



From genes to minds to cultures: Evolutionary approaches to leadership

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ABSTRACT

Evolutionary perspectives are part of any comprehensive explanation of leadership and, more generally, hierarchy formation in groups. This editorial describes contributions to a special issue on the theme of “The evolution and biology of leadership: A new synthesis”, and we reach four main conclusions. First, leadership has been a powerful force in the biological and cultural evolution of human sociality. Humans have evolved a range of cognitive and behavioral mechanisms (adaptations) that facilitate leader-follower relations, including safeguards against overly dominant leaders. Second, how these adaptations interact with local ecological and cultural contexts produces cultural variation in leadership preferences, and in the structure of human organizations more broadly. Third, an evolutionary perspective creates consilience between the social and natural sciences, by integrating leadership theory from diverse fields such as biology, psychology, neuroscience, anthropology, economics, and political science. Fourth, evolutionary approaches – and specifically the collection of articles in this theme issue – produce and test novel hypotheses, such as regards (i) the critical role of leadership in cooperation, (ii) the importance of contextual factors in leader emergence and effectiveness, (iii) interactions between genetic and cultural influences on leadership, and (iv) obstacles and opportunities for women leaders.

Introduction

Evolutionary and biological scientists have long been interested in studying collective behavior in different social species, from migration patterns in ungulates to conflict management in non-human primates (Smith et al., 2016). Many of these collective behaviors either directly or indirectly involve leadership. Evolutionary approaches are increasingly visible in the social science literature on leadership too. For instance, evolutionary perspectives feature prominently in recent textbooks on leadership (e.g., Antonakis & Day, 2017) and the latest version of the Handbook of Evolutionary Psychology (Buss, 2015) devotes several chapters to leadership and hierarchy. Recently evolutionary perspectives have also been applied to leadership processes in work organizations, politics, and sports (Elgar, 2016; Knapen, Pollet, & van Vugt, 2019; Kniffin, Bogan, & Just, 2019). Evolutionary thinking has also influenced cognitive neuroscientists in studying the neural underpinnings of leadership and followership (Boyatzis, 2014; Lee, Senior, & Butler, 2012; Molenberghs, Prochilo, Steffens, Zacher, & Haslam, 2017; Van Vugt, 2014; Waldman, Balthazard, & Peterson, 2011).

Nevertheless, these advances – and their implications – may not be evident to many members of the academic leadership community. Indeed, even enthusiasts of evolutionary approaches may be unfamiliar

with many of the new directions that are emerging in this field. It is primarily for this reason that we, an evolutionary psychologist (Mark van Vugt) and biological anthropologist (Chris von Rueden), have assembled this special issue, titled “The evolution and biology of leadership: A new synthesis.”

The special issue comprises a heterogeneous collection of 15 original articles, 14 core papers and 1 commentary, ranging from theoretical to empirical contributions and representing a diverse set of methods, from experimental psychology to ethnographic and historical data. The featured articles come from research teams operating across the world, containing both senior and junior researchers, men and women, and people from many different national and cultural backgrounds. For readers who are new to evolutionary perspectives, these articles may provide a useful introduction to the many insights that can be gleaned from an evolutionary approach. For readers already familiar with such perspectives, these articles provide a stimulating and diverse sample of new ideas and findings that are indicative of the many creative ways evolutionary theory can be applied productively to the study of leadership.

This editorial is structured as follows. We first familiarize readers with natural selection and tie the evolution of leadership to the evolution of cooperation and competition in groups. We then discuss

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common sets of questions and methods that evolutionary scientists employ to do research on leadership and provide some illustrative examples. Then we focus on the articles in the special issue and the insights they provide in understanding leadership, according to four key themes: (i) the evolved functions of leader-follower relationships; (ii) the importance of context (iii) the interaction of biological and cultural evolution in shaping leadership; and (iv) the evolved and cultural roots of gender differences in leadership. We conclude by summarizing the strengths of an evolutionary approach and identifying various gaps in our current knowledge.

Natural selection and the evolution of leadership

Evolutionary approaches to leadership make predictions inspired by Darwin's theory of evolution by natural selection. Natural selection is the process by which genes (or to be more precise genetic variants called alleles) decline, are maintained, or spread in a population by virtue of their effects on the reproduction of individual organisms. Evolution through natural selection operates on the basis of three very simple rules:

- There is variation in traits between individuals of the same population (principle of variation)
- Some of this variation is due to heritable genetic differences – producing similarity between parents and offspring (principle of heritability)
- Heritable traits that cause individuals to produce more offspring that survive to maturity relative to other individuals (i.e. reproductive success) will tend to spread in the population (principle of selection).

Genetically-influenced traits that help organisms solve reproductive challenges recurrent in their environments are called adaptations. Some of these adaptations concern the physical features of organisms. Take the long neck of the giraffe, which may have evolved in part because ancestral giraffes with genes for longer necks had an advantage in obtaining food (access to the leaves on the large trees of the savannah) that were unavailable to other ungulates without these gene variants. Hence, the long-necked giraffes were able to acquire more resources, enabling them to leave more offspring who also had longer necks. Over time, this long-necked gene variant spread through the population until it became a universal feature of the giraffe's phenotype.

Importantly, when evolutionary biologists talk about a gene for trait X or Y this is overly simplistic because most traits are underpinned by multiple genes operating in complex combinations (human height, for example, is influenced by hundreds of genes according to genome wide association studies: [Yengo et al., 2018](#)). And rarely do genes on their own determine anything. Natural selection spreads genes which, *in the presence of or interaction with particular features of an organism's environment*, increases the organism's relative reproductive success. Also, when evolutionary biologists talk about traits, they refer to any feature of an organism that is expressed when an organism's genes interact with the environment, including physical features, neurophysiological mechanisms (hormones, neurotransmitters, brain regions), psychological mechanisms (cognitions, emotions), overt behaviors and even social structures. Natural selection can operate on any aspect of an organism as long as it is under the influence of genes.

Furthermore, adaptations can emerge in response to features not just of the physical environment (e.g., location and availability of food) but also the social environment (e.g., social competition, opportunity for cooperation). Many species evolved adaptations that facilitate living in groups, because of benefits of collectively defending important resources, minimizing predation risk, and sharing knowledge and resources. Adaptations for group life include changes to physiological features such as immune function ([Nunn & Altizer, 2006](#)) as well as psychological adaptations instantiated in neural tissue, particularly

psychological adaptations that minimize conflict and facilitate cooperation ([Harcourt & de Waal, 1992](#)).

Hierarchy formation is a principal means by which group-living animals minimize conflict. Social animals possess psychological adaptations that facilitate hierarchy formation, including mechanisms for assessing competitive ability and displaying deference towards individuals perceived as more dominant ([Arnott & Elwood, 2009](#); [Van Vugt & Tybur, 2015](#)). Deference is beneficial because it avoids costs of repeated competition over food and mates ([Maynard Smith & Price, 1973](#)). It is in the context of dominance hierarchies that leader-follower relationships often emerge, though whether leaders tend to be dominant individuals varies by context and by species. Leadership can be defined as differential influence within a group over decision-making, logistics of coordination, monitoring of effort, reward or punishment ([Day & Antonakis, 2012](#); [Van Vugt, 2006](#); [von Rueden, Gurven, Kaplan, & Stieglitz, 2014](#)). Leadership has been documented in various species, from ants to fish to mammals like elephants and whales, and in different domains of social interaction, from collective movement to intergroup competition to policing of intra-group conflict ([Smith et al., 2016](#)). Leaders' influence can derive from their position in the dominance hierarchy, but this need not be the case. In many species, individuals become leaders because they have valuable knowledge or motivation to act first, which helps coordinate other group members. Thus, the evolution of leadership is not tantamount to the evolution of dominance hierarchy, and this is particularly true in the case of humans. In general, social species have evolved motivations to adopt leader-follower relationships to resolve coordination and collective action problems, often to the mutual benefit of group members ([Glowacki & von Rueden, 2015](#); [Bastardoz and Van Vugt, 2019](#); [King, Johnson, & Van Vugt, 2009](#)).

Asking the right questions, finding the right methods

An evolutionary approach to leadership has attracted scholars from a diversity of theoretical and methodological backgrounds, from biologists, geneticists, and anthropologists to psychologists, neuroscientists and management scholars. While evolutionary approaches to leadership are not uniform, a common thread is the ambition to generate predictions based on hypothesized selection pressures and hypothesized adaptations rather than on more process-based explanations like LMX-relations or impressions of leader integrity. This is not to say evolutionary approaches supplant these more proximate explanations, but rather integrate them into a wider theoretical frame. The biologist Niko Tinbergen is famous for arguing that a behavior is only fully understood by asking four complementary, non-exclusive questions, each requiring unique methodologies (see also Brian Spisak, this issue).

The functions of leadership

The first question concerns the evolutionary functions of leadership. Did psychological traits that facilitate leader-follower relationships evolve because they increased group members' reproductive success? To realize the benefits of group living, group members must often surmount coordination and collective action problems ([Glowacki & von Rueden, 2015](#); [King et al., 2009](#)). Game theoretic and other analytical models (e.g. [Couzin, Krause, Franks, & Levin, 2005](#); [Gavrilets, Auerbach, & Van Vugt, 2016](#); [Hooper, Kaplan, & Boone, 2010](#)) as well as experimental paradigms (e.g. [Baldassarri & Grossman, 2011](#); [Dyer, Johansson, Helbing, Couzin, & Krause, 2009](#)) have been important in demonstrating that leader-follower relationships can be uniquely instrumental in surmounting coordination and collective action problems. The evidence is consistent with the argument that natural selection favors (context-dependent) adoption of leader-follower relationships within group-living animals.

Coordination and collective action problems differ in their incentive structures, and thus also in the kind of leader-follower relationship that

will be more successful. In pure coordination situations, group members have uniform preferences, but how to coordinate behavior can still be tricky. In such situations, it can pay to coordinate by simply following the “first mover” (Cartwright, Gillet, & van Vugt, 2013). In groups with heterogeneous preferences or heterogeneous knowledge, stubborn individuals that are the least likely to change their position (Gavrilets et al., 2016), dominant individuals (King et al., 2009), or individuals with more task-relevant knowledge (Couzin et al., 2005) can be instrumental in catalyzing effective coordination. In collective actions, in contrast, group members have incentive to “free-ride” on the efforts of others, by under-contributing to a collective good while still benefiting from it. With enough free-riding, collective action fails. Here, group members may derive greater benefit from granting leaders some degree of coercive authority, in order to deter and punish free-riding (Glowacki & von Rueden, 2015; Hooper et al., 2010; King et al., 2009; O’Gorman, Henrich, & Van Vugt, 2009).

The question of leadership’s evolutionary function must also consider why leaders would take on any costs to leading. Costs may be energetic costs, opportunity costs, or risks to health or reputation. Dominant individuals may recoup their costs by coordinating decision-making in ways that directly benefits them more than other group members. Often, coordination or collective action provides no differential benefit to leaders (Smith et al., 2016). Thus, leader emergence itself can be a collective action problem. One functional solution to this “second-order” collective action problem is when, via the collective goods they help produce, leaders benefit their kin, who share leaders’ genes with some probability. This is the logic of kin selection, whereby genes for altruism can evolve to the extent the altruism is targeted towards individuals with those same genes (Hamilton, 1964). Another functional solution is that leaders build reputations for dominance or prestige via their leadership, which motivates group members to reward leaders with sex, alliance, or deference (von Rueden et al., 2014).

The phylogeny of leadership

A second kind of theoretical question concerns the evolutionary history of leadership - the phylogeny-question. How did leadership emerge and change over the evolutionary history of different species, particularly our ape ancestors? While we lack a time machine, comparative research offers clues. In multiple species from insects to humans, dominant individuals have been observed to police their groups, e.g. impartially intervene in fights (Singh & Boomsma, 2015). In studies of macaques and chimpanzees, policing by dominants resulted in greater social connectivity and stability of their groups (Flack, Girvan, de Waal, & Krakauer, 2006; von Rohr, Koski, Burkart, et al., 2012). Such connectivity and stability is a public good that may benefit all group members but be particularly beneficial to dominants, who increase their mating opportunity. A complementary explanation is that policing evolved because, by policing, dominants thwart the ability of competitors to gain status.

Leadership and followership also evolved in the context of migration or group movement towards valuable resources. In some species, dominants tend to initiate such movement. For example, studies of chacma baboons (King et al., 2009) and black and white ruffed lemurs (Overdorff, Erhart and Mutschler, 2005) found that group members would typically follow the most dominant individual to new food patches, even though the dominant would get the most food. Subordinates would nevertheless avoid even worse payoffs from discoordination. In species where expert ecological knowledge is important, individuals who have unique knowledge often receive deference during group movement. For example, elephants benefit by following the oldest females, who have knowledge of watering holes and other resources that may be particularly useful during periods of scarcity (McComb, Shannon, Durant, et al., 2011). Where expert ecological knowledge is less important to group movement, it can pay to coordinate by simply following the “first mover”. For example, zebra herds often follow the

lead of lactating zebras, who are most likely to be the first to move in new directions because of their greater water or energy needs (Fischhoff, Sundaresan, Cordingley, et al., 2007; Van Vugt, 2006). Thus, depending on the context and the species, different sorts of leaders emerge. The use of phylogenetic trees, which map the genetic relatedness between species, can establish whether similarities in leadership between species are due to phylogenetic consistency – the trait is present in the last common ancestor – or to homology – both species have come up with the same solution independently (e.g. bats and birds have evolved wings independently).

When we look at hierarchy and leadership in humans, they appear to be somewhat unique. Sometime since the split from our last common ancestor with bonobos and chimpanzees, some 6 million years ago, our human or even earlier hominin ancestors became more egalitarian, largely by forming group-wide coalitions against dominants (Boehm, 1999; Gavrilets, Duenez-Guzman, & Vose, 2008). Such large-scale coalition-building was facilitated by the evolution of a more complex theory-of-mind via which individuals can simultaneously represent the intentions of multiple other individuals, as well as language abilities to improve coordination (Dunbar, 2018; Tomasello, 2009). Humans also evolved motivations to engage in relatively monogamous pair-bonding, which may have decreased competition among prospective coalition partners (Chapais, 2008).

Inferences about the egalitarianism of our ancestors have been made in part via observation of modern hunter-gatherers and other small-scale societies. While many such societies are quite egalitarian, they still show evidence of informal status differentiation and leadership (Anderson et al., 2015; von Rueden & Van Vugt, 2015). Certain individuals tend to be granted more active influence in collective decision-making, not because they dominate others but because they have demonstrated their value to others, that is, they have prestige (Henrich & Gil-White, 2001). Prestige likely contributes more to human hierarchy and leadership relative to other animals, not just because humans are good at forming coalitions against dominants, but also because humans are so interdependent. Humans rely on more extractive means of producing food that requires sharing, coordination in groups, and culturally acquired knowledge (Kaplan, Hill, Lancaster, & Hurtado, 2000). As a result, reputations for knowledge, skill, and especially generosity influence individuals’ choice of whom to marry, befriend, or follow (Bliede Bird & Power, 2015; von Rueden, Redhead, O’Gorman, Kaplan, & Gurven, 2019). Even in egalitarian human societies, where there is minimal variation in status and wealth and where dominance is suppressed, individuals who are prestigious or who are recognized as leaders often have greater reproductive success (von Rueden & Jaeggi, 2016). Thus, traits that facilitated the acquisition of leadership likely experienced positive natural selection throughout recent human evolution. In contrast, chimpanzees and bonobos show less interest in maintaining or rewarding reputations for generosity (Engelmann, Hermann, & Tomasello, 2012; Krupenye & Hare, 2018).

The ontogeny of leadership

Both function and phylogeny are questions about deep evolutionary time, but a third question concerns the developmental aspects of leadership and followership – this is called the ontogenetic question. Twin studies reveal that about 40% of variation in leadership emergence between individuals is due to genetic factors, suggesting a substantial heritable component (Chaturvedi, Zyphur, Arvey, Avolio, & Larsson, 2012). This does not mean that 40% of leadership is explained by genes, but rather that 40% of differences in who emerges as a leader can be explained by the *different* genes they have (within the particular population studied). Genes always play a role in any behavior, whether they vary across individuals or not. And the interplay of genes and environments can be complex. Gene-by-environment interactions shape leader emergence (Zhang, Ilies, & Arvey, 2009), and genes can influence the environments individuals create or select into over

development (De Neve, Mikhaylov, Dawes, Christakis, & Fowler, 2013). Why there is variation in genes related to leader emergence (or anything else) requires more explication than this review can provide, but candidate explanations include mutation in relevant genes or to natural selection processes like balancing selection (e.g. Penke and Jokela, 2016).

Developmental psychology studies provide evidence of when and how preferences for particular leaders emerge over childhood. For instance, there is evidence that even infants already differentiate between leaders and bullies when they get to see them operate in a puppet play (Margoni, Baillargeon, & Surian, 2018). Further, children from as young as 5 years of age have cognitive templates of leadership that enable them to successfully predict actual election outcomes based on facial cues of the political candidates (Antonakis & Dalgas, 2009). Survey data suggest that voters with preferences for more dominant-appearing leaders tended to experience more harsh and unpredictable childhood environments (Safra et al., 2017). The latter study articulates with a broader theoretical perspective rooted in evolutionary history called life history theory (Giudice, Gangestad, & Kaplan, 2015), which predicts how organisms mature given their early life experiences.

The mechanisms of leadership

Tinbergen's fourth question concerns the precise mechanisms by which leader-follower relationships come about. This more proximate question is what regular readers of *The Leadership Quarterly* are probably most familiar with. For instance, psychological experiments enable researchers to examine the impact of leaders' emotional displays, like anger, happiness or sadness, on followers' support (Lewis, 2000). Furthermore, neuroscience studies can help to understand the hormonal, physiological and brain processes involved when leaders try to recruit followers. For instance, high levels of basal testosterone have been linked to a dominant leadership style (Van der Meij, Schaveling, & van Vugt, 2016). Exposure to particularly charismatic leaders has been linked to a deactivation in prefrontal cortex activity among followers (Schjoedt, Stødkilde-Jørgensen, Geertz, Lund, & Roepstorff, 2011). Finally, eye-tracking methods can predict leadership emergence by considering the gaze patterns of followers (Gerpott, Lehman-Willenbrock, Silvis, & Van Vugt, 2018).

In general, evolutionary approaches predict humans possess a suite of evolved psychological mechanisms that are underpinned by genes and enable them to form and maintain productive leader-follower relations in order to overcome different kinds of coordination and collective action challenges. This is not a deterministic view, however. How leaders emerge and what determines effective leadership is context-dependent. Adaptive psychological mechanisms are predicted to operate as if-then decision rules that are activated in appropriate environments. As just one example of such an evolved decision rule, evidence is accumulating that followers prefer leaders who are physically dominant in situations when their groups experience existential threats, such as in wartime (Van Vugt & Spisak, 2008). This decision rule may in part reflect expectations that physically formidable leaders are more capable coordinators or punishers (Blaker et al., 2013; von Rueden et al., 2014). This is clearly not a preference for the dominance hierarchies that structure other animal societies, but rather an intuition that targeted application of dominance on the part of leaders can bring benefits to the group. As another example, the extent to which leaders act prosocially appears contingent on whether leaders perceive followers as willing and able to displace them (Maner, 2017).

An evolutionary approach makes clear that leadership and followership are not necessarily the result of deliberate, rational decision-making. In solving the problems associated with survival and reproduction (such as the food we prefer and the mates we are attracted to) evolution has mostly done the thinking for us. Decision rules about who are effective leaders in a particular context are reasonably intuitive (System 1 thinking; Kahneman, 2011), and sub-consciously influence

more rational, deliberate justifications of one's decisions (System 2). An implication is that followers will endorse certain leaders based on cues or signals associated with effective leadership in ancestral environments – like following a leader with a strong physique or aggressive personality to catalyze collective action in small groups in the face of inter-group conflict. However, it is good to realize that such cues are not necessarily indicative of a leaders' effectiveness in modern, large-scale societies, or in the face of evolutionary novel threats (such as terrorism, infectious disease or climate change). This is the notion of evolutionary mismatch, an important concept in evolutionary biology and evolutionary psychology (Giphart & Van Vugt, 2018; Li, van Vugt, & Colarelli, 2018).

It should be clear that the answers to Tinbergen's four questions are not mutually exclusive. Through employing different research methods with different designs, they offer complimentary answers at different evolutionary time scales (Sapolsky, 2017). So, for instance, if we want to explain why Greta Thunberg, a child climate activist leader, has been able to attract so many followers worldwide we could consider analyzing the contents of her speeches or the immediate neural reactions of her followers to these speeches (mechanism). Yet we can also go back further in time to find out what combination of genetics and environmental factors drove her and her followers towards environmental activism (ontogeny). Or, to understand why certain traits predispose leadership or followership in particular contexts, and why we can be inspired by charismatic leaders like Greta, we can look at the patterning of leadership across species (evolutionary history), and model the evolutionary consequences of adopting leader-follower relationships (function).

Insights from special issue

It is evident from the articles in this special issue that an evolutionary approach represents an enormously diverse set of theoretical, methodological, and analytical perspectives, quite literally from genes to culture. The theoretical and methodological pluralism results in part from the fact that scientists in many diverse disciplines with an unusually diverse range of backgrounds work on the evolution of leadership, aiming to build consilience between their disciplines – consilience is the idea that evidence from independent, unrelated sources can converge on strong conclusions (Wilson, 1999). In addition, the diversity in concepts, methods and data is a functional response to the requirements for generating and testing evolutionary predictions. Reconstructing ancestral selection pressures requires much induction, based on tools from evolutionary biology, animal behavior, anthropology, and other disciplines. While some methods may be familiar to leadership scholars (e.g., psychological experiments, survey methods) others (e.g., comparative methods, ethnographies, hormonal data, agent-based models) may not be as they do not often appear in outlets such as *The Leadership Quarterly*.

The collection of articles in this special issue shows that an evolutionary approach offers many new ideas for leadership theory and research. Below we organize our comments on the special issue articles according to four principal conclusions: (i) leadership is critical for solving coordination/collective action dilemmas in groups; (ii) context matters in leadership emergence and effectiveness; (iii) both biological and cultural evolutionary processes shape leadership, including (iv) gender differences in leadership. Together, these special issue articles show the generativity of an evolutionary approach to leadership.

Need for leadership

Using methods from economic games, Ghufuran Ahmad and Christoph Loch (this special issue) demonstrate experimentally how the more difficult the coordination or collective action problem gets, the more group members desire leadership and the more leadership benefits the group. Their results bolster the argument that motivations to

adopt leader-follower relationships evolved to realize the benefits of cooperation, which would otherwise be unobtainable due to coordination and collective action problems (Glowacki & von Rueden, 2015). There are also meta-coordination problems: how to coordinate decision-making about which action plan to coordinate on. Leadership can also help solve this problem of meta-coordination, when multiple would-be leaders market different action plans and followers choose among them, as David Pietraszewski (this special issue) shows.

Once leadership has been established in groups and leader-followers relations have been formed a social exchange process develops whereby leaders and followers weigh the merits of their relationship. Ray Sparrowe (this special issue) uses the evolutionary theory of welfare trade-off ratios to interpret work on leader-member exchanges (LMX) in terms of psychological adaptations for weighing others' welfare against one's own. This paper is a good example of how more proximate models of leadership can be linked to more fundamental evolutionary principles and methods. Another example is the contribution by Alexandra Cook, Alexander Zill, and Bertolt Meyer (this special issue). They call for shared leadership theory to incorporate theory and methodology from animal behavior studies, especially observation and interaction methods. Whereas much of the research on shared leadership relies on subjective perceptions they argue that an ethological approach with a focus on observable behaviors, both verbal and non-verbal, can add valuable knowledge about leadership. Collecting social network data and using social sensing data (via sociometric badges) should complement self-reported data.

Context matters

Evolutionary behavioral scientists increasingly distinguish between two means of acquiring social status in human hierarchies: dominance and prestige (Cheng, Tracy, & Henrich, 2010; Henrich & Gil-White, 2001). Dominance is based on a willingness and ability of individuals to inflict costs on other group members, for instance, by using (threats of) force, punishment and intimidation. In contrast, prestige accrues according to a willingness and ability to deliver benefits to other group members, for example, by providing valued knowledge or resources. The prestige-dominance distinction can be used to distinguish between different leadership archetypes and the influence strategies they use to recruit and mobilize followers (Van Vugt & Smith, 2019). This differentiation bears some similarity to different power bases discussed by French, Raven, and Cartwright (1959) and other distinctions between autocratic-democratic or transactional-transformational leadership styles. Yet the prestige-dominance model in some ways improves on these taxonomies, because it is (i) theoretically-motivated rather than principally descriptive, and (ii) able to describe leadership processes in (a) both humans and non-human groups and (b) in large, complex industrialized societies as well as in non-WEIRD small scale human societies.

In contexts with challenging collective action problems, accumulating evidence suggests group members increase their preference for leaders whose traits are conducive to dominance (von Rueden & Van Vugt, 2015). Increased risk of free-riding or where free-riding can pose an existential threat to groups, as in collective defense against other groups, may cause followers to decrease their wariness of dominant individuals as leaders, whose ability and willingness to coerce can expedite collective action and deter freeriding (von Rueden & Van Vugt, 2015). This is not a preference for the dominance hierarchies that structure many other animal societies, but rather an intuition that targeted application of dominance on the part of leaders can bring benefits to the group as a whole. As in other species, physical size intuitively affects humans' estimation of each other's capacity for dominance (Blaker et al., 2013; Lukaszewski, Simmons, Anderson, & Roney, 2015). Psychological studies find that perceived risk of free-riders within groups or conflict between groups can increase preferences for more dominant-looking leaders – leaders who have more masculinized

facial features, indicative of physical formidability (Boggild & Laustsen, 2016; Laustsen & Petersen, 2017; Van Vugt & Spisak, 2008). Lasse Laustsen and Michael Bang Petersen (this special issue) show that these preferences are more apparent in right-wing voters, who are more likely to view the world as a dangerous, conflict-laden place.

Economic inequality can also potentiate dominance-based leadership, whether due to shifts in group members' desired characteristics in leaders, for instance, during an economic recession (Kakkar & Sivanathan, 2017), or in the potential personal benefits to individuals pursuing a more dominant form of leadership under conditions of inequality as Richard Ronay, William Maddux, and Bill von Hippel (this special issue) argue persuasively. The nature of leader-follower relationships is rarely driven only by follower interests. Threats and crises create opportunities for leaders to strategically manipulate the emotions of group members, in order to forge cohesive political identities for personal if not collective gain (Rose McDermott, this special issue). Because group members are particularly motivated to defer to leadership in the context of collective defense, leaders whose interests include aggression towards other groups often take pains to reframe such aggression as defense in order to generate collective action (Anthony Lopez, this special issue). Examples of this abound, such as the political justifications by the Bush administration for the American invasion of Iraq in 2003.

Deferring to leaders with traits conducive to dominance involves a trade-off (De Waal-Andrews and Van Vugt, 2019). Because of the risk of exploitation by leaders, group members employ various anti-exploitation devices to curtail the powers of their leaders (Boehm, 1999). History is replete with examples of leaders who sought to extend their dominance-based leadership beyond wartime, and met with resistance or even assassination, for instance, Julius Caesar and, more recently, Colonel Gaddafi. Anti-exploitation mechanisms include disrupting leaders' coalitional support and building coalitions against them, via gossip, ridicule and public protest (Boehm, 1999; Van Vugt & Ronay, 2014). The content of such criticism often includes purported examples of procedural unfairness in leaders. There is much evidence that humans evolved a specialized cognitive system for detecting rule violators, independent of domain-general reasoning ability (Cosmides & Tooby, 1992).

Political scientist Troels Boggild (this special issue) argues that humans' attention to leaders' procedural fairness is an adaptation that builds on this cheater-detection system. Because the long-term effects of leaders' decisions are often unclear, group members look to see whether leaders follow decision-making rules consistent with a concern for procedural fairness. For example, leaders should listen to the opinions of diverse group members rather than appear to be solicitous only to close friends and family. Communicating with other group members about evidence of leaders' procedural unfairness is a powerful coordination tool for establishing leaders as illegitimate and undermining their power.

Finally, preferences for leaders who look more facially dominant and who appear larger and stronger have been interpreted as examples of evolutionary mismatch, because physical formidability may have minimal relevance for leaders' effectiveness in modern societies where political leaders effect action via policy rather than face-to-face interactions with constituents or rivals (Blaker et al., 2013; Li et al., 2018; Murray & Schmitz, 2011; Van Vugt & Ronay, 2014). What still requires testing is whether preferences for physical formidability in leaders are primarily driven by evolved intuitions about the role of body size in interpersonal influence (which may still be a factor when politicians meet), or whether such preferences are targeting the personality and behavioral tendencies that tend to correlate with such physical attributes, such as facets of extraversion (Lukaszewski & von Rueden, 2015), charisma (Grabo, Spisak, & van Vugt, 2017) or anger (Sell, Tooby, & Cosmides, 2009). Alexander Bor (this special issue) proposes another mismatch: Economic conditions affect voters' perception of the competence of leaders, despite lack of concrete evidence connecting the

two, in part because evaluating leaders' performance based on the resources available to group members may have improved followers' fitness ancestrally. That this evolved heuristic is still applied today to evaluate leader's performance in large-scale modern economies suggests that voters do not make rational decisions when it comes to leader selection.

Importance of cultural evolution

Differences between leadership structures and preferences around the world are likely the result of interactions between genetically evolved decision rules and local cultural and ecological conditions (cf. gene-culture coevolution). Leadership in humans is complex in that evolved adaptations for leader-follower relationships shape and interact with ecological contexts, cultural norms and institutions regulating leadership (Garfield et al., 2018). As human societies grew larger, denser, and wealthier – particularly after the spread of agriculture beginning some 12,000 years ago – political leadership was more likely to be institutionalized in the form of chiefs, kings, judges, presidents and CEO's (Van Vugt, Hogan, & Kaiser, 2008; von Rueden, 2019). This formalization of leadership contrasts with the more ad hoc, informal leadership common to more egalitarian, small-scale societies (von Rueden et al., 2014). Such historical change was partly due to wealthy, powerful families codifying their rights to engage in coercive and exploitative politics (Mattison, Smith, Shenk, & Cochrane, 2016). Collective action against coercive leaders was tempered by economic dependency on leaders' patronage and the absence of exit options.

At the same time, follower's evolved decision-making heuristics may have found institutionalized leadership attractive to manage the problems of life in larger, denser, more complex and unequal societies (Hooper et al., 2010). According a leader formal punitive powers (as is also the case in modern democracies) is instrumental to the functioning of large-scale societies with their large-scale coordination and collective action problems (Van Vugt & Smith, 2019; von Rueden, 2019). Evidence that emergence of more institutionalized leadership is not simply a product of elite coercion can be seen in those societies, like Plains Indians of North America (Lowie, 1948), who elected leaders with coercive power during times when group size swelled, yet eschewed such dominance-based leadership at other times. Conflict resolution may have been the domain of leadership first to institutionalize in human societies, because internal conflicts that occur within a society can trigger feuds or lead to group fission and undermine all other collective action, including those activities necessary for subsistence, collective defense, or collective aggression (Glowacki & von Rueden, 2015). This scholarship originating in anthropology has much consilience with the experimental research described in the previous section, on the context specificity of preferences for dominance-based leadership.

Sirio Lonati (this special issue) finds that members of societies whose ancestors practiced more intensive forms of agriculture, a cultural innovation which associates with greater population densities, wealth and power differences – endorse more directive, less participative leadership in the workplace today. Cultural models of leadership, including implicit leader theories (Rush, Thomas, & Lord, 1977), that emerged historically as a result of evolved decision-making heuristics interacting with local contexts, can be reinforced across the generations via teaching, imitation, and other forms of cultural learning. These kinds of dynamics may also explain the relationship between the prevalence of infectious diseases – an ecological threat that varies between nations – and the endorsement of strict social norms and authoritarian leadership (Gelfand et al., 2011; Murray, Schaller, & Suedfeld, 2013).

Other models of leadership in modern large-scale societies may show less variation, because alternative norms and institutions conflict with evolved decision-making heuristics and make organizations less competitive. For example, firms and governments tend to be structured as bureaucracies with multi-tiered leadership structures, which

guarantees face-to-face leader-follower relationships at each level of the hierarchy (Richerson & Boyd, 1999). If those intimate contacts are missing, organizations usually pay the price (Van Vugt & Ronay, 2014).

Gender and leadership

In human societies, men tend to acquire greater status than women, in terms of overt leadership in community or state-level politics (Low, 1992; von Rueden, Alami, Kaplan, & Gurven, 2018). To place this trend in comparative context, biologist Jennifer Smith and colleagues (this special issue) review leadership across many different mammalian societies, looking for conditions that favor female leadership. Although relatively uncommon, female leaders emerge in those few species where females are dominant to males (e.g. lemurs and spotted hyenas), where females acquire ecological knowledge valuable to other group members, and where females live in close proximity to other female relatives.

These patterns are analogous to the conditions that favor men as leaders in small-scale human societies. A recent study of the Tsimane horticulturalists of Amazonian Bolivia found that – from least to most relevant traits – larger body size and strength, greater access to education, and greater access to social support privilege men as informal leaders during community debates (von Rueden et al., 2018). Gender differences in body size are largely a product of sexual selection – the different selection pressures ancestral men and women experienced due to opportunities and constraints of their different reproductive biologies (e.g., pregnancy, lactation). Ipek Kocoglu and Murad Mithani (this special issue) invoke Darwin's sexual selection theory – the idea that some traits evolved because they give an edge in the competition for sexual partners – to explain a double standard they find in their research: The perceived leadership ability of male CEOs is enhanced by the attractiveness of their romantic partner, while female CEOs' leadership is downgraded in the presence of an attractive partner.

Sexual selection may have also contributed to greater motivation among men compared to women to build large coalitions for competitive purposes (Benenson & Markovits, 2014; David-Barrett, Rotkirch, Carney, et al., 2015) – the male warrior hypothesis (Van Vugt, Cremer, & Janssen, 2007). Sexually selected cooperation strategies may contribute to sex differences in ability to mobilize social support and acquire leadership positions. Evaluating this hypothesis is difficult, because various cultural institutions often constrain women's ability to network. These institutions include patrilocal residence patterns and, more universally, a gender division of labor, in which women are expected to perform more intra-household labor, including childcare. The gender division of labor also contributes to normative expectations that women assume less agentic and less competitive roles in groups (Eagly & Karau, 2002). This social role perspective is often contrasted with evolutionary models of sexual selection to sex differences, but social role theory and evolutionary theory are compatible. Evolved sex differences in size, strength, and social behavior may help explain (but certainly not justify) the emergence, persistence, and cross-cultural patterning of the gender division of labor and gender-related cultural norms. In short, the balance of political power between women and men is the interplay of evolved sex differences with local ecology and cultural norms (Low, 2005).

Studies of leadership in small-scale, relatively egalitarian societies suggest that gender is not the most important predictor of leadership once accounting for other predictors such as physical size and network size, and the traits that associate with men's and women's leadership are similar – see Zach Garfield and Ed Hagen (this special issue; also von Rueden et al., 2018). Gender inequality in leadership is not some intrinsic property of human nature. Rather, policy can redress gender inequality in political leadership by attending to the influence of physical formidability on leader evaluation, addressing the constraints imposed on women by a gender division of labor and associated norms,

recognizing how sex differences in social networking create unequal opportunity, and, in many parts of the world, expanding access to education for women, as Jennifer Smith et al. (this special issue) suggest.

Some final considerations

First, evolutionary approaches have the potential to offer a more complete understanding of a particular leadership process or phenomenon. A more complete account follows naturally from the theoretical and methodological pluralism that the field offers by integrating evidence obtained at different levels of analysis and at different timescales (cf. evolutionary leadership theory; Van Vugt & Ahuja, 2011). If we want to understand the appeal of charismatic leadership we can invoke Tinbergen's four questions approach (Spisak, this special issue) and study first the core functions of such charismatic leadership, such as via game-theory and computer simulations to model its fitness effects on leaders and followers (Grabo et al., 2017). We can then infer the phylogenetic roots of charisma by comparing to its analogues in non-humans and to small-scale human societies. Developmental psychology experiments can tell us whether children differentiate charismatic from other forms of attempted influence, and at what age. Finally, neuroscience and observation studies can help illuminate the neural, hormonal, and cognitive pathways through which particularly charismatic individuals exercise influence on followers, and via what tactics, e.g. metaphor, gesture, emotional appeal, etc. (Antonakis, Fenley, & Liechti, 2011).

Second, an evolutionary approach can help overcome biases and blind-spots in the leadership literature. Research is biased towards studying leadership in modern, complex organizations such as in corporates, governments and armies. As a consequence, there is an obsessive interest in CEO's, managers, presidents and officers. Yet an evolutionary approach makes clear that leadership happens at all levels of society, including in families, communities and other informal social networks. Another implication is that more effort should be made to collect leadership data in non-WEIRD (non-Western, Educated, Industrialized, Rich and Democratic) societies as these can indicate what aspects of leadership are truly universal, and which are culturally patterned (Garfield & Hagen, this special issue; von Rueden & Van Vugt, 2015). Another blind-spot is the emphasis in research on the virtuous aspects of leadership such as ethical, transformational, authentic leadership (Alvesson & Einola, 2019). Although there are certainly situations in which followers want their leaders to be ethical or visionary there are also situations in which followers trade-off honesty and integrity for less benign traits such as dominance, hostility, anger, and aggression – in conflict between groups, for example.

Third, an evolutionary approach can be used to deduce many novel hypotheses bearing on topical leadership phenomena. For example, insights from evolutionary anthropology and research on small-scale societies can be applied to understand the levelling mechanisms that groups apply to avoid exploitation by leaders. Examples of such anti-exploitation devices are those that are relatively cost-free such as gossip about leaders to more costly ones such as public criticism or the replacement of poorly functioning leaders. Research could develop predictions about how mechanisms like gossip, ridicule and collective protest affects leader-follower relations and the decision-making powers of leaders. Evolutionary analyses also point to interesting developmental processes that increase people's propensities to follow particular leaders or lead themselves. It would be interesting to consider how ontogenetic factors such as the death of a parent or caregiver may affect someone's leadership preferences and leadership styles.

Another promising area for an evolutionary approach is the increased digitalization of leadership in the work place, which increases social distance (Antonakis & Atwater, 2002). As leaders and followers increasingly find themselves in different places and even different time zones (such as in multinational operating companies) the question is

how effective remote forms of leadership are in motivating and instructing workers. As humans have evolved to be influenced primarily by face-to-face interactions (Dunbar, 2018), the lack of direct physical contact may limit remote leadership influence attempts (via email, Skype or texting). This then suggests that new technologies for remote forms of leadership need to better incorporate face cues (such as by increasing eye gaze cues when using video-conferencing) to be instrumental.

Relatedly, as more leadership is being conducted either with the support of algorithms or leaders are replaced by algorithms an important question is whether human followers willingly accept such interventions. An evolutionary mismatch hypothesis (Li et al., 2018) suggests that humans may have a hard time accepting decisions that are derived from machine learning principles, such as in selection and promotion decisions, although they may be objectively better than those emerging from individual leaders (as they may be less prone to individual errors and biases).

Conclusion

In sum, an evolutionary approach provides a new set of theories, methodologies and tools to understand leadership and followership more completely, help overcome biases and blind-spots in the literature, and turn our attention to investigate novel leadership trends and phenomena. Adopting an evolutionary perspective has rich implications for public policy, particularly for thinking about how we culturally design our organizations and institutions to avoid exploitative leadership and create healthy, productive leader-follower relationships. The articles in this special issue attest to these claims.

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