.* 8) *Department of Political Science, Baylor University, One Bear Place #97276, Waco, Texas 76798, USA.*

Knowing how to send and interpret signals is an essential part of both diplomacy and war. Political scientists have recognized that costly signals—gestures and actions that involve significant cost or risk—are central to politics and diplomacy since modeling doyen James Fearon built his Ph. D. thesis around the concept in the 1990s. Because these signaling systems are pervasive in nature (many of these strategies arise independently and repeatedly to solve common problems suggesting evolutionary pressure to select strategies offering the most success at the least cost), their underlying strategic logic has important implications to foreign policy challenges we face today. By capitalizing on solutions derived by evolution over 3.5 billion years of life on Earth, we may identify ideas that otherwise might not have been explored in a policy context potentially offering quick, novel, and effective options to increase strategic and combat effectiveness. Here we present 8 lessons from evolution for political science.

Corresponding author's e-mail: marmots@ucla.edu

Citation: Blumstein, Daniel T., et al. 2012. The Peacock's Tale: Lessons from evolution for effective signaling in international politics (*with comment*). *Clodynamics* 3: 191–214.

Lesson 1. *Honest signals will be costly*

The power of costly signaling in the animal world is captured in the famous example of the peacock's tail. A series of studies have demonstrated that females select males with the longest and most elaborate tails. The benefits of such a selection criterion are clear: males that are able to allocate sufficient resources to grow this long tail, make it colorful, and keep it clean and healthy looking, survive despite their handicap. Males that can do this have energy to burn; they radiate their quality. The tail is thus an honest advertisement of the skills of acquiring food, avoiding predators, and controlling parasites and pathogens. Females choosing these showy males will ensure high quality genes being transmitted to their offspring

Indeed, from this and many other studies of signaling and communication in a diversity of mammals, birds, fishes, and insects, we can conclude that a common feature of animal communication is that costly signaling is valued by receivers, not just the sender, and in a wide range of settings. This biological rule has important implications for several aspects of foreign policy including making positive gestures during negotiations.

An effective negotiator must communicate honesty to the receiver, thereby inducing trust. Negotiations proceed with repeated positive feedback: the receiver needs to honestly signal trust back to the negotiator. Complicating this interaction is the cross-cultural nature of diplomacy that may result in the misinterpretation of honest signals. Positive gestures are one way of building trust. To be effective in the long term, positive gestures must be costly, yet many positive gestures in foreign policy are ritualized into protocol whereby there are formal and invariant rules by which states, and their emissaries, interact. If they are expected as routine, they are unlikely to be valued—seen as a result of the situation rather than any cooperative disposition of the actor.

Lesson 2: *Ritualized signals may have little value, but may be used strategically*

In animal systems, ritualized signals contain little information and do not vary much from individual to individual; consider the first, stereotypical behaviors in a courtship sequence. To avoid confusion, such displays are often ritualized. This lack of variation means that there is less of an opportunity for a receiver to associate a display with its underlying cost. And, while ritualized gestures might be commonplace ways of building trust—consider shaking hands, smiling, engaging in small talk—these displays may not be as effective as a genuinely costly display. This is not to entirely discount the importance of these displays, because effective cooperation between individuals is costly in that it takes time to develop and requires individuals to evaluate each other's reputations that are built over time. However, for now, let's consider isolated responses.

Systematically reducing the value of a signal to a receiver may be used strategically. The Egyptians capitalized on what became to Israelis a ritualized signal—maneuvers on the Israeli border in the months preceding the Yom Kippur War. Before attacking Israel, Egypt ran 40 military exercises on Israel's borders. This led Israel to discount the threat of a troop buildup on their border and enhanced its vulnerability.

However, there are also costs to ritualization. The recently scrapped Homeland Security Threat Level remained unchanged for years before being eliminated. What message did this invariant ritualized message send to travelers—or to prospective terrorists? Indeed, one lesson from nature is that one must consider the nature of the recipient in order to properly design a signal. And, in some cases, such ritualized signals may become meaningless and counterproductive.

Lesson 3: *Unexpected signals may be more effective*

Following a natural disaster, nations offer assistance to other countries. An offer of one million dollars in aid from a poor country is a much more meaningful contribution than the same offer from a wealthy one. And, individual citizens lining up to spontaneously help others (as often occurs following natural disasters) are truly meaningful gestures. For instance, following devastating 1999 and 2011 earthquakes in Turkey, members of the Israeli public spontaneously and immediately organized to collect food, clothing and other emergency necessities for Turkish citizens. While many governments formally responded, including the Israeli government, such responses are difficult to interpret since they are routine and likely to be strategically motivated. The spontaneity of the Israeli public response however appeared to be a sincere offer of help. The key insight is that it is not the absolute value, but rather the value relative to ability, and the sincerity of the donation that is likely to define a trustworthy display. Humans suffer from the so-called 'correspondence bias', which makes us more likely to assume the behavior of other actors is a result of their fundamental character, whereas our own behavior is a result of reacting to the situation—especially if the act impacts on us negatively. However, when the act impacts on us positively, we are more likely to assume the actor was motivated by situational constraints.

Lesson 4: *Threats should be costly*

Conversely, natural systems show us that negative gestures such as threats may also have to be costly to be effective. A striking lesson from evolution is that adversaries should organize their threats into a gradually escalating sequence, resorting to all-out fighting only if the less costly, earlier signals fail to induce their opponent to back down. Red deer competing for mates strut threateningly side-by-side, then bellow at each other, and only then lock antlers if one individual does not back away. The logic is impeccable: if the

adversaries are badly mismatched, they will realize it during the first phase and back down quickly, saving both from wasting further time and energy. If the payoff for winning is not great, individuals should not escalate. But, if the payoff is great, more subtle differences will be detected at the second stage, again a mutually beneficial outcome. Truly dangerous fights will only occur when both have proved themselves to be so evenly matched that signaling alone cannot distinguish between them. Over millions of years, natural selection has crafted a finely-tuned 'playbook' of signaling and escalation for species' to work from as they attempt to resolve their conflicts of interest without getting killed in the process.

Humans face similar problems, and bargaining theories of war have investigated similar problems of incremental signals. However, evolution offers a useful new perspective on this because we face types of conflict that our ancestors never encountered, and thus to which our responses have not been molded by selection. In a world of cyber-warfare, weapons that kill at a distance, and remote command and control far from the battlefield, our evolved signaling mechanisms neither convey messages to the enemy nor bring us direct feedback (e.g., drone pilots fight thousands of miles from the battlefield, the sources of computer worms like Stuxnet are opaque and difficult to trace). This means we may expect an evolutionary 'mismatch' between our behavior and our environment and may lead to unintended and un-checked escalation. Rival states may exchange costly signals prior to launching into war, for example military parades that display cutting edge technology, power projection through naval port calls, elevating level of alert status for forces as well as funding levels for security and defensive activities. However, different strategies and their deployment between adversaries in a crisis may lead to confusion and potentially catastrophic outcomes. Considering the stakes in incidents such as the nuclear alerts ordered by President Kennedy in the Cuban Missile Crisis, by Nixon during the Yom Kippur War of 1973, or North Korea's response to accusations that it torpedoed and sank a South Korean warship in March 2010—the question becomes a very urgent one.

Evolutionary thinking provides guidelines for formulating an appropriate policy response, particularly when it is unclear whether adversaries are following the same rules. Just as in conflicts in natural systems, honest signaling of intention in a series of reciprocal steps is the best way to obtain a peaceful resolution. And, developing a reputation for honest signaling is a powerful force in obtaining trust. In the absence of a reputation for honest signaling, it is difficult to know whether to escalate up or down in negotiations.

Lesson 5: State apologies should be costly

To be successful apologies must be costly. The cost of an apology is the political risk to the person or administration apologizing, and broader costs to pride

and well-being within an apologizing society. This may explain why meaningful apologies are not very common, and most apologies happen long after the incident that stimulated it. Apologizing, after all, is a political calculation. Waiting until there is no political cost because opponents have died or moved on to some other issue lessens the value of an apology. In 1998, President Clinton apologized for his administration's inaction during the Rwandan genocide four years earlier—an unusual and costly act for a President still in office. Israel and Germany have good diplomatic relations and there is also friendship among the populations (many Germans travel to Israel) and this is remarkable given the devastation in the living memory of so many Jews and Israelis. At least three factors were probably important: 1) public apologies which were followed up by real costs such as 2) reparation payments, and 3) a schooling system that makes German children more educated about the Holocaust than probably any other children outside Israel in the world. Nelson Mandela probably recognized the huge value of costly apologies when he set up the reconciliation commissions in South Africa after the fall of the apartheid. Rather than sending all whites involved in the apartheid state to jail, he created a forum for them to apologize face to face with their victims and wipe the slate clean.

Insincere apologies may be particularly costly. Then Secretary of Defense Donald Rumsfeld's apology about the Abu Ghraib prisoner abuse backfired when he tried to also explain that there was Arab mis-understanding of American culture which could not condone such behavior. This apology was widely regarded as a flop. Japan's apologies for atrocities in China during World War II remain unvalued by the Chinese because of Japanese dignitaries' visiting the Yasukuni Shrine to Japanese war dead, which includes the remains of convicted war criminals.

Lesson 6: *Humans (and animals) are not necessarily rational: symbolic concessions may be useful*

Studies of animals (and humans) also show us that in certain circumstances, individuals do not make economically rational decisions. There is healthy debate about whether these are indeed costly mistakes or evolved strategies. However, there are some lessons from this observation for security and policy.

One of these is that low cost actions may sometimes have a high value to recipients of these actions and, as Jeremy Ginges and colleagues found, the economically rational offers are not necessarily what people will accept. Indeed, people's core values must be recognized, often by symbolic concessions. In their research asking both Palestinians and Israelis about what sort of incentives might help move a peace process forward, they found that financial incentives were viewed very negatively, but symbolic concessions, such as apologies for past actions and removing anti-Semitic material from textbooks, went far both with leaders and citizens. Indeed, offers of reparation

without the necessary symbolic concessions were viewed negatively. Here again, Nelson Mandela recognized the importance of symbolic concessions when he publicly supported the Springbok rugby team, even though, initially, his black supporters wanted to disband this symbol of apartheid. Understanding that economically irrational behavior is common and that symbolic concessions have great value may be essential in negotiating through seemingly intractable political quagmires (e.g., such as those in North Korea, Iran, and, as Atran and Ginges write—Israel/Palestine).

Lesson 7: *Weaker parties will advertise the strength of their conviction*

Obviously not all diplomatic interactions and conflicts are between state actors. Are there unique insights for interactions with non-state actors? A characteristic of a state interacting with a non-state actor is power asymmetry. Consider the rapid spread of suicide terrorism among weak and disenfranchised organizations fighting a stronger state. With the exception of Kamikaze pilots in WWII, we have not seen two strong opponents in the 20th century use suicide attacks as a military strategy. Indeed, one could argue that the Japanese only resorted to Kamikaze pilots once they realized they were losing because of a loss of pilots, fuel, and weapons. One interpretation of this is that being able to marshal legions of self-sacrificial volunteers creates an honest indicator of the amount of displeasure and the intention to continue fighting that the weaker party faces. When non-state actors fight against democratic state actors, the public opinion is as much a target as the military and the weaker party often wins by turning public opinion against ongoing conflict. Thus, in such asymmetrical combat, such as Chechens against the Russians, Hamas against Israel, or the LTTE against the Sri Lankan government, we should expect the weaker party to work hard to impress upon the stronger party the strength of their conviction. Suicide terrorism may be such a potent signal because it is an unbluffable signal of commitment.

Political scientists have recently recognized this, and have characterized five distinct ways in which terrorists use costly signals to advance their agenda: attrition (wearing down the enemy), intimidation (of opponents in their own population), provocation (of the enemy to violence and collateral damage that consolidates resistance against it), spoiling (of a peace process), and outbidding (of domestic rival parties). Moreover, natural systems show us that self-sacrifice is often associated with high relatedness. Social insect workers will die to help their highly-related group persist and the same logic might explain situations in which tightly knit groups, bound by kinship and religion, are willing to make the ultimate sacrifice. Holding this lens over the problem of terrorism clarifies the strategic logic that should guide a policy response.

Lesson 8: *Signals are often species specific: it's essential to know your audience*

Species differ in their signals that are often directed to conspecifics. Indeed, divergent communication signals are used to 'isolate' species from each other and prevent costly, but mis-guided fights, and potentially wasteful reproductive attempts with the wrong species. The final insight comes from the widespread evolution of species-specific signals: it's essential to know your audience in order to communicate effectively to it and the same signal may mean very different things to different audiences.

Consider how two populations may have difficulties communicating. The United States botched the messaging to the Muslim world after killing Osama bin Laden. To the audience in the United States there was a low cost propaganda release of video of bin Laden sitting on the floor watching a small TV aimed at demonstrating what a miserable and pathetic fellow the man was. But to would-be jihadis, the actual effect was the opposite. They saw a leader living in humble conditions—a positive image under Muslim law. It was a low cost, culturally blind signal sent by the United States that was filtered and amplified through Islamic culture and tradition into a demonstration of the ultimate high-cost sacrifice of the man for his people.

The lesson is clear: be sure you know who your audience is before signaling and realize that the same message can be interpreted quite differently by different audiences. A low-cost signal to one audience could illustrate high-cost behavior to another audience.

Conclusions

While humans, like every other organism, have a unique evolutionary history, the rules of evolution and natural selection act on us all. More work is needed to disentangle the logic of individual versus group selected mechanisms on policy, but identifying these rules will inevitably create more insights about successful strategic behavior. Importantly, nature's rules are all around us just waiting to be discovered and explored to see whether they have modern-day applications.

Acknowledgment

In addition to their primary affiliations, the authors are members of the Natural Security Working Group (www.naturalsecurity.arizona.edu) that has been supported by the National Center for Ecological Analysis and Synthesis, and the Office of Naval Research-Global.

References

Atran, Scott, and Jeremy Ginges. 2009. How words could end war. *New York Times* 24 January:WK12 (New York Edition).

- Fearon, James D. 1995. Rationalist explanations for war. *International Organization* 49(3):379-414.
- Ginges, Jeremy, Atran, Scott, Medin, Douglas, and Khalil Shikaki. 2007. Sacred bounds on rational resolution of violent political conflict. *Proceedings of the National Academy of Sciences* 104(18):7357-7360.
- Husain, Ed. 2011. Did U. S. botch message with bin Laden videos? <http://www.cfr.org/terrorism/did-us-botch-message-bin-laden-videos/p24939>
- Kydd, Andrew H., and Barbara F. Walter. 2006. The strategies of terrorism. *International Security* 31(1):49–80.
- Rabinovich, Abraham. 2004. *The Yom Kippur War: The Epic Encounter That Transformed the Middle East*. New York: Schocken Books.
- Sagarin, Raphael D., and Terrence Taylor (eds.) 2008. *Natural Security: A Darwinian Approach to a Dangerous World*. Berkeley: University of California Press.
- Schmitt, Eric. 2010. U. S. offers aid to rescue Pakistanis and reclaim image. *New York Times*, 15 August:A6 (New York Edition).

Commentaries

James Fearon

Stanford University

e-mail: jfearon@stanford.edu

Blumstein et al. look to evolutionary theory regarding signaling in animal species to try to draw out some general rules of thumb that they think might be useful for diplomats and politicians in matters of foreign policy. The rationale for the exercise is that “By capitalizing on solutions derived by evolution over 3.5 billion year of life of Earth, we may identify ideas that otherwise might not have been explored in a policy context potentially offering quick, novel and effective options to increase strategic and combat effectiveness.”

None of the eight rules of thumb, however, are novel propositions or observations, and some—like the eighth, ‘it’s essential to know your audience’—are mainstays of international relations literatures and diplomatic folklore or commonsense. (Not to say such wisdom is always acted on!) The core idea in several of them is that signals will not reliably convey their message unless they are actions (or words) that would be more costly for a potential bluffer to take. This idea has been familiar in Economics and Political Science research for some time now, and in this specific formulation it derives not from evolutionary theory but from developments in information economics in the late 1960s and early 1970s.

There are indeed some significant parallels between the strategic problems facing animals competing over territory or mates and that between two states, or a state and non-state group, at odds over territory or public policy. In both cases violent conflict is typically costly and thus something both sides would like to avoid. But both sides would also prefer that the other side concede more of whatever resources or goods (which might be symbolic, in the human case) are at stake. In both contexts, then, all can ideally be made better off if they can develop some kind of signaling system that allows the more motivated or strong types to credibly reveal this, so avoiding violent contests when a stronger or more motivated party faces a weaker or less motivated antagonist. It is fascinating—though perhaps not so surprising, once we have seen the analogy and realized that evolution can sometimes select ‘best reply’ strategies even without cognition—that animal contests (including sexual selection) often exhibit complex strategies of costly signaling.

What is less clear is whether there are specific findings from the study of signaling in (non-human) animal systems that have interesting or novel implications for diplomats and politicians engaged in international affairs. As

noted, none of these eight general rules of thumb are results or arguments that did not already emerge from social science studies of signaling in human contexts. Perhaps, however, as the study of signaling in animal contexts proceeds it will produce findings that suggest novel ideas about signaling in human contexts.

For example, the canonical story about the peacock's tail has, according to more recent research, gotten somewhat murkier. There has always been the following theoretical objection: If a bigger tail with more eyespots signals greater quality, then greater fitness should select out variation in tails so that residual variation in tail quality is not correlated with fitness. Thus, in evolutionary equilibrium, expected fitness must be equal across larger and small tails, with the handicap of a larger train exactly compensating for a bird's greater underlying quality.

Empirically, the original study found a correlation between number of eyespots and mating success in a population in Britain. However, more recent studies based on populations in France and Japan reached different conclusions. In the French group, number of eyespots was unrelated to mating success, but the length of the train was. In the Japanese birds, there was no correlation for either one. In studies of three different North American populations there was also no correlation between number of eyespots and mating success (at least until almost the bird's eyespots were clipped off).

It could be that some other feature of the tail is a signal of mate quality. According to Erol Akçay, an evolutionary biologist who is my source for this information, we just don't know, and we also don't have studies that directly test whether the peacock's tail is a costly signal, since cost has not been measured and related to 'quality.' Akçay (personal communication) thinks it is likely that peacock's tail is a signal of some kind, since it is hard to see it evolving without having some adaptive value. But he thinks "what exactly it is a signal of and whether it is honest because it's costly are open questions at this point."

So perhaps things are not so straightforward. This is surely also the case for diplomacy. For example, it is not uniformly true that "honest signals will be costly" (Lesson 1) or that (Lesson 4) "threats should be costly." At a minimum, these claims depend on a prior assumption that we are talking about a situation in which the signaler can have a strong incentive to misrepresent its preferences or type—to bluff—to the target. In some diplomatic contexts, 'cheap talk' can be informative because the parties' interests are sufficiently aligned that misrepresentation can be counterproductive. Or, it can be the case that in signaling between governments there are so many sources of publicly available information about what is going on that misrepresentation is not a big concern. Finally, when states are signaling over multiple dimensions of policy, which is often the case, cheap talk can be informative even when there are incentives to misrepresent.

A final comment is that to the extent that we do put stock in these costly signaling claims as rules of thumb, they may actually argue against the notion that evolutionary (or economic) theory can increase diplomats' tactical success in contests. The point of these arguments is that contests are like auctions in which the side that is genuinely more resolved or more capable is more likely to win. The advice "Make your signals of resolve (or reassurance, if seeking peace) costly!" only makes sense if you actually are that resolved or you are that willing to risk a disadvantage in order to get to peace. There is a parallel here with "Lesson 3: Unexpected signals may be more effective," where the authors suggest that "individual citizens lining up to help others (as often occurs after natural disasters) are truly meaningful gestures." The advice "deliberately make your gestures of reconciliation spontaneous in order to make them effective!" is a bit of contradiction in terms.

Evolutionary theory regarding signaling in animal contests may yet produce novel and interesting insights into signaling in roughly parallel human contexts. Given the incredible complexity and diversity of animal signaling systems, I would expect that this could be the case. But I'm not sure if these very high level rules of thumb optimally exploit the potential in this area.

Olivier Morin: *Why Cheap and Ambiguous Signals May Serve Diplomacy Better than Credible Commitments*
Central European University
e-mail: olivier@treizh.net

In this interesting paper, Blumstein et al. argue for a view of diplomacy based on credible commitments, honest signals, and the prevention of misunderstandings caused by cultural distance. They hope to enlighten politicians with lessons drawn from evolutionary biology (though one might note that credible commitment was explored by Clausewitz before Darwin, and costly signaling is found in Thomas Schelling before Amos Zahavi). This comment challenges two points made by their article.

First, I argue that misdirection, ambiguity and provocation are worthy tools in a politician's toolbox. Yes, such strategies may lead to military escalation — but sometimes that is precisely the point. I shall illustrate this with the story of the Ems dispatch, one of the most famous episodes of diplomatic signaling. Second, I will argue that Blumstein et al. misuse the notion of costly signaling,

as used in economics and evolutionary biology (Zahavi, 1977). A costly signal in the strict sense is so costly to produce that the fact of producing it provides a credible information. Peacock's tails and nuclear tests are costly signals *sensu stricto*. Threats, promises, symbolic gestures, and most other diplomatic moves are not costly in that sense. As a result, their informational value is different.

The Ems dispatch

In the summer of 1870, Chancellor Bismarck made a diplomatic move that would eventually make him the unifier of Germany and the victor of the Franco-Prussian war (Howard 2001). The move began when he encouraged a cousin of the King of Prussia to become candidate for the throne of Spain. A Hohenzollern in Madrid — that would mean an encirclement of France by friends of Prussia, a notoriously hostile power. Bismarck knew this. He knew this may cause violent reactions from the French, even a war in which Paris would play the part of the aggressor. Such a war would fit well into Bismarck's plans for national unification.

Yet Napoleon III deftly defused the crisis. He uncovered Bismarck's plan and managed to have the Hohenzollern claim to the Spanish throne withdrawn, with the agreement of the King of Prussia. A French agent went to Ems-Baden to seal the deal with the King. Bismarck, seeing his plan unraveling under his eyes, refused to be present at the meeting, and threatened to resign if the meeting took place. All in vain.

On the thirteenth of July, on the promenade of Ems, the King had a tense but courteous talk with the French ambassador. He confirmed the withdrawal of the Hohenzollern candidacy. Unbeknownst to Napoleon III, the French secretary of State had ordered the ambassador to take a hard line. The ambassador tried to push his advantage and obtain a commitment for the future. The King politely declined, and telegraphed Bismarck that the incident was over. The Chancellor did not react. He was nowhere to be found.

Bismarck was busy exploiting a mistake in the ambassador's strategy. The King had satisfied one French request, but not the other. Bismarck cut and rephrased the King's telegram to showcase the King's refusal. His version of the Ems telegram, sent to major French and German newspapers, depicts a harsh and bitter encounter. Nationalists on both sides further distorted the message. The dispatch humiliated Prussia, whose King had been harassed with an arrogant ultimatum. It incensed the French, who declared war on Prussia less than a week later. Bismarck had won his first move.

The Chancellor's tactics may interest Daniel Blumstein and his coauthors, since it turns most of their advice on its head. Bismarck did not pay attention to Blumstein et al. 's lessons 1 and 4. He produced few signals, most of them deceptive. He did not intend to resign if the Ems meeting took place. The Ems dispatch itself was a deliberately distorted signal.

Oblivious to Blumstein et al. 's lessons 2 and 3, Bismarck used historical precedent in a predictable, almost boring way. Unifying German imperial powers with the Spanish throne had been a classic geostrategic move in European history since the time of Charles V. It had always been interpreted as an attempt to isolate France, and Bismarck used this common knowledge to provoke the French.

Against lesson 8, Bismarck knew that the Ems dispatch would give rise to divergent interpretations on both sides of the Rhine, with everyone distorting and amplifying the dispatch to suit their purposes (as he himself did). Yet he did not try to limit or control the disagreements, as he did not see them as obstacles. Quite the contrary.

'Costly' signals?

Yet, one might reply, Bismarck seems to follow at least one of Blumstein et al. 's lessons. In a way, he uses 'costly' signals: every time he communicates something, he takes a risk. His foreign policy is like the peacock's tail in this respect: it is a signal with a cost.

The analogy is misleading, though. The costly signals of modern costly signaling theory are not merely signals that have a cost to the producer. The point of costly signals is that certain signals are more reliable than others since their *production* is costly (Veblen 1899/1973, Schelling 1960, Zahavi 1977). For instance, a peacock's tail is a reliable indicator of a peacock's fitness because it would be hard to grow a beautiful tail without a good immune system. Or possessing two luxury cars is a reliable indicator of wealth because possessing such cars without being wealthy would be difficult. Those signals are especially reliable because they reveal a cost that has already been paid.

Compare those costly-to-produce signals with signals that are cheap to produce, though the emitters take risks when emitting them. Uttering a sentence, in itself, is easy, whether the sentence is true or not. Lying may have costly consequences, of course, but those costs lie in the future. However near that future might be, the costs are not paid by the liar when he pronounces his lie. Thus the production of a sentence, by itself, says nothing about its truth. In contrast, the mere fact of producing a beautiful tail is a good indicator of the reproductive potential that the tail indicates.

Blumstein et al. are right to note that politicians sometimes use such signals, like military parades or nuclear tests. But most diplomatic threats and promises are not costly signals in the biological sense. They are not costly and honest in the way a peacock's tail is costly and honest. Bismarck's threat to resign if the Ems meeting took place was just cheap words. His utterance of the threat was not an honest signal of his intention to resign. Indeed, nothing Bismarck could have *said* could be a costly signal in the biological sense.

Technical or moral advice?

Bismarck's warmongering was, of course, objectionable in many ways. A moral person would usually prefer diplomatic strategies based on credible commitment, and a careful avoidance of escalation and misunderstandings. Since the Cold War, this way of doing politics seems the least destructive on the global scale. Yet individual politicians do not necessarily have peace and security as their first objective. Credible commitment is a useful tool for them, but sometimes ambiguity and deception serve them better. Even for peace-making: Charles de Gaulle solved the Algerian crisis by appearing utterly uncommitted and unpredictable. Thus, while I share the moral outlook of Blumstein et al. and agree with them on ethical grounds, I do not think we should commend their strategic solutions to actual politicians — unless we make it clear that we are not giving technical advice to diplomats, but promoting one particular view of what international relations should look like.

References

- Michael Howard, 2001. *The Franco-Prussian War: The German Invasion of France 1870-1871*. Oxford: Routledge.
- Thomas Schelling, 1960. *The Strategy of Conflict*. Cambridge: Harvard University Press.
- Thorstein Veblen, 1899/1973. *The Theory of the Leisure Class*. Boston: Houghton Mifflin.
- Amos Zahavi, 1977. The cost of honesty (Further remarks on the handicap principle). *Journal of Theoretical Biology*, 67: 603-605.

Rebecca Sear

London School of Hygiene and Tropical Medicine

e-mail: rebecca.sear@lshtm.ac.uk

The application of evolutionary theory to the real world has the potential to be one of the most exciting developments in the human evolutionary behavioral sciences. Most research over the last few decades using an evolutionary framework to understand human behavior has been largely of theoretical interest, so to see researchers actively engage with how this research can be applied in settings such as international politics is an important step forward.

While I am an enthusiastic supporter of such attempts, a question which interests me, and which is not dealt with in this particular article, is how to put these academic ideas into practice. The authors list 8 lessons that politicians can learn from evolutionary theory which will help them send and interpret signals in both diplomacy and war. But how does one get the actors involved in international politics to learn these lessons? The majority of such individuals are unlikely to have much training in evolutionary theory, or any other kind of science for that matter. No member of the British Cabinet, for example, has a science degree, and only one member of the House of Commons is apparently educated to PhD level in science. So it seems that researchers interested in persuading politicians that the insights of evolutionary theory may be of use to them need to get involved in lobbying and actively engaging with the political community, to bring this research to their attention. Generating greater interdisciplinary links within academia, and getting evolutionary ideas onto the syllabi of social science and humanities degrees would also help lay the groundwork, as the social sciences and humanities tend to be the educational route most UK politicians, at least, take (but see Mesoudi et al 2010 for a discussion of the challenges involved in this endeavor). A solid grounding in science and evolutionary theory during school-level education would also be a very good start, though possibly even more challenging.

To lobby and engage successfully with politicians, I'd also suggest researchers need to consider carefully exactly how their research may be applied in the real world. I suspect what may hold some evolutionary behavioral scientists back from doing so is a lack of understanding of how the theory-driven, hypothesis-testing research they do can be usefully applied to real world settings (at least, this is a significant reason for my own reluctance to engage substantially with policy-makers). The authors of this article have done just that by including examples of how past political events can be interpreted through the lens of evolutionary theory. What might be even more useful is to consider how evolution can be applied to developing future policy. This necessarily involves considerable dialogue with politicians and policy-makers. Applied work is clearly becoming an active area of interest for the evolutionary community as suggested, for example, by the special issue of *Human Nature* on 'The human behavioral ecology of contemporary world issues' (Tucker, 2007); the recent book on *Applied Evolutionary Psychology* (Roberts 2011); and the recent workshop on *Applied Evolutionary Anthropology* held at the University of Bristol in September 2011.¹ While these examples largely involve academics keen to apply their work, rather than policy-makers keen to apply it, Curtis and her colleagues at the London School of Hygiene and Tropical Medicine have been successful in promoting their

¹ <http://www.bris.ac.uk/arts/research/events/2011/641.html>

'Darwinian approach to health promotion' in the real world (see e.g. Curtis, de Barra et al 2011; Curtis, Schmidt et al 2011); she helped found, for example, the Global Public-Private Partnership for Handwashing with Soap.²

Something else perhaps to consider, is how to convince politicians of the added value evolutionary theory can bring to the table. Certain sections of academia have had success in persuading politicians that their discipline can be used in the formulation of policy, for example, 'nudge' economics has been successfully promoted by behavioral economists (Thaler and Sunstein 2008). How might we convince politicians that the evolutionary behavioral sciences have anything to add to the voices of behavioral economists and psychologists working on human decision-making? One solution might be to combine evolutionary theory with disciplines more familiar to policy-makers: Tucker's approach, for example of combining human behavioral ecology with behavioral economics to apply to conservation and development issues does just that (Tucker, 2007).

An important part of any endeavor applying academic research to the real world is likely to be the evaluation of policies which have been informed by such research. This may not be easy, since randomized control trials are clearly not possible in the field of international politics, but might it be possible to use 'natural experiments' where policies known to have been influenced with evolutionary ideas could be compared to those who have not (though this of course assumes that it is possible to identify policies which have been informed by evolution, perhaps not easy to determine in itself)?

I welcome any endeavor which attempts to develop evolutionary research for application to real world human affairs, and would be very interested to hear more about the practicalities of such endeavors from those currently engaged in them: how is evolution being put into practice?

References

- Curtis, V., M. de Barra, et al. (2011). Disgust as an adaptive system for disease avoidance behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**(1563): 389-401.
- Curtis, V., W. Schmidt, et al. (2011). Hygiene: new hopes, new horizons. *The Lancet Infectious Diseases* **11**(4): 312-321.
- Mesoudi, A., D. Veldhuis, et al. (2010). Why aren't the social sciences Darwinian? *Journal of Evolutionary Psychology* **8**(2): 93-104. Introduction to a special issue on this topic; see also other papers in this volume.
- Roberts, S. C. (2011) Applied Evolutionary Psychology. Oxford University Press.

² <http://www.lshtm.ac.uk/aboutus/people/curtis.val>

- Thaler, R. H. and Sunstein, C. R. (2008) Nudge: Improving Decisions About Health, Wealth and Happiness. Yale University Press
- Tucker, B. and L. R. Taylor (2007). The human behavioral ecology of contemporary world issues: applications to public policy and international development. *Human Nature* **18**: 181-189. Introduction to a special issue on this topic; see also other papers in this volume.
- Tucker, B. (2007). Applying behavioral ecology and behavioral economics to conservation and development planning: An example from the Mikea forest, Madagascar. *Human Nature* **18**: 190-208.

Armando Geller

Scensei and George Mason University

e-mail: ageller@scensei.com

Students of international relations have applied signaling models to a variety of problems: decision to go to war (Morrow 1992), dispute resolution (Holler and Lindner 2004), foreign policy (Fearon 1997) and crisis bargaining (Taran and Leventoglu 2008), to name a few. The eminent authors, Daniel T. Blumstein, Scott Atran, Scott Field, Michael E. Hochberg, Dominic D. P. Johnson, Raphael Sagarin, Richard Sosis, and Bradley Thayer, argue that studying signaling in nature reveals much about the underlying mechanisms of signaling in international politics. I remain skeptical: Humans use language purposively not only to formulate thoughts, but also thoughts about thoughts, knowingly distinguishing themselves from peacocks or deer. Consequently, signaling systems along with their associated behavior have emerged as outcomes of purposive interactions among human entities. For example, diplomatic behaviors such as trust building, deception and escalation have come about not as merely evolutionarily superior behaviors, but as products of groups of humans reflecting on their own and on one another's thoughts that are assumed to represent, express, and reason about behaviors.

Do we find signaling systems with equally high-dimensional reflection in nature? I believe not. The degree of human cognitive capability and organizational machineries required for signaling in international politics render the evolutionary concepts in Blumstein et al. weak candidates for explaining international political behavior. For example, comparing escalation mechanisms among deer with the escalation ladder described by Kahn (1965) quickly turns into a futile exercise. Some evidence may point to 'notional' similarities between mechanisms of signaling in international politics and

those in nature. However, relying on such evidence to prescribe certain policies and specific behaviors is ill-advised.

Call me conventional, but I have a hard time believing that a negotiator must communicate honestly in order to be effective as dictated by the peacock's tail. I also find it difficult to derive policy from signaling systems in nature that can answer questions such as when should states apologize, individuals commit suicide terrorism, and Al-Qaeda kill a hostage; at least at this stage of scientific inquiry. So lessons from evolution (for example for signaling) should be underpinned empirically and perhaps even experimentally if they are to evolve into more than a catch phrase for military-industrial circles, as was 'complexity'.

As an undergraduate student I was once rebuked by a professor for using a scene from an Asterix and Obelix comic book to illustrate cultural variation in the usage of time in the High Middle Ages. He thought it was a bad analogy because it lacked contextual correspondence. So what to take away from the article? That some evolutionary signaling mechanisms appear relevant for explaining signaling in international politics? That may be true. Yet, far more evidence should be brought to the fore to link signaling in nature with that in international politics empirically. Beginning with the differences between the two phenomena is perhaps a way forward.

References

- Fearon, James D. (1997) Signaling Foreign Policy Interests. Tying Hands versus Sinking Costs. *Journal of Conflict Resolution* 41(1):68-90.
- Holler Manfred J. and Ines Lindner (2004) Mediation as Signal. *European Journal of Law and Economics* 17(2):165-173.
- Kahn, Herman (1965) *On Escalation: Metaphors and Scenarios*. New York: Praeger.
- Morrow, James D. (1992) Signaling Difficulties with Linkage in Crisis Bargaining. *International Studies Quarterly* 36(2):153-172.
- Tarar, Ahmed and Bahar Leventoglu (2008) Bargaining and Signaling in International Crises. Unpublished paper.

Reply

Blumstein et al.: *The Peacock's Tale: New Ideas Require Quantitative Evaluation*

Speak softly and carry a big stick.

—Theodore Roosevelt

We were thrilled to receive four extremely thoughtful and constructively critical commentaries on our focus article. Apart from anything else, we are pleased to see that all respondents recognized the importance of strategic signaling in both nature and international politics, and the value of exploring their differences and similarities.

We especially appreciated Rebecca Sear's goal to ask big picture questions about how one would overcome the obstacles of getting evolutionary insights out of the labs of biologists and into the laps of policymakers. As with the growing field of evolutionary medicine, we agree that an evidence-based experimental approach will be the best way to identify and hone effective strategies—the proof of the utility of these ideas is in the pudding. Can they improve our predictions and success in international politics?

Armando Geller is concerned to point out that humans are a very complex species, but we disagree that this means there are no insights from successful strategies in other species. The key point is that 3.5 billion years of life on Earth reveals recurrent behavioral, organizational and mathematical patterns that appear across contexts and species, and transcend cognitive sophistication. For example, although human brains are remarkably complex, the movement of crowds can be modeled with surprisingly simple rules.

Humans are clever, but this hardly makes us immune to fundamental principles of nature. Almost every line drawn in the sand between humans and non-humans—tool use, language, deliberate planning for the future, sense of self—has dissolved with further examination of the animal world, or the realization that basic mechanisms of interaction trump cognition. We are different, but not as different as we'd like to believe. The advantage of analogies in natural history is in part through the sheer diversity of biology—ideas generalized from biology have been tested in all sorts of environments by all sorts of organisms. As with all generalized analogies, exceptions can be found and contingencies must be considered, but this same argument could be applied to generalized theories of international relationships that contain no evolutionary or biological guidance.

Geller is correct that human cognition adds a complicating dimension in applying signaling theory to human behavior, but cognitive capacity does not nullify the predictions of signaling models. Evolutionary models (e.g., ESS models, optimal foraging theory, life history theory) offer predictions about phenotypic strategies that often ignore the underlying mechanisms, including cognition, physiology, and even genetics, that produce these strategies, as long as these proximate mechanisms do not significantly constrain optimal outcomes. These models allow us to determine the selective pressures that favor successful strategies. While human cognition may enable humans to devise uniquely sophisticated signaling strategies, there is no reason to believe that human signals are somehow outside the reach of selection pressures.

From the opposite perspective, the critique that past theories of international relationships and politics have essentially come to similar conclusions as some of our evolutionarily inspired insights (as noted by Fearon) is not troubling to us—rather, it goes to support our claim that there are fundamental patterns that know no species boundaries. The tragedy is that different disciplines are reinventing the wheel. Biologists observe numerous examples of ‘convergent evolution’ where very similar structures or behaviors arose through very different evolutionary pathways. Where our suppositions align with those resulting from separate intellectual thought processes would seem to strengthen their conclusions, not weaken them. Nonetheless, we would argue that a biologically-based theory has the distinct advantage of a large empirical database populated by the diversity of life, and thus knowledge of how such systems vary across a wide variety of contexts, and its use of signaling and communication to survive for billions of years in hostile and unpredictable environments.

Note also that, crucially, signaling mechanisms may arise from a variety of selection mechanisms. Humans are different from deer, and one such difference is that we can observe and copy successful strategies (of, say, signaling). However, this process of selection and replication is just another evolutionary process—cultural evolution instead of genetic evolution. The consequence? Equilibria are the same (all else being equal), but evolution is faster. Geller writes that “signaling systems ... have emerged as outcomes of purposive interactions among human entities”. This is certainly the case, but (1) those outcomes are influenced by evolved psychology (which may include the products of genetic evolution of signaling mechanisms).

Focusing on the differences between human and non-human signaling systems, as Geller advises, is indeed an important part of our analysis. However, the beauty of evolutionary biology is it gives us a framework against which to compare when and what our one species does differently from the millions of others.

Olivier Morin offers a fascinating example of lying working in the interests of the state. However, there are two very important problems with using this example as a weapon against the importance of costly signaling.

First, we know from evolutionary game theory that cheaters can (and often will) exist at a low frequency—an example of frequency dependent selection. Indeed, models show that costly signaling, specifically, can remain perfectly stable in the presence of cheats who do not emit costly signals (Johnstone 1997; Searcy & Nowicki 2005). Thus, a Bismarck or two does nothing to upset the fact that costly signaling prevails among the majority.

Second, this one example (about Bismarck), compelling as it is, worked precisely because other actors expected dishonesty. Indeed, diplomatic history is marked more by stringent etiquette than the violations that undermine them. More striking than cases like this are the widespread rules to which they are exceptions. Those widespread rules of the game are, among other things, honest signals: they persist even if they are sometimes breached. We agree with Morin that signalers may benefit by manipulating information. But this is only possible where honest signaling is the norm. There has to be an expectation for cheats to exploit it. As Teddy Roosevelt would advise us, if you carry a big stick, most of the time you do not have to shout.

It may also be worth noting that such cheats do not always succeed as Bismarck did. During the Vietnam war, Nixon came up with what he called the 'mad man' strategy (Sagan & Suri 2003), in which he tried to convince Ho Chi Minh that he was crazy enough to consider the use of nuclear weapons against North Vietnam if negotiations failed. If Ho believed it, the war could be ended early. However, Nixon failed to convince Ho that this was the case. Deceptive signals do not always work.

Morin raised an excellent point when he noted that cost implies reliability and it works by indicating past, rather than future investment. While, as the saying goes, "past returns do not predict future performance", this is valuable information in a Bayesian context and permits one to modify actions accordingly. We would argue, especially in our information-dense age that 'merely' stating a position does indeed carry enormous immediate costs. Just consider how quickly simple, often symbolic gestures—President Obama apologizing to Afghanistan for U. S. troops burning Korans or Rush Limbaugh calling a birth-control advocate a 'slut'—result in political and economic repercussions. In fact, in political observation, it is often seen as a sign of a strong leader that they are able to 'speak their mind' and by contrast, one who is seen as continually parsing their words to 'feel the political winds' is usually considered to be in a position of weakness. Building up a body of strong statements and yet maintaining a leadership position is certainly perceived as both a signal of past and current strength.

Finally, we contest the idea that "most diplomatic threats and promises are not costly signals in the biological sense [i.e., signals that are costly to

produce]”. Indeed, it is also important to recognize that not all signals require significant costs to ensure reliability. For example, conventional signals, such as symbolic gestures, can be reliable, if dishonest signalers experience differential benefits. More promising for political signaling are models that demonstrate the importance of future interactions for maintaining low-cost reliable signals. In a study on rhesus macaques, for example, Silk et al. (2000) show that low-cost vocal signals, what the authors refer to as ‘cheap talk’, can be honest and stabilize even when interests conflict, as long as there is a high expectation of future interaction. These conditions would seem to parallel the reality of many political interactions; the likelihood of future interactions are particularly high, since governments and nations usually survive beyond the lives of their leaders.

Whether states follow through on their threats or commitments is laid bare for all to see in the pages of history, so there are reputational (and domestic political) costs to making claims that are unrealistic or unbelievable. But furthermore, threats and commitments very often require massive costs, in shoring up political capital to make them, binding alliance treaties, and military deployments. The United States only signaled that it was serious about invading Iraq in 1991 when there were half a million troops on the ground.

The importance of information in strategic signaling and negotiation was also recognized by James Fearon; a political scientist who has thought deeply about these ideas for a number of years and has incorporated perspectives from other disciplines. His main point is that our predictions are not surprising because they have already been arrived at in political science and economics only means that there are fundamental patterns that transcend species and context. In the context of international relations, these same successful strategies may in fact have arisen precisely because they have been shaped by a process of (cultural) evolution. Our essay attempts to explain why and how those effective strategies were selected.

Fearon also notes that signals vary widely in international relations as well as in biology. Biological insights may be useful for this reason alone: the plethora of examples of signaling in nature allow us to generate predictions for what kind of signals are likely to emerge (and be successful) in a variety of different contexts. The key parameters are probably much more varied in nature than they are in politics.

Fearon might be more persuaded by the utility of evolution in its novel predictions for understanding of when and where signaling may succeed or fail. Although above we have stressed the system-level, that is, some selection mechanism generating costly signaling among interacting entities, costly signaling is thought to have been an important part of human cognitive evolution as well. If so, humans may be predisposed to making costly signals of commitment when interacting with other humans (including other state leaders). Thus, states may not need to wait for a process of socialization to

generate signals: state leaders will do it anyway. This can be a useful insight, because the proximate mechanisms that cause costly signaling have not changed from the Pleistocene to today, but the social and technological context has changed beyond recognition. This means that an understanding of the evolution of signaling mechanisms can generate predictions for 'evolutionary mismatch'—the contexts in which our proximate mechanisms for signaling will be triggered but lead to detrimental outcomes in the modern world.

Fearon may be right to note that 'rules of thumb' are unlikely to lead to the optimal exploitation of signals in international politics. This is because rules of thumb work on average, over time, but make many individual errors along the way. Because humans are clever, they should in principle be able to work out what to do on a case-by-case basis rather than having a blanket strategy that works well on the whole but often makes mistakes (perhaps causing wars or disasters in the process). But this does not make the stable strategy less important to understand. In fact, it makes it more important to understand, because only by understanding the likely strategies of other states can we determine when to play by the rules or to seize the opportunity to bluff and win cheaply.

Lastly (he made so many important points!), we can defend his penultimate criticism of our suggestion to "deliberately make your gestures of reconciliation spontaneous in order to make them effective". As he says, this may seem a contradiction—how can you plan something spontaneous? Again, evolution may be way ahead of us here. Robert Trivers's new book suggests that humans have evolved not just deception, but self-deception, and this is an adaptive strategy to better deceive others (Trivers 2011). Deliberate deception can be ineffective because 'behavioral leakage' can give the game away. Genuinely believing you are confident of victory, or willing to reconcile, even if you are not, is more likely to bluff an adversary. Long ago, economist Robert Frank made related arguments about emotions being a strategic device to deter enemies. Rational choice cannot match it because it is too predictable. Nature discovered this many millions of years ago.

We end with an analogy that illustrates the conservative nature of integrating disparate disciplines. The field of evolutionary medicine could be said to have begun with the 1990 Quarterly Review of Biology article showing how and why the field of medicine would benefit from the incorporation of evolutionary thinking and knowledge. Twenty-two years on, there are textbooks, edited volumes, and studies showing how evolutionary ideas can enhance medicine and public health, yet in the US there are no evolutionary medicine degrees, physicians are not trained in evolution, and most medical schools have no evolutionary biologists on their faculty (R. Nesse, pers. comm.). Indeed, many of the recommendations are high-level suggestions for future study. While there have been a number of 'actionable' discoveries,

evolutionary medicine sets the stage for proper empirical studies; all of which must be tested before application.

We believe that nature has similar insights for political science and that when questions can be focused to be more actionable, they can be studied and their successes and failures evaluated. Just like a doctor wouldn't want to use evolutionary logic alone without a double-blind study to determine treatment strategies, diplomats and negotiators might not want to immediately jump in and adopt our suggestions. However, those that take lessons from life and study their effectiveness might find that 3.5 billion years of life has created effective time-tested strategies (Sagarin & Taylor 2008; Sagarin et al. 2010). It is a short step to investigate whether these work today as well.

References

- Johnstone, R. A. 1997. The Evolution of Animal Signals. In *Behavioural Ecology: An Evolutionary Approach* (ed. J. R. Krebs & Davies). Oxford: Blackwell Science.
- Sagan, S. D. & Suri, J. 2003. The madman nuclear alert: Secrecy, signaling, and safety in October 1969. *International Security* 27, 150-183.
- Sagarin, R. D., and T. Taylor (eds.) 2008. *Natural Security: A Darwinian Approach to a Dangerous World*. Berkeley: University of California Press.
- Sagarin, R. D., Alcorta, C. S., Atran, S., Blumstein, D. T., Dietl, G. P., Hochberg, M. E., Johnson, D. D. P., Levin, S., Madin, E. P., Madin, J. S., Prescott, E. M., Sosis, R., Taylor, T., Toby, J. and G. Vermeij. 2010. OPINION: Decentralise, adapt and cooperate. *Nature* 465, 292-293.
- Searcy, W. A. & Nowicki, S. 2005. *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton: Princeton University Press.
- Silk, J. B., E. Kaldor, and R. Boyd 2000. Cheap talk when interests conflict. *Animal Behaviour* 59, 423-432.
- Trivers, R. L. 2011. *Deceit and Self-Deception: Fooling Yourself the Better to Fool Others*. London: Allen Lane.