Contents lists available at ScienceDirect

# The Leadership Quarterly

journal homepage: www.elsevier.com/locate/leagua

# Full Length Article

# The evolution of leadership: Leadership and followership as a solution to the problem of creating and executing successful coordination and cooperation enterprises

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ARTICLE INFO	A B S T R A C T
Keywords: Leadership Followership Evolutionary Psychology Coordination Cooperation	This paper proposes that leadership and followership are not just evolved solutions to the problem of co- ordinating what to do once a group exists. Rather, leadership and followership also solve the problem of creating a group in the first place. Creating a group is a problem of meta-coordination: coordinating with others about what to coordinate about. Of all possible bases for coordinating or cooperating, only a tiny fraction will be embraced by others, and smaller fraction still will be successfully implemented and executed. No one individual has enough information to solve this problem on one's own. Leadership and followership solve this problem by creating a social marketplace, in which leaders propose possible coordination and cooperation enterprises, and followers evaluate and choose among these offered possibilities. This marketplace—in which different in- dividuals propose and evaluate different coordination and cooperation enterprises—solves the problem of meta- coordination by exposing possible enterprises to the broader social market, which serves as a selective or culling regime. Leadership and followership are evolved information-processing roles within this social marketplace. Consequently, understanding the evolutionary psychology of leadership and followership requires under- standing the challenges and opportunities inherent in this market dynamic. The present paper analyzes the tasks that must be carried out to successfully navigate this dynamic. This task analysis predicts a number of novel information-processing functions for the roles of leadership and followership, and suggests that leadership and followership are a broader set of phenomena than currently conceptualized. This broadened conceptualization has a number of important implications for future research, and suggests that leadership and followership may have played a more central role in the evolution of human coordination and cooperation than has been ap- preciated.

# Introduction

In 1937, the Nobel-prize-winning economist Ronald Coase posed the deceptively simple question, "Why do firms exist?" For example, why would an automobile manufacturer ever exist? Why do the engineers, welders, upholsterers, and marketers all coalesce into the entity that we call a company, rather than offering their services independently from one another? Coase's insight was to see the coordination and transaction costs of establishing such relationships: To find the right people and bring them together with the right tools and materials takes time, energy, and money. If this constellation of relationships were to be disbanded after every order for a car, the costs of re-establishing them each time would be astronomical. This would be like hiring a chef and wait staff each time that you wanted to eat at a restaurant.

Coase's less appreciated insight was to see the relationships that can

be established within such a firm. Not only can horizontal relationships be established—for the engineer, welder, designer, and upholsterer to share the fruits of their labor—but so too can vertical or hierarchical relationships. Freed from direct labor, someone can manage and coordinate the workers more efficiently. An entrepreneurial role can also be established to seek out new contracts and anticipate future market demands. At the heart of these vertical and hierarchical relationships lies a specific kind of division of labor: Some parties agree to give up their autonomy in order to be told what to do and how to do it, on the understanding that they will share in the profits. The entrepreneur, manager, and the workers all specialize. None could do the full-time job of the other. Each role is necessary, and they succeed or fail as a unit.

A natural question then arises: has natural selection stumbled upon this insight, such that a capacity to engage in vertical and hierarchical social relationships is reflected in our evolved psychology? Although

https://doi.org/10.1016/j.leaqua.2019.05.006 Received 25 April 2018; Received in revised form 21 May 2019; Accepted 23 May 2019 Available online 19 June 2019 1048-9843/ © 2019 Published by Elsevier Inc.





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Coase (1937) never used the terms, when considering vertical and hierarchical relationships he was of course talking about leadership and followership. Those who instruct others about what to do are leaders. Those who follow those instructions are followers. Questions about vertical or hierarchical relationships then fundamentally resolve to questions about leadership and followership.

In the past ten years, leadership and followership has begun to be studied through the lens of evolution (e.g., Van Vugt, Hogan, & Kaiser, 2008). The insights from this body of work so far include the following:

- 1. Leadership and followership phenomena are found in non-human animals. Certain individuals initiate movement in herds, intervene in conflicts, and communicate their idiosyncratic knowledge to others, thereby disproportionately affecting the behaviors of others (Couzin, Krause, Franks, & Levin, 2005; Hurwitz, 2018; Smith, 2017; Smith et al., 2016).
- In humans, leadership occurs not just in hierarchical, large-scale industrial societies, but also in small-scale, relatively egalitarian non-industrial societies (von Rueden & Van Vugt, 2015).
- Leadership solves coordination problems, a sub-set of which includes collective action problems (Glowacki & von Rueden, 2015; Van Vugt, 2006).
- 4. Evolved cognitive capacities for leadership and followership are tailored to the coordination and collective action problems that humans would have faced over evolutionary time within a small-scale social environment (Van Vugt, 2006; von Rueden & Van Vugt, 2015).
- In order for these cognitive capacities to evolve, the roles of leadership and/or followership must entail some net benefits on balance. Evolved decision rules for navigating these roles must therefore take costs and benefits in account (Glowacki & von Rueden, 2015; Price & Van Vugt, 2014a).

These observations offer principled grounds for expecting the human mind to contain evolved information-processing structures for establishing vertical and hierarchical relationships-even on strict a view of human evolutionary history that does not concede an influence of large-scale societies on the structure of the mind. In this respect, leadership and followership may be a bit like gears, motors, and Velcro: Each may appear to be a recent invention borne out of the excesses of large-scale industrialization, but each was likely stumbled upon by natural selection far earlier than its newer and more modern manifestations.<sup>1</sup> Although of course the kinds of leadership and followership that one finds in modern hyper-specialized societies-such as the roles found in an automobile manufacturer-are exaggerated forms of the phenomenon (Day & Antonakis, 2017; Graen & Uhl-Bien, 1995; Uhl-Bien, 2006). And these likely deviate in important ways from the kinds of leadership and followership dynamics that played out throughout most of our evolutionary history (Van Vugt et al., 2008).

# What are we missing in our current evolutionary analyses of leadership and followership?

Until now, there have been two important gaps in how leadership and followership have been studied from an evolutionary perspective.

#### Phenomenon-first versus adaptive-problem-first

First, nearly all analyses to date have taken a *phenomena-first* approach. In this kind of approach, one starts with the known

phenomenon—leadership and followership—and then characterizes where the phenomenon appears and what attributes tend to co-occur with it. Typical questions include, *in which situations does one find leadership*? (such as in food acquisition, decisions about movement, conflicts within and between groups, and so on; e.g., Smith et al., 2016) and *what are the attributes of people who become leaders*? (such as being high or low on initiative taking, social intelligence, Machiavellianism, health, and so on.; e.g., Van Vugt, 2006). It is this phenomenon-first approach that has led us to the view that leadership and followership are likely the expressions of cognitive adaptations for solving coordination and collective action problems.

Here, in contrast, we build upon the hard-won efforts of the phenomenon-first approach to instead take an *adaptive-problem-first* approach. In this approach, one begins with the conclusions of the phenomenon-first approach: that leadership and followership appear to solve coordination and collective action problems. One then sets aside the phenomenon of leadership and followership altogether, and then thoroughly analyzes the problems posed by solving coordination and collective action problems. Once these are characterized, one next considers what solutions to these problems would look like. These solutions then provide a functional description of what the evolved phenotype of leadership and followership are. This functional description then constitutes a set of theory-driven predictions or hypotheses about what should be found within the phenotype (see Fig. 1).

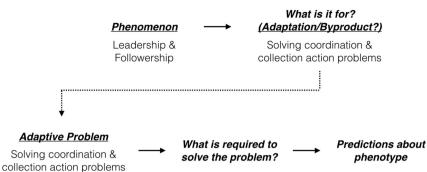
Transitioning to an adaptive-problem-first approach is critical because it allows researchers to conceptualize a phenomenon more thoroughly and rigorously than is possible during the more informal phenomenon-first phase of investigation. As an analogy, consider a group of alien anthropologists who visit earth and have noticed a conspicuous instance of human communication: *public speaking*. They note that a single person tends to speak, and a large group of people tend to listen. Thus, they conclude that there are two kinds of people: *speakers* and *listeners*. They then look to see where this speaking and listening phenomenon appears in different domains of human life; they characterize the costs and benefits associated with either being a speaker or a listener, and document the attributes of the people who tend to become one or the other.

While such an approach would be productive, it would become restrictive in the long-term. Indeed, if these aliens believed that they were studying the vast majority of human speaking and listening with this approach they would of course be mistaken. In fact, most people communicate in a decentralized way most of the time, most people are both speakers and listeners. And while conspicuous public speakers embody particular attributes, these attributes do not exhaust the list attributes of successful speakers in day-to-day, decentralized interactions.

The conclusions of the present analysis will suggest that we have been doing something analogous in our studies of leadership and followership: We have started with the most obvious and conspicuous instances of leadership and followership-instances in which we understand leaders to be types of people (for example, a chief directing a tribe or the manager of an auto firm directing laborers)-and then approached this as if it were the entirety of leadership and followership. Like our alien anthropologists, we have then assumed that leaders and followers are types of people. This assumption defines what we look for when we are looking for instances of leadership and followership, and it leads naturally to the most typical approach to leadership and followership-the search for individual attributes that predict who becomes a leader and who becomes a follower. Indeed, even operational definitions of distributed leadership import the notion that leadership resides within particular individuals within particular interactions (e.g., Smith et al., 2016).

However, an analysis of the problems of coordination and collective action suggests that leadership and followership—like speaking and listening—is a much more pervasive and decentralized phenomenon than its most conspicuous and public instances. Furthermore, just as

<sup>&</sup>lt;sup>1</sup> Gears are found in jumping insects (Burrows & Sutton, 2013), rotary motors in bacterial flagella (Berg & Anderson, 1973), and Velcro in the burdock plant (genus *Acrtium*)—the last serving as direct inspiration for the modern manifestation.



**Fig. 1.** An evolutionary approach to a phenomenon typically starts phenomenon-first (the top row). This approach provides initial guidance. Eventually, there is a transition to an adaptive-problem-first approach (bottom-row). This is a longer-term enterprise that generally produces the most detailed knowledge of the phenomenon and the phenotype producing it. In the current paper, we are shifting from the process depicted in the top row to the process in the bottom row.

speaking and listening are roles within a conversation, so too are leadership and followership roles within coordination and collective actions. These conclusions suggest that large swathes of the phenomena of leadership and followership have until now sat undetected and unstudied, and that there is a fundamentally different way to conceptualize and study the evolved psychology of leadership and followership.

The assumption that leaders and followers are types of people is not the only assumption brought to light by an adaptive-problem-first analysis. Another is the pre-existence of the "group". That is, nearly all past work on leadership has assumed the pre-existence of the group that is being led. For example, leadership is often defined as "taking a central role in the group's decision-making" (Van Vugt, 2006, p. 356). Consequently, the starting point of inquiry are questions such as, *what would be required to make decision-making work within the group*? or, *who will be more likely to be the leader of the group*? Likewise, in existing empirical and modeling work, both the group and the domain of coordination (within and between group conflict, movement, food, and so on) are all assumed to exist ahead of time.

However, an adaptive-problem-first-approach highlights the fundamental problem that groups do not exist until individual minds represent their possible existence and then take steps to create them. If someone has an idea for how to do something that will require more than just their own individual efforts, they will have to communicate this proposal to others (for example, "A bunch of us should go raid the neighboring village."). Others will then have to adopt that proposal for it to come to fruition. Therefore, by assuming that the group already exists, we are assuming away a large part of what leadership is for: for creating groups in the first place (see also Van Vugt, 2017).

If groups do not exist in the first place, then their continued existence cannot be taken for granted either. Maintaining a group requires not only fighting against non-participation but also against the onslaught of competing interests of the agents within the group, which requires vigilance against temptations and threats coming from both within and outside of the group.

The logical entailment of this analysis is that solving these two problems—creating and then maintaining groups—is going to be a large part of the evolved function of leadership and followership. This expanded notion of what leadership and followership are for suggests a number of novel, testable predictions about (1) the evolved psychology of leadership and followership, (2) the within-generation social dynamics created by this evolved psychology, and (3) the across-generation selection dynamics that produced this evolved psychology. These predictions will be highlighted throughout the paper.

In summary:

- Leadership and followership are best conceptualized not as types of people—which is a special case—but rather as evolved informationprocessing roles.
- Leadership and followership are not just roles within a pre-existing group; they are also roles that produce and maintain groups.

#### Actuarial versus mechanistic

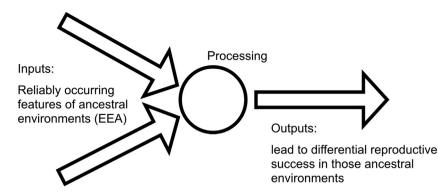
None of the above insights can be adequately studied without a second shift in approach. To date, nearly all evolutionary analyses of leadership and followership have taken an *actuarial* approach, whereas our approach here will be *mechanistic*. To understand the distinction, it is helpful to consider the analogy of how one might approach studying automobiles. One way would be to document the costs and benefits that accrue to people who use automobiles compared to those who do not. Another would be to describe when and where automobiles are found on the road. So, too, could each automobiles' average speed and direction be documented. All of these are *actuarial* approaches: in which one describes factors or elements that correlate to varying degrees with the automobile. In these examples, the relationship between automobiles and money, and between automobiles and location, speed, and direction are all being documented.

However, such investigations could be extended forever without ever approaching the question of how automobiles work. This is a mechanistic question-a question about how a particular phenomenon is produced by describing the sub-entities involved and their casual relationships with one another (Bechtel, 2008). In the case of the automobile, this would require describing various systems-such as the brakes, drivetrain, suspension, and so on-in terms of what they are for (their function) and how they work. If one didn't already know these things, one way to proceed would then be to conduct a task-analysis: to ask what functions must exist within cars given their broad function of transporting humans. For example, one might expect to find mechanisms for receiving inputs about direction and speed from the driver. One could then start looking for things within automobiles that appear welldesigned for executing these functions (for example, systems for turning, systems for stopping, and so on). Once identified, these systems could then be examined at ever finer and finer-grained levels of detail.

Here, we will adopt the same kind of mechanistic approach towards the evolved psychology of leadership and followership. However, rather than systems in a car, we are looking for systems in the mind. Because we don't yet know what these are, we will conduct an analogous taskanalysis: asking what functions must in principle exist within the mind, given the broad function of solving coordination and collective action problems. Thinking in detail about what these functions might be then gives us something to look for.

Given that are no brakes or steering wheels within the mind, what does it mean to characterize systems or mechanisms? Here, we rely on one of the great insights of the twentieth-century: that all informationprocessing devices can be characterized as a set of mechanistic if-then contingency rules. This was one of Turing's (1950) central insights that paved the way for modern computing technology. Consequently, all psychological mechanisms for producing behavior can be described as sets of nested if/then contingency rules. This input/output level of description is called a *computational level description* (Marr, 1982).

Evolution dictates what we are allowed to predict about the human phenotype at this level of description (Cosmides & Tooby, 1987, 1994). Because natural selection is the only known force that creates biological



complexity, and because natural selection works in a particular way, we can a priori state that all input/output mechanisms in the human phenotype will be structured in the following way: (1) that they will take as inputs those features of the environment that were reliably present over multiple generations of evolutionary time, and (2) that they will generate outputs that would have been selected for within that environment—where the environment refers to those features that are stable enough to have interacted with mechanisms over multiple generations, thereby shaping the structure of those mechanisms (See Fig. 2).

Here, our goal is to characterize the information-processing functions that are entailed by solving coordination and collective action problems over evolutionary time. This input/output level of description gives our adaptive-problem-first approach predictive teeth. In particular, when we stipulate information-processing solutions to coordination and collective action problems throughout this paper, we will be making the following predictions in each instance:

- 1. Current human phenotypes will contain input/output mechanisms for executing the information-processing functions. Thus, experimental and/or observational work should find evidence for these input/ output relationships (for example, in the dependent and independent variables of experimental laboratory set-ups, or in the observed relationships occurring within natural ecologies).
- 2. These input/output mechanisms were naturally-selected. Thus, the input/output mechanisms will be selected for compared to alternative phenotypes or strategies within evolutionary models. (For example, they will be selected for in agent-based simulations compared to alternatives or their absence within a population, or will be analytic solutions/evolutionarily stable strategies within evolutionary game theory under a range of reasonable assumptions).

An example will make this concrete: One enduring feature of collective actions is that they sometimes they fail, and these failures are often costly to those who have invested in them. Therefore, we may expect to find information-processing mechanisms within the mind whose function is to monitor for signs of likely failure. As researchers, we can then ask what on-the-ground cues over evolutionary time might serve as inputs to such mechanisms (such as exponentially-increasing signals of dissatisfaction from other members, increasing rates of freeriding, and so on). We can also ask what outputs would have been selected for over evolutionary time (such as assessing the viability alternative collective actions, calculating the costs and benefits of remaining in or withdrawing from the collective action, and so on). Each proposed information-processing function therefore allows us to generate a number of candidate input/output relationships that can subsequently be tested.

The long-term goal of a mechanistic approach is to adequatelyspecify the full suite of evolved input/output mechanisms that exist in the mind. What *adequately-specify* means is that if the description of the input/output mechanisms were to be implemented (say in an artificial **Fig. 2.** Within a mechanistic approach, the evolved phenotype can be characterized as a set of nested if/then contingency rules. These are described in the language of inputs, processing, and outputs. This level of description can be applied to all element of humans' evolved phenotype, including those elements responsible for producing the phenomenon of leadership and followership.

intelligence), then one would observe the stipulated functions occurring without any intervention from an exogenous agent. At this level of specificity, there are likely hundreds if not thousands of input/output relationships embodied within the evolved psychology of leadership and followership (or more). Each one of these should in principle be discoverable.

Although there are a number of excellent empirical studies that essentially embody this input/output logic (see Grabo & Van Vugt, 2016; Lukaszewski, Simmons, Anderson, & Roney, 2016; Patton, 1996, 2000; Sell, 2011; von Rueden, Alami, Kaplan, & Gurven, 2018; von Rueden & Gurven, 2012), the evolutionary study of leadership has been almost entirely devoid of an explicit mechanistic account of how the evolved psychology would work. (The most extensive task analysis presented to date is cursory and appears on p.184 of Van Vugt et al., 2008). Thus, the time is ripe for an explicit, mechanistic account of the psychology of leadership and followership. In this paper, a number of novel predictions about candidate input/output mechanisms will be presented. Each one of these awaits empirical-tests of the kind outlined in predictions 1 and 2 above.

In summary:

• Leadership and followership are phenomena produced by evolved cognitive mechanisms. The existence and evolvability of these mechanisms can be tested rigorously to the degree they are specified in terms their functional (i.e., input and output) logic.

## Combining mechanistic and adaptive-problem-first approaches: An evolutionary task analysis of leadership and followership

The combination of taking both an adaptive-problem-first and a mechanistic approach to a particular phenomenon has been variously called a task analysis, an evolutionary functional analysis, or a computational theory (Cosmides, 1989; Cosmides & Tooby, 1987, 1989; Cosmides et al., 1992; Marr, 1982; Tooby & Cosmides, 1992, 2015)—and what we will call here an evolutionary task analysis. The task analysis is divided into four parts: Part one analyzes the problems inherent in coordination and collective action over evolutionary time. Part two analyzes the information-processing functions that are entailed by solving these problems. Part three considers what outcomes and dynamics these information-processing functions would produce within each generation over evolutionary time. Part four then describes how the content of the preceding sections can be used to think about and study leadership and followership going forward. (While this task analysis is specific to humans, certain elements of it will likely apply to other species as well).

To anticipate the conclusions, the following are the primary, novel, testable insights derived from this task analysis:

• Adequately solving coordination and collective action problems implicates a host of novel information-processing functions within the mind, most of which have yet to be tested for either experimentally or modeled using evolutionary game theory.

• The identification of these information-processing functions allows us to re-define the evolved psychology of leadership and followership as a set of information-processing roles, rather than as kinds of people. This re-definition adds considerably more precision and testability to our present conceptualizations of leadership and followership.

Moreover, once these information-processing roles are identified, it becomes clear that they will produce an interesting and largely unexplored dynamic:

- As they interact in the world with one another, these informationprocessing roles of leadership and followership will create a withingeneration market dynamic. This market allows coordination and collective action enterprises to come to fruition that could not have otherwise been arrived at, thereby solving the problem of metacoordination: of how to coordinate about what to coordinate about.
- In particular, within each generation over evolutionary time, proposals of different coordination and collective action enterprises create a marketplace in which competing proposals are considered by consumers of those proposals. These consumers—by calculating their own idiosyncratic cost/benefit analysis before deciding to join in the enterprise—create a de facto culling regime. Thus, only those enterprises that are acceptable to the required number of other people will be initiated, and an even smaller number still will continue to exist for any length of time. Critically, no one individual can know ahead of time which coordination and collective action proposals will be acceptable to others without first offering up the proposal into the market and then allowing others to respond.
- Within this market, leadership is the role of proposing different enterprises. Followership is role of evaluating these different proposals.
- Solving the problem of meta-coordination is hypothesized to be an important reason for why a psychology of leadership and followership evolved. The dynamics of the market that they create may also help resolve certain long-standing issues related to the evolution of sociality and cooperation, including the second-order free-rider problem.

# Part I of the task analysis: What are the problems inherent in coordination and collective action?

Raiding a village, building a well, establishing a norm for sharing food—these are all coordination and collective action problems. Although the dynamics of each are different, here we are asking what dynamics hold generation after generation among *all* instances of coordination and collective action problems. These determine what the evolved psychology of leadership and followership will need to be.

# Problem 1: The free-rider problem

When benefits are a public resource or are not monopolizable by those who create it, an individual who opts out of contributing can nevertheless reap the same benefits as those who contributed. Because they forgo the costs of contribution, these non-contributors accrue a greater net benefit than those who do contribute. This is the classic *freerider problem* in the evolution of cooperation (Axelrod, 1984; Axelrod & Hamilton, 1981; Hume, 1739). There are two solutions to this problem. First is for a phenotype to be structured in a way that it avoids contributing to those enterprises in which failures to contribute cannot be avoided or punished. Second is for contributions to be accompanied by additional mechanisms for (i) detecting instances of free-riding and (ii) motivating punishment and/or avoidance (Boyd & Richerson, 1988, 1992; Cosmides, 1989; Cosmides, Barrett, & Tooby, 2010; Kiyonari & Barclay, 2008; Panchanathan & Boyd, 2004; Price, 2005).

#### Problem 2: The problem of representing the coalition and its consequences

Agents who enter into a contingent exchange of costs—such as in a trade or an outlay of costs such as in a work project—constitute a *coalition.*<sup>2</sup> Who belongs within the coalition, why those particular agents are coming together, and what is expected of them, must all be represented at some level in the evolved psychology in order to predict the actions and behaviors of others, and coordinate with them.

## Problem 3: The problem that multiple coalitions exist

The number of possible coalitions is as large as the potential ways in which two more agents may enter into a coordination or cooperation relationship with one another (Patton, 1996, 2000). Thus, even in a small group of 50 people there may be several thousand virtual "groups" or coalitions, each of which comprises a particular set of relationships. For example, those agents who will respond to an outside attack from any enemy may be different than the agents with whom one shares one's food, which may be different than the agents with whom one allies to displace a social rival, and so on. This world of multiple, co-existing coalitions has several important attributes. First, each individual agent sits at the nexus of a cloud of nested, overlapping coalitions. Second, coalitions will vary in terms of the broadness of their goals. Third, very few individuals will share the exact same coalition cloud with each other. Fourth, only a subset of all coalitions will be activated or in use at all times.

### Problem 4: The problem of coalitional entrepreneurship

A coordination or cooperation enterprise cannot exist until someone has the idea of it. At some point then, for a coalition to exist, someone had to arrive at the idea of it and then communicate that idea to others. This problem of imagining and then communicating possible coalitional enterprises to others is the problem of *coalitional entrepreneurship* (Lopez, McDermott, & Petersen, 2011).

Moreover, coalitions cannot exist without the individual members all changing their behavior in accordance with the enterprise and goal of the coalition. This means that some part of the member's psychology must hold some representation of that goal or enterprise. In the case of coalitions defined by behavioral coordination, such a representation may be as minimal as the representation of the behavior (for example, *walk to the watering hole in the south*). Yet even in these minimal cases, such a representation must come from somewhere. Some may already exist in the social environment, such in as culturally-transmitted representations that extend across generations, as in the case of local norms, practices, and tribal and national identities. They may also be created de novo in the mind of another person and then communicated, as in when a new goal not yet achieved is imagined and communicated, such as to kill Caesar or to build a well (Haslam, Reicher, & Platon, 2011).

#### Problem 5: The problem of coalition maintenance

Once a coalition is proposed, it be must be created, invested in, and maintained. Maintaining a coalition is not easy for several reasons. First, some people will benefit more than others from the enterprise of the coalition. Thus, there will differing levels of investment from each individual, depending on how much they each have to gain (Tooby, Cosmides, & Price, 2006). Second, each individual within a coalition will also belong to other coalitions, and these different coalitions may

 $<sup>^2</sup>$  We will use the word "coalition", rather than "group", to avoid the conceptual baggage associated with the word "group". Here, "coalition" simply means a set of agents coordinating or cooperating in the broadest possible sense.

often have competing interests. For example, the members of a coup (say to kill Caesar)—may be aligned in their interests to achieve this particular goal. However, once achieved, each may have different ideas about what should happen next. Both issues are compounded by a third problem—the free-rider problem, in which each individual will be selected to avoid over-contributing relative to others within the coalition, which will tend to corrode the existence of the coalition over time.

### Problem 6: What to do with an existing coalition

Each coalition is defined by a particular goal or enterprise, around which a particular set of individuals form. However, this is an oversimplification, which can be seen once we consider how such a coalition will play out dynamically over time. For example, once such a coalition-defined-by-goal exists, two things will happen. First, coalitions can be chosen not because of its goals, but rather because of who is a member. Second—and mirroring Coase's insight about the origin of firms—the relationships formed among the members of a coalition can become the thing itself to be preserved, above and beyond or even independent of any particular goals or enterprises (Tooby et al., 2006).

# Part II of the task analysis: What information-processing functions are entailed by solving these problems?

We next consider what information-processing functions would be required to solve the above problems. Doing so allows to more precisely characterize the evolved psychology of leadership and followership. The following is a truncated treatment of these predicted informationprocessing functions (for additional design feature considerations, see Part A of the SOM):

### Broad function 1: Creation of coalitions

If there are gains to be had in either leading or following based on some coordination or collective action enterprise, there must be information-processing to imagine and then communicate such possible coalitions.

# • Prediction 1: An evolved psychology for representing current coalitions Novel coalitions will always arise in the context of currently existing coalitions. Consequently, the psychology of generating novel coalitions requires representing the coalitions that already exist.

•. Prediction 2: An evolved psychology for evaluating current coalitions

All coalitions will naturally vary along a number of attributes: their goals, their efficiency in achieving those goals, the satisfaction of the members, the level of conflict and coordination within the coalition and between the coalition and those outside of it, and so on. All of these attributes are predicted to be represented by psychological mechanisms.

•. Prediction 3: An evolved psychology for imagining novel coalitions

Psychological mechanisms are predicted to not only generate counterfactual elements of existing coalitions, but to also generate representations of possible novel coalitions that do not yet exist.

•. Prediction 4: An evolved psychology for communicating novel coalitions Some mental representation must be created in the minds of others if a coalition is to exist. Therefore, candidate novel coalitional representations need to be eventually communicated to others. Psychological mechanisms must implement this transition from internal private representation to public communication.

•. Prediction 5: An evolved psychology for evaluating possible novel coalitions

Choosing a coordination or collective action enterprise that fails is

costly—particularly when that choice entails social, resource, or opportunity costs. Therefore, a fundamental task for evolved psychological mechanisms is to choose a successful coalition.

#### Broad function 2: Coalition execution and maintenance

If gains in coordination and collective action enterprises are to come to fruition, some subset of all possible novel coalitions will need to be chosen and then executed. This requires information-processing mechanisms to determine what execution means and looks like for each coalition—which will vary depending on the nature of the goal or enterprise.

# • Prediction 6: An evolved psychology for representing the candidate coalition

Some representation of the goals of the coalitions, or minimally the behavioral expectations of the individuals within the coalition, must be held.

# Prediction 7: An evolved psychology for motivating and guiding coalition execution

The goals or behaviors that constitute the coalition must eventually be executed. For example, a group of agents who represent that they have all agreed to go on raid of a neighboring village must at some point put that plan into motion. Such outcomes require the involvement of planning and motivation mechanisms.

# • Prediction 8: An evolved psychology for implementing contingencies once the coalition is underway

Mechanisms are also required to monitor the current status of the coalition and determine what may be needed to either preserve it or improve it over time. For example, a set of agents who enter into an agreement of common defense must monitor for threats to that agreement, such as internal fighting or changes in loyalty. They must then also be motivated to do something about such threats.

Characterizing the evolved psychology of leadership and followership more precisely

The identification of these information-processing functions allows us to now more precisely re-define the evolved psychology of leadership and followership as a set of information-processing roles, rather than as kinds of people. In particular:

• The functions described above (and in SOM, Part A) are predicted to be the central information-processing functions that constitute the evolved psychology of leadership and followership.

Thus, if we want to understanding the evolved psychology of leadership and followership, we must understand the mechanisms producing these functions. Furthermore, if we take seriously the notion that leadership and followership is a division of labor (Hooper, Kaplan, & Boone, 2010; Kurzban & Van Vugt, 2007; Price & Van Vugt, 2014a, 2014b; Tooby et al., 2006), then we can define those aspects of leadership and followership that are asymmetric as follows:

- Broad function 1: Creation of coalitions
  - Leadership is the information-processing role of generating and/or communicating possible novel coalitions, including the motivation to do so.
  - Followership is the information-processing role of evaluating the possible novel coalitions proposed by others, including an appetite for consuming and evaluating such offerings.
- Broad function 2: Coalition execution and maintenance
- Leadership is the information-processing role of: having a mental representation of the coalition, maintaining the necessary or

sufficient representations of the coalition in others, directing and monitoring the behaviors and division of labor within the coalition, monitoring motivation and investment in coalition execution, sanctioning under-contribution, and orchestrating high-level responses to obstacles and opportunities—including shifting the coalition's goals, and serving as spokesperson for the coalition's interests with respect to both members of the coalition and to those outside of it (Lukaszewski et al., 2016; von Rueden, Gurven, Kaplan, & Steiglitz, 2014).

- Followership is the information-processing role of: mentally representing one's own expected contribution (and/or behaviors) with respect to the coalition, executing those behaviors, representing and responding to direction from leaders about one's own and others' contributions, and representing and responding to leader-directed changes to the coalition's goals and membership.

### The distribution and adoption of leadership and followership roles

Now that leadership and followership are more precisely defined as information-processing roles, what can we infer about their likely distribution over evolutionary time? First, because each individual will belong to a large cloud or array of coalitions, both leader and follower information-processing roles are likely be implemented in each individual body. Consequently, the potential to adopt either role will be part of a universal psychological endowment (Price & Van Vugt, 2014a, 2014b).

Second, and importantly, there is no entailment that each leadership function must be carried out by just one individual. Instead, different functions—such as the creation of goals, managing and directing goal execution, sanctioning under-contribution, and so on—may be implemented by different individuals. For example, skills in articulating a goal or a vision for the coalition may be different than the skills and knowledge required to execute the tasks relevant to the coalition (Price & Van Vugt, 2014b). Thus, initial individual differences and subsequent specialization may canalize certain individuals to occupy particular roles more often.

Third, each individual will belong to many different coalitions. Thus, it is unlikely that they will occupy the same role within each coalition that they belong to. For example, the same individual who can best sanction under-contribution within a small-scale cooperative endeavor (because they are physically strongest among the members of that coalition) may not be the same person who sanctions under-contribution during a large-scale defense of one's village (because they are not the strongest among this larger coalition, or lack the necessary social capital and influence at this largerscale).

Thus, leadership can be implemented across different bodies—and in fact, will often be when different individuals have different relative strengths and skills. Moreover, the same function may even be executed by one member one day, or by another member another day. Or, multiple individuals may coordinate to execute any particular function at the exact same time (as would be the case in egalitarian groups). Thus, there will be tremendous variation in (i) how much leadership functions are bound within particular individual bodies and (ii) how stable that body-to-function mapping is for any coalition (for convergence on this idea from another perspective, see Hurwitz, 2018).

#### Distributed monitoring of leadership and followership roles

Every individual will monitor their own cost/benefit investment within the coalition.<sup>3</sup> This monitoring will include a representation of

what leadership and followership roles are occurring, along with a determination of how effective these are. This monitoring is carried out by information-processing mechanisms. These work by being sensitive to the on-the-ground cues of the different functions or manifestations of leadership. That is, the mind is predicted to contain an implicit taxonomy of the kinds of roles necessary for each type of coalition.

To understand how this psychology likely works, we must next consider what different manifestations of leadership will in principle occur within each generation over evolutionary time (for additional details, see Part B of the SOM).

# The different manifestations of leadership roles

#### •. Leadership as mentorship

What to do and how to do it are perennial problems to solved every generation, particularly as humans occupy diverse social and ecological niches, relying on individual improvisation and cumulative cultural knowledge transmitted over generations (Boyd & Richerson, 1985). Asymmetries in knowledge, experience, skills, and so on will produce different options in terms of who to learn from and who to emulate (Henrich, Chudek, & Boyd, 2015; Henrich & Gil-White, 2001). Consequently, one leadership and followership dynamic will involve leadership emitting (either intentionally or incidentally) variants of what to do and how to do it. Followership will involve considering and selecting among these variants (Couzin et al., 2005; Smith et al., 2016).

#### •. Leadership as rhetoric

The role of leadership fundamentally involves convincing other agents to change their behaviors according to some representation that you yourself have. Each individual will evaluate such inducements and invitations in light of their own unique constellation of existing interests, calculating the likely cost/benefit repercussions of making such changes. Consequently, a large part of leadership involves choosing what to communicate to others, and how to communicate it in such a way that clarifies what to do and why it should be done.

### •. Leadership as task management

The time and energy required to achieve some goal (dig a well, raid a village, and so on) precludes doing other things-including coordinating the contributions of different individuals. An over-arching director can increase efficiency by assigning different tasks to individuals with different strengths, minimize duplication and wastes of effort, allocate investment where and when it is needed, and so on. As Coase (1937) observed, these functions of leadership are seen in modern, large-scale institutions. But the same principles apply at all scales of social interaction and enterprise, and would be evolutionarilyrecurrent (Van Vugt et al., 2008; von Rueden et al., 2018; von Rueden & Van Vugt, 2015). Such functions require: understanding the tasks to be done, the relative strengths and weaknesses of individuals, generating task and effort counterfactuals, effectively communicating goals and tasks for others to do and convincing them to carry them out, seeking out information about who has and is currently doing what (and how well), and receiving information related to unforeseen exigencies.

#### •. Leadership as policing

Every individual—both within and also outside of each coalition—will have his or her own unique constellation of interests. This means that there will be constant testing of agreed upon or negotiated tradeoffs of costs and benefits, such that each individual will want to accrue more benefits and incur fewer costs. The leadership role is then to monitor coalition members' cost/benefit flows in light of the

<sup>&</sup>lt;sup>3</sup> Cost and benefit are defined as within-generation proximate cues that track the ultimate, differential reproductive success of design variants compared to alternate designs within the population (Gardner & Grafen, 2009; West, Griffin, & Gardner, 2007). More plainly: the level of selection is neither an individual or

<sup>(</sup>footnote continued)

a group, but the preservation of the design of input/output mechanisms that will exist across different individual bodies within and across generations.

negotiated agreements, and to coordinate and sanction punishment and enforcement (Price & Van Vugt, 2014a, 2014b; Tooby et al., 2006). Individual members will also want to generate their own ideas about what to do and how to do it, which may or may not harm the dynamics or violate the norms of the coalition. The leadership role is then to monitor for these introduced variants and determine if they should be preserved or rejected.

### •. Leadership as coalition representative

Almost all coalitions will be represented by others outside of it (that is, outsiders will mentally-represent that the coalition exists, who its members are, and so on). Outsiders will also have interactions with members of the coalition, and will hold some representation of how much they value the coalition and are willing to impose costs on its members. The leadership role is then to monitor these levels and work to increase them. That is, the leadership role represents the interests of the coalition to those outside of it, working to negotiate the best possible treatment of the coalition as it interfaces with the rest of the world (Lukaszewski et al., 2016; von Rueden et al., 2014). Further, alternative coalitions represent both opportunities and threats: Compatible coalitions can be merged, neutral coalitions can be convinced to value one's own coalition more they currently do, and rival coalitions can be defended against and undermined. Possible new and attractive individual members can also be courted while unattractive potential members dissuaded. Investment and resources directed to the coalition can be maximized. These are all tasks pursued by the leadership role.

In summary:

• Prediction 9: The evolved psychology of leadership and followership contains information-processing procedures for enabling each of the above manifestations of leadership, including monitoring for their existence and effectiveness.

## Part III of the task analysis: The dynamic that plays out between leadership and followership roles

The above information-processing occurs in individual bodies which in turn interact with one another. We next consider how these interactions would in principle play out within each generation over evolutionary time. This next step of the analysis is the source of the conclusion that leadership and followership create a within-generation market dynamic that solves the problem of meta-coordination.

# The evolved psychology of leadership and followership creates a market dynamic

Evolved information-processing mechanisms are expected to represent both counterfactual coalitions and counterfactual leadership and followership roles within those coalitions. Thus, when a weakness in an existing coalition is perceived, or an opportunity to establish an imagined coalition becomes available, individuals will become motivated to act in a way that realizes these counterfactuals (indeed, this is why these counterfactuals are generated in the first place). For example, cues that a leader has become feckless in convincing others should unleash counterfactual mental representations in the minds of followers about alternative leaders, and unleash motivation for action in the minds of alternate candidates for that leadership role.

Consequently, within each generation over evolutionary time, leadership and followership roles will create a market dynamic. The market will be game-theoretic, meaning that what is offered at time one can lead to a change in the market at time two (Noë & Hammerstein, 1995). That is, each individual can react to the current state of the market by producing their own novel leadership and followership offering. For example, someone may use an instance of poor followership in a coalition that they would like to join to demonstrate their own (better) followership attributes. In so doing, they expand the market of followers from which that coalition can choose. Likewise, the proposing of different coordination and collective action enterprises will create a marketplace in which competing proposals can be evaluated by consumers (leadership being the role of proposing these different enterprises, and followership being the role of evaluating them).

In summary:

• Prediction 10: The evolved psychology of leadership and followership creates a market dynamic. The benefits created by this market dynamic are hypothesized to be part of why the evolved psychology of leadership and followership exist.

Next, we will consider how the psychology of attempting to garner benefits while avoiding exploitation drives this market dynamic.

### How the psychology of leadership and followership drives the leadership and followership market

Because there are more possible coalitions than can ever be realized, there will be competition among leaders<sup>4</sup> to attract followers, and competition among followers to select the best leaders. What constitutes a good follower is determined by how a leader could be exploited by a follower, and what constitutes a good leader is determined by how a follower could be exploited by a leader.

#### How a leader can be exploited

Followers may be incompetent, feckless, or unable or unwilling to perform the tasks or behaviors required of them. Leaders may also fail to get credit for their contributions to the coalition from the perspective of followers. In particular, the contributions of a leader may be cryptic or hidden from the view of followers, such that any one follower sees only a small sample (or even none) of what the leader contributes in their day-to-day activities.

In the case of mentorship, exploitation may particularly be a concern when the skillset or basis of emulation is only short-term-such that the followers can consume the leader's skills and consequently divest in valuing the leader thereafter. In the case of rhetoric, followers may be inattentive to what they should do and why-either because (i) they do not have sufficient knowledge or skills to incorporate the information, or (ii) because they have motivations and goals that are rival with the interests of the rest of the coalition. In the case of policing, each individual follower would like the leader to more lenient on themselves the other followers, such that if the leader did this with each follower the coalition would either dissolve or produce at a low enough level that it would harm the interests of the leader. Consequently, followers will be incentivized to be the recipient of asymmetric benefits and/or leniency, which can be accomplished by hiding failures, oversignaling contributions, and so on. In the case of coalition representation-representing the interests of the coalition to outsiders-coalition members may produce behaviors that harm the reputation or diplomatic efforts of the leader with respect to the rest of the world (i.e., "they make the rest of us look bad").

#### What makes a good follower from the perspective of a leader?

A good follower from the perspective of a leader manifests attributes that are opposite of the ways in which a leader can be exploited by a follower. Consequently, a good follower is one who: is able to perform the tasks required of them; acknowledges the contributions of the leader; trusts that the leader is contributing to the interests of the coalition; is attentive to and quickly internalize instructions; has

<sup>&</sup>lt;sup>4</sup> Shorthand for "individuals occupying leadership roles" (likewise for followership roles).

interests that align with the rest of the coalition; minimizes signaling their own achievements; readily communicates their mistakes, failures, and moments of under-contribution; at minimum, wants to be evaluated according the same standards that others in the coalition are also evaluated; demands little from the coalition; and produces outcomes that advance the interests of the coalition from the perspective of outside observers.

 Prediction 11: The evolved psychology of leadership and followership contains a metric for evaluating the quality of followership roles, which can be understood by analyzing how leadership roles may be exploited over evolutionary time.

#### How a follower can be exploited

Leaders can exploit followers by being either inept or exploitative, or both. Leadership is inept if it offers coalitions that either dissolve prematurely or produce no net benefits to members. For example, in the case of mentorship, a leader can be wrong about the right thing to do, and a follower may emulate that error at a cost to themselves. A weaker form of the same problem involves joining a worse coalition in lieu of a better realizable alternative (for example, backing an unsuccessful political candidate).

In the case of rhetoric, a leader may fail in articulating what to do and why. This will produce mistrust or lack of confidence in the goals, vision, or long-term enterprise of the coalition. In the case of management, a leader may not fully-utilize the relevant skills and abilities of the members of the coalition, and may direct them to do things that are neither efficient nor productive. Leaders may also fail to understand the workings and dynamics of the situations over which they are ostensibly directing, and will fail to respond to the exigencies that arise within them. In the case of policing, a leader may fail to monitor for undercontribution from followers. Or, they will be unable to successfully address under-contribution when it is detected. In the case of coalition representation, a leader may not adequately represent the interests of the coalition and may harm the status and reputation of those in it. Generally, an unsuccessful leader will be someone who cannot convince others (either within or outside of the coalition) to modify their behaviors; a leader who is ignored is no leader at all.

In addition to ineptitude, a leader may also exploit followers. Leaders gain status by being followed and emulated and by influencing others. Status, in turn, fundamentally derives from the ability to get others to do what you want (either because they want to, or because you are forcing them to; Henrich & Gil-White, 2001). Consequently, followers are de facto ceding status to leaders when they follow. This gives leaders power, both within the leader/followership relationship and also in the minds of third parties who observe that relationship. Just as followers will be incentivized to maximize their gains when participating within the coalition, so too will leaders. Therefore, leaders can use this power to further their own idiosyncratic ends, which may be either neutral or actively counter to the interests of the coalition. Because leaders are already likely to have intrinsic or conferred bargaining power with respect to followers, they can then use that power to extract more benefits from the coalition than was otherwise agreed upon (Price & Van Vugt, 2014a, 2014b). This problem is compounded to the degree that the leader's investment in the coalition, and the benefits they extract from it, are opaque to or hidden from followers, and to the degree that the leader has differential access to the coalition's social and material resources.

#### What makes a good leader from the perspective of a follower?

A good leader from the perspective of a follower manifests attributes that are opposite of the ways in which a follower can be exploited by a leader. Consequently, a good leader is one who: maintains the continuity and integrity of the coalition; chooses goals and enterprises that

generate benefits for the members of the coalition; is correct about what to do; leads the best possible coalition of its type among the realizable alternatives offered; clearly articulates what to do and why; instills confidence and trust in the goals, vision, and long-term enterprise of the coalition; fully utilizes the skills and abilities of the members of the coalition; directs tasks in a way that is efficient and productive; fully understands the situations over which they exert direction; responds effectively to the exigencies that arise within the coalition; monitors for under-contribution among followers and effectively addresses this when it does occur; represents the interests of the coalition in a way that lifts the status and reputation of those in it; can convince others to modify their behaviors: does not use their status within the coalition to further their own idiosyncratic interests; minimizes the opacity of the benefits that they extract from the coalition; is trusted in terms of what they contribute to the coalition and take from it; and minimizes their use of the coalition's resources.

• Prediction 12: The evolved psychology of leadership and followership contains a metric for evaluating the quality of leadership roles, which can be understood by analyzing how followership roles may be exploited over evolutionary time.

#### Information-processing checks on exploitation

Consequently, evolved information-processing mechanisms for monitoring for cues of good and bad leadership and followership are expected to exist. Moreover, one can anticipate how these mechanisms may work by analyzing what on-the-ground cues would allow individuals to infer the above criteria. For example, one subroutine of these mechanisms is expected to monitor for demonstrations that someone can convince others to change their minds about either what they want to do, or how they feel towards something. Such demonstrations should affect something like an ability-to-persuade-others index, for example, which would be part of the mental representation that each agent holds about others in their social world (and may also feed into something like a general leadership index; see Grabo, Spisak, & Van Vugt, 2017). Such a representation would be called up when considering each agent's particular strengths and weaknesses for various leadership and followership roles. The criteria listed above imply the existence of a large number of similar kinds of mental representations, most of which have yet to be explored.

These representations and their down-stream effects serve as information-processing checks on exploitation. However, the effectiveness of these checks depends almost entirely on the state of the market. For example, evolved decision-rules are expected to register when the benefits of replacing a poor leader outweigh the costs. Consequently, the presence of a viable alternative will lower the costs of leadership replacement, and such a change will be more likely to occur. Generally, when leaders are more replaceable there will be less exploitation of followers. The same holds for followership. To the degree that a follower provides a uniquely-valuable service, they may be permitted to exploit leadership roles to some degree (or at least can expect a higher rate of relative benefits from the coalition). Consequently, the magnitude of exploitation and conflict found within a coalition will be a function of the current state of the leadership and followership market (see also Price & Van Vugt, 2014b).

 Prediction 13: The magnitude of exploitation and conflict found within a coalition will be a function of the current state of the leadership and followership market.

### How the market dynamic helps solve the problems inherent in coordination and collective action

We will next revisit the initial problems posed by coordination and collective action, and consider how the evolved psychology of leadership and followership and the market dynamic it creates may help solve these problems. In the process, several additional problems not covered in the initial task analysis will also be addressed.

• Prediction 14: The leadership and followership market helps solve the problem of coalitional entrepreneurship.

The leadership and followership marketplace appears to solve the problem of coalitional entrepreneurship in a way that no purely, topdown centralized process could. In particular, the roles of leadership and followership create a trial-and-error process that discovers coordination and cooperation relationships that are workable (acceptable to others), but that would not be discovered otherwise, because the information about what is workable is locked away in individual minds, and because each agent sits at a unique locus of intersecting interests.

Another way of putting this is that natural selection cannot prespecify with complete detail the basis around which cooperation and coordination should exist, because doing so would require knowledge of details that vary within every generation. So instead, what can be "seen" by natural selection is that the division of labor of leadership and followership drives the sussing out of those relationships more than does perfect parity of roles between agents. In other words, by allowing leadership offerings and followership choices to play out within a particular social environment (the market), an otherwise untapped possibility space is opened up.

The immune system offers a useful analogy: The immune system recapitulates natural selection within a generation by creating variants of antibody proteins, each of which are then let free to fight against a particular pathogen. The most effective of these variants are retained (Boehm, 2011). In the same way, leadership and followership create a within-generation selective regime in which coordination and cooperation variants are generated, and those that are acceptable to the larger social environment are retained. In this way, leadership and followership help solve a meta-coordination problem: how to coordinate about what to coordinate about.

• Prediction 15: The leadership and followership market helps solve the problem of coalition execution and maintenance, including vigilance against free-riding.

The asymmetrical dynamic of leadership and followership within the market also appears to be well-suited to solving the problems of maintaining and executing coalitions in two important ways. First—and as observed by generations of scholars—leadership and followership produce a division of labor that can more effectively execute goals. The reason why is the same reason that hierarchical organization is endemic throughout complex biological and social systems—because "no 'demon' or other local process can know enough about the overall situation to make good decision; but no top-level manager can know enough details either" (Minsky, 1974, p.60; see also Coase, 1937; Lorenz, 1948/1996; Simon, 1962, 1969/1996). That is, leaders are free to worry about *what* to do, because followers are free to worry about *how* to do it.

Second, the combined perspectives of leadership and followership can better capture instances of under-contribution, and better determine why it is happening and what to do about it, than can either on their own (Tooby et al., 2006). Leaders will tend to have a better sense of who is assigned to what task, and what is expected of them. Followers will tend to have better information about the performance of their fellow followers. Consequently, followers will tend to be better *detectors* of under-contribution in followers, whereas leaders will tend to be better *responders* to that under-contribution. In particular, because of their broader access to information, leaders will often be better able to attribute under-contribution to its correct cause. For example, was an apparent case of under-contribution due to free-riding, or due to a different expectation between the different followers about what is expected of them? Such information will be more opaque to followers than it will be to leaders.

Moreover, the conflicts of interests between leaders and followers, and among followers themselves, will reinforce this sensitivity to freeriding. The underlying principle is very similar to the dynamics of parent-offspring conflict (Trivers, 1974): just as siblings perceive more slights from the other sibling than they would if they expected equal treatment, so too will followers. This self-advantageous bias will produce overly-sensitive under-contribution detection on the part of followers from the perspective of the leader. However, this conflict between followers can be buffered against if both leaders and followers agree to let the leader respond to instances of perceived under-contribution by followers. That is, all else equal, followers should be motivated to let the leader know about under-contributions from other followers, but at the same time should be willing to yield to the decision of the leader as to how to respond, if at all. It can be net beneficial for followers to agree to this: Both leader and follower can't do the job alone, so both are incentivized to maintain their division of labor.

This division-of-labor benefit offsets the demand among followers to do a bit less than everyone else. Or in other words, the leader does not benefit from under-contribution in the same way that another follower does. Therefore, followers should be more willing to believe the leaders' judgment about the relative under-contribution among different followers. From the "objective" perspective of the coalition, the leader's perceptive is in fact more correct or, more precisely, better for the maintenance of the coalition.

In this way, leadership and followership help solve the free-rider problem, and coordinate the contributions of different members within the coalition (Price & Van Vugt, 2014a, 2014b). Left to their own devices, a set of leader-less individuals—even if starting out giving equal contributions—will slowly corrode itself because each individual will feel that they are over-contributing compared to everyone else, because from their perspective, they are. Left unchecked, such sentiments typically lead to a ratcheting down of contributions and investment, until the coalition is extinguished. This is why an absence of leadership often creates disloyalty.

• Prediction 16: The leadership and followership market helps solve the 2nd-order free-rider problem

The classic free-rider problem involves under-contribution and/or over-extraction of benefits from the coalition. The leadership role helps solves this problem by coordinating punishment and monitoring contribution levels.<sup>5</sup> However, a second-order free-rider problem then arises: Given that someone is monitoring and sanctioning free-riding, who is monitoring the sanctioner? Who, in other words, is policing the police? The division of labor in leadership and followership roles helps solve this problem in two ways.

First, and foremost, followers will serve as a check on second-order free-riding. Any follower who is under-contributing represents a cost to other followers (insofar as those other followers do not share in the benefits of that under-contribution). Consequently, others followers are incentivized to monitor for effective leader sanctioning. That is, they will police the police. Moreover, leaders who fail to effectively sanction that free-riding will satisfy the input conditions of inept or exploitative

<sup>&</sup>lt;sup>5</sup> Leadership is also the information-processing role of determining who is in good standing with respect to the coalition, and who is not. This role is crucial for the evolution of collective action, because the sanctioning of under-contribution in a collective action can look like regular non-reciprocation from the perspective of anyone who does not know about the under-contribution (Panchanathan & Boyd, 2004). Consequently, some information-processing role needs to communicate or embody the causal link between under-contribution at time one and subsequent non-reciprocity towards the under-contribution at time two. Otherwise, the psychology of reciprocity will oppose the evolution of collective action. Leadership is such a role.

leadership, to which each follower's psychology should be vigilant. Followers can then respond by doing any number of things, including withdrawing their services or shifting their followership onto another coalition or leader (see also Barclay, 2013).

Second, other potential leaders can also serve as a check on secondorder free-riding. In particular, those individuals who are interested in a leadership role will monitor for failures of leadership—including failure to sanction under-contribution—because these represent opportunities to shift support away from the current leader over to oneself. Secondorder free-riding on the part of leaders therefore creates opportunities for rivals. Consequently, and in general, when followers can police the leader or there are feasible replacements for that leader, there will less second-order free-riding on the part of the leader. Conversely, when followers cannot readily police the leader or if there are no feasible replacements for that leader, then there will tend to be more secondorder free-riding on the part of the leader.

# • Prediction 17: The leadership and followership market helps solve the opacity-of-coordination problem

Although the first and second-order free-rider problems are wellknown, the opacity-of-coordination problem is less so. This problem refers to the fact that it is often unclear how to gauge the likely success or failure of any particular coordination or collective action enterprise. This is because such enterprises often involve many moving parts which must be integrated together. The leadership and followership market dynamic appears well-designed to solve this problem as well (for the explanation, see Part C of the SOM).

#### Summary of the market dynamic

From the cost/benefit perspective of natural selection, leadership and followership is a mutually-beneficial division of labor<sup>6</sup> (Price & Van Vugt, 2014a, 2014b): Both roles stand to benefit from the products of leadership and followership-leveraging the abilities, knowledge, and power of multiple agents to achieve things that could not be done by individuals-including, but not limited to, the creation or extraction of resources from the environment, and the promise and delivery of social or physical costs and benefits to others (Hooper et al., 2010; Kurzban & Van Vugt, 2007; Price & Van Vugt, 2014a, 2014b; Tooby et al., 2006). This potential to benefit, however, exposes both roles to costly mistakes, and even active exploitation. Consequently, the psychology of both leadership and followership must not only create and be attentive to opportunities to benefit, they must also monitor for signs of mistakes and exploitation. The execution of these information-processing functions then creates a within-generation culling regime. This regime opens up a possibility space of coordination and collective action enterprises that could not exist otherwise, because no one agent could determine on their own which coordination enterprises would be successful. Thus, by virtue of the market dynamic they create, leadership and followership roles solve the problem of meta-coordination: how to coordinate about what to coordinate about.

# Part IV of the task analysis: What does this task analysis offer to future studies of leadership and followership?

#### A mechanistic study of the evolved psychology of leadership and followership

Every information-processing function characterized in this paper—and there are several hundred if one considers that functions entail sub-functions, and so on—is expected to be implemented in the human mind. Consequently, a research program may commence to empirically test for the existence of these functions. This would be done by generating and testing hypotheses about these functions at the level of inputs and outputs (for additional details, see Part E of the SOM).

# A more precise phenotype for evolutionary models of leadership and followership

The present task analysis makes novel claims about what fitness benefits the division of leadership and followership roles provided over evolutionary time (Or, more precisely, it makes more detailed claims about what design variants should be inserted into evolutionary simulations, game theory, and analytic models of evolvability). These claims can be tested in future mathematical and simulation models of the evolution of leadership and followership. For example, the notion of a decentralized culling regime borne out of the kinds of informationprocessing suggested here can be implemented and tested.

Broadly speaking, tests of *evolvability* (that is, of what can evolve given the logic of how natural selection and other evolutionary processes work) can only be as sophisticated as their assumptions about the phenotype. By characterizing the phenotype as a broader and more precise set of contingent responses emanating across different individual agents, a richer and more complex analysis of the evolution of leadership and followership can be conducted. For example, past and current evolutionary models of the evolution of leadership (that is, of heterogeneity and hierarchy in collective actions, such as in Olson, 1971; Gavrilets, 2015; Hooper et al., 2010, and so on) model the costs and benefits of monitoring and enforcement within already-existing collective actions. Thus, these models by and large assume away the psychology of the evolving agents—which is thus far entirely appropriate (although see Gavrilets, Auerbach, & Van Vugt, 2016 for the addition of some psychological representations).

However, the role of the evolved psychology cannot be ignored when it comes to initiating collective actions in the first place. Future modeling will therefore need to incorporate variables related to different agents who can represent different possible collective actions, communicate those representations to others, and so on. At minimum, and to start, agents will need to be able to both initiate and evaluate collective action proposals, and do so all according to some internal model of expected costs and benefits. However, in the long term, all of the design features of the psychology outlined within this paper will need to be incorporated if we are to model how collective actions are initiated and maintained with precision and fidelity.

#### Thinking differently about leadership and followership and how to study it

The present task analysis adopts a mechanistic approach that is also universal. This means that all humans are expected to have an evolved psychology for executing the functions of described in this task analysis.<sup>7</sup> On this approach, a complete understanding of leadership and followership will need to include a description of the input/output mechanisms that makes each of the functions and roles described in this task analysis possible. Such an analysis constitutes a *cognitive psychology* of leadership and followership—of which we currently know next to nothing.

<sup>&</sup>lt;sup>6</sup> It has been suggested that it is somewhat of a mystery as to why everyone is not always motivated to be a leader (Van Vugt et al., 2008). Roger's paradox provides an analogy to the natural check that will operate within the market dynamic that may help explain why this would be the case—even holding individual differences in skills and talents constant. See Part D of the SOM for details.

<sup>&</sup>lt;sup>7</sup> Certain elements of this task analysis will apply to other species as well.

However, a different approach is to predict or describe the distribution of leadership and followership phenomena (what we have called an *actuarial* approach). The current task analysis informs this actuarial approach as well. First, and consistent with an emerging trend in leadership studies (e.g. Hurwitz, 2018), the current task analysis suggests that leadership is more than just the trope of a dominant manager standing over and directing a group of followers. Leadership is also imagining and communicating what can be done; it is the ability to create representations in the minds of others; it is doing or saying something that captures the attention of others; it is to embody knowledge and skills that others incorporate into their own behavior; it is contingently responding to followership offerings and behaviors; and competing with rival instances of leadership information-processing.

Followership, in turn, is not just dutifully-following instructions. Followership is also the desire to be part of some greater goal or purpose; to contribute to something beyond oneself; to monitor how well one is being led; it is to be a student or a disciple; to follow the rules; and to evaluate, compare, and select among possible leadership offerings.

This broadened conceptualization implies that the canonical trope of a single, publicly-represented leader, with much greater status and dominance than followers, is only a small subset of the entirety of the leadership and followership phenomenon-even in small-scale societies. Thus, leadership and followership can also exist in private, smallscale interactions. This has a number of important implications. Female leadership, for example, is likely to involve more of this cryptic, private type of leadership, given that women have lower levels of intrinsic physical bargaining power compared to men, but equal-if not higher-levels of relationship knowledge and competence (Benenson, 2013: Krems, personal communication). Consequently, female leadership will tend to be less obvious than will men's, biasing the study of leadership away from women. For example, in small-small societies, long-term trust and a deep knowledge of the local social community is often required to observe or infer instances of female leadership (Patton, personal communication; see also Dobbins & Platz, 1986). Existing work on leadership-and in particular evolutionary approaches to leadership-therefore probably grossly underestimate female leadership in terms of kind, scope, and impact. A broader conceptualization of what leadership looks like may help to start correct this bias (see also Smith, Ortiz, Buhbe, & van Vugt, 2018).

An evolutionary approach, moreover, suggests that not all aspects of leadership and followership will be universal. In particular, while the underlying input/output mechanisms are likely to be universal, barring developmental insults, the manifestations of leadership and followership will vary considerably across contexts and cultures (Price & Van Vugt, 2014a, 2014b; Van Vugt, 2017). The current task analysis suggests two sources of this variation: (1) different coordination and collective action enterprises will require different kinds of leadership and followership, and (2) the leadership and followership market will determine what will be tolerated on behalf of leaders and followers within a given social marketplace. Consequently, an evolutionary approach does not lead one to necessarily expect universality in terms of who becomes a leader or a follower, nor even what leadership and followership look like. Instead, variation will be expected according to what each coalition is for, the social context in which that coalition is occurring, and what kind of alternative leadership and followership offering are available to choose from. These principles will determine what leadership and followership look like, including the attributes of the individual bodies that fill each of these roles. Thus, on first principles, we should not expect to find leadership to be a homogenous phenomenon.

For example, a context in which agents do not have a rich and longterm representation of each other's characteristics and attributes will cause them to favor leaders with superficial bargaining power. Less quickly-discernible attributes—such having skills that are difficult to signal to others, or having strong but hidden social alliances—will become subservient to immediately-obvious attributes such as boldness, assertiveness, and professed competence. Conversely, a social world in which all agents have a deep interaction history with each other, know each other's hidden strengths and weaknesses, and have tested the honesty of various signals and posturing will produce leaders who posture far less and may even appear to be superficially less "impressive", but in fact have true bargaining power in the form of knowledge, skills, and alliances (Patton, personal communication). Moreover, some attributes, such as physical strength and attractiveness, will be a source of bargaining power in both kinds of social worlds, and consequently will be found as attributes of leaders in both kinds of social contexts (von Rueden et al., 2014, 2018; von Rueden & Van Vugt, 2015). Researchers will consequently find different answers to the question, "What kind of person is a leader?" within these two social contexts.

The leadership and followership market dynamic will introduce further variability. In particular, the attributes that constitute good leadership will depend on followers' expectations. For example, some individuals may expect coalitions to involve conflicts of interest, whereas others may expect more cooperation. These different expectations will produce different conceptualizations of the ideal leader (e.g., Lausten & Petersen, 2015). In turn, these different expectations will be the result of dynamics including the vagaries of history and cultural norms and processes. Consequently, invariance in leadership attributes will be found in underlying causal principles-such as those found in the prestige-for-leadership model (Price & Van Vugt, 2014a, 2014b), partner choice models (Barclay, 2013; Barclay & Raihani, 2016; Raihani & Barcaly, 2016), and in the design of the underlying evolved psychology-but not in terms of universal outcomes. This makes it all the more important that future leadership studies begin to focus on the underlying evolved psychology that make these contingencies possible.

Moreover, the scope of study for leadership and followership may be expanded on a broader conceptualization of what the underlying evolved psychology is for. The evolved psychology of leadership and followership likely produces not just obvious leadership and followership behaviors, but also motivations to consume and produce things like art, science, historical narratives, and to evaluate and criticize public representations of people and their ideas, and so on. In other words, the evolved psychology of leadership and followership is likely important to a number of domains of modern life that do not, upon first glance, seem to have much to do with leadership and followership.

#### Leadership and followership as central to the evolution of human sociality

Finally, the current task analysis suggests that leadership and followership is not just some ancillary constraint on how individuals successfully pool contributions and reach a consensus. Rather, leadership and followership are likely central to how our evolved psychology has solved the fundamental problems of coordinating and cooperating. This insight comes from viewing leadership and followership as not just the execution of coordination and collective action, but also as the crucible out of which coordination and collective action possibilities are born, evaluated, maintained, and even abandoned.

The centrality of leadership and followership to the evolution of coordination and collective action has far-reaching implications. For example, much has been made of punishment's role in the evolution of cooperation (e.g., Pedersen, Kurzban, & McCullough, 2013), but far less attention has been paid to leadership and followership. Consequently, most studies on the evolution of cooperation offer participants disembodied cooperation opportunities delivered on high from the experimenter. These methods violate the ecologically-valid dynamics that occur during real coordination and cooperation enterprises. In particular, they fail to capture and convey the leadership and followership market dynamic. In the real world, coordination and cooperation opportunities are delivered by specific people (either in the form of an

explicit offer, or simply because of what some people are already doing, often after a process of communication and bargaining). Thus, when a person is considering whether or not to engage in particular enterprise (for example, building a well), they are not only evaluating the enterprise itself, but also what they know about the person(s) proposing and coordinating it. Consequently, willingness to invest will not just be impacted by punishment, but also by the leadership roles present—including individual reputations for initiating and carrying out successful enterprises, knowledge about what those leaders have to gain or lose, and the alternative choices available to followers. Insofar as theories, models, and empirical tests (such as economic games) fail to include a leader/follower market dynamic, we are likely missing out on a complete understanding of how the psychology of multi-agent coordination and cooperation evolved (for notable exceptions see Barclay, 2013; Barclay & Raihani, 2016; Raihani & Barclay, 2016).

In sum, leadership and followership are in some sense then nature's research and design wing for coordination and collective action: they provide a mechanism whereby the possibility space of coordination and collective action enterprises can be explored and then narrowed down to those that are most likely to succeed. They create a within-generation trial-and-error process, in which candidate coalitions are proposed and then tested out in the larger social world. Each individual in the social word can then monitor for subsequent cues of success or failure, as described above. From a gene's-eye-view, using this kind of trail-and-error process to narrow down what to do and how to do it is tolerated by natural selection to the degree that the process of generating variants is not too costly, and that feedback about success and failure can be seen and acted upon within each generation.

#### Conclusions

A consideration of the adaptive problem of proposing, evaluating, executing, and maintaining sets of coordinating or cooperating individuals implies a set of universal information-processing mechanisms. These constitute the pan-human, universal psychology of leadership and followership. Determining how this psychology works at a mechanistic, input/output level of description represents an important direction for future studies of leadership and followership. The present evolutionary task analysis furthermore suggests that leadership and followership are a broader class of phenomena than previously conceptualized. Leadership in particular is likely to be a more de-centralized, cryptic, and thus more prevalent phenomenon than is currently assumed.

Conceptualizing leadership and followership as information-processing roles suggests new ways to think about and study leadership and followership. These roles are not just epiphenomenon borne out of individual differences, but are rather fundamental solutions to the problem of how to create, maintain, and execute coordination and collective action enterprises that span across multiple agents. So conceived, leadership and followership are likely much more central to the evolution of human sociality than has yet been appreciated. Further, the scope of phenomena that fall under the rubric of leadership and followership has likely been vastly underestimated, so too has the power and prevalence of female leadership.

### Acknowledgements

Aaron Goetz, Jaimie Krems, Tomás Legarraga, Aaron Lukaszewski, and Jan Woike all provided helpful comments on previous versions of this manuscript. Tomás Legarraga pointed out the relevance of Coase's work.

#### Supplementary online materials

Supplementary online materials (SOM) can be found at https://doi.org/10.1016/j.leaqua.2019.05.006.

#### References

Axelrod, R. (1984). The evolution of cooperation. New York: Basic Books.

- Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. Science, 211, 1390–1396.
- Barclay, P. (2013). Strategies for cooperation in biological markets, especially for humans. Evolution and Human Behavior, 34, 164–175.
- Barclay, P., & Raihani, N. (2016). Partner choice versus punishment in human prisoner's dilemmas. Evolution and Human Behavior, 37, 263–271.
- Bechtel, W. (2008). Mental mechanisms: Philosophical perspectives on cognitive neuroscience. New York: Routledge.
- Benenson, J. F. (2013). The development of human female competition: Allies and adversaries. Philosophical Transactions of the Royal Society B, 368, 20130079.
- Berg, H. C., & Anderson, R. A. (1973). Bacteria swim by rotating their flagellar filaments. *Nature*, 245, 380–382.
- Boehm, T. (2011). Design principles of adaptive immune systems. Nature Reviews Immunology, 11, 307–317.
- Boyd, R., & Richerson, P. J. (1985). Culture and the evolutionary process. Chicago, IL: University of Chicago Press.
- Boyd, R., & Richerson, P. J. (1988). The evolution of reciprocity in sizable groups. Journal of Theoretical Biology, 132, 337–356.
- Boyd, R., & Richerson, P. J. (1992). Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology*, 13, 171–195.
- Burrows, M., & Sutton, G. (2013). Interacting gears synchronize propulsive leg movements in a jumping insect. Science, 341, 1254–1256.
- Coase, R. H. (1973). The nature of the firm. Economica, 4, 386-405.
- Cosmides, L. (1989). The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition*, 31, 187–276.
- Cosmides, L., Tooby, J., & Barkow, J. (1992). Evolutionary psychology and conceptual integration. In J. Barkow, L. Cosmides, & J. Tooby (Eds.). *The adapted mind: Evolutionary psychology and the generation*` of culture (pp. 3–15). New York: Oxford University Press.
- Cosmides, L., Barrett, H. C., & Tooby, J. (2010). Adaptive specializations, social exchange, and the evolution of human intelligence. *Proceedings of the National Academy of Sciences*, 107, 9007–9014.
- Cosmides, L., & Tooby, J. (1987). From evolution to behavior: Evolutionary psychology as the missing link. In J. Dupré (Ed.). *The latest on the best: Essays on evolution and optimality* (pp. 277–306). Cambridge, MA: MIT Press.
- Cosmides, L., & Tooby, J. (1989). Evolutionary psychology and the generation of culture, part II. Case study: A computational theory of social exchange. *Ethology & Sociobiology*, 10, 51–97.
- Cosmides, L., & Tooby, J. (1994). Beyond intuition and instinct blindness: Toward an evolutionarily rigorous cognitive science. *Cognition*, 50, 41–77.
- Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision- making in animal groups on the move. *Nature*, 433, 513–516.
- Day, D. V., & Antonakis, J. (Eds.). (2017). The nature of leadership(3rd ed.). Thousand Oaks: Sage.
- Dobbins, G. H., & Platz, S. J. (1986). Sex differences in leadership: How real are they? The Academy of Management Review, 11, 118–127.
- Gardner, A., & Grafen, A. (2009). Capturing the superorganism: A formal theory of group adaptation. Journal of Evolutionary Biology, 22, 659–671.
- Gavrilets, S. (2015). Collective action problem in heterogeneous groups. Philosophical Transactions of the Royal Society, B, 370, 20150016.
- Gavrilets, S., Auerbach, J., & Van Vugt, M. (2016). Convergence to consensus in heterogenous groups and the emergence of informal leadership. *Scientific Reports*. https://doi.org/10.1038/srep29704.
- Glowacki, L., & von Rueden, C. (2015). Leadership solves collective action problems in small- scale societies. *Philosophical Transactions of the Royal Society B*, 370(2015,0010).
- Grabo, A., Spisak, B. R., & Van Vugt, M. (2017). Charisma as signal: An evolutionary perspective on charismatic leadership. *The Leadership Quarterly*, 28, 473–485.
- Grabo, A., & Van Vugt, M. (2016). Charismatic leadership and the evolution of cooperation. Evolution and Human Behavior, 37, 399–406.
- Graen, G. B., & Uhl-Bien, M. (1995). Relationship-based approach to leadership: Development of leader-member exchange (LMX) theory of leadership over 25 years: Applying a multi- level multi-domain perspective. *Leadership Quarterly*, 6, 219–247.
- Haslam, S. A., Reicher, S. D., & Platon, M. J. (2011). The new psychology of leadership: Identity, Influence, and Power. New York: Psychology Press.
- Henrich, J., Chudek, M., & Boyd, R. (2015). The big man mechanism: How prestige fosters cooperation and creates prosocial leaders. *Philosophical Transactions of the Royal Society B*, 370, 2015.0013.
- Henrich, J., & Gil-White (2001). The evolution of prestige: Freely-conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, 22, 165–196.
- Hooper, P. L., Kaplan, H. S., & Boone, J. L. (2010). A theory of leadership in human cooperative groups. *Journal of Theoretical Biology*, 265, 633–646.
- Hume, D. (1739/1896). A treatise of human nature. Oxford: Claredon Press.
- Hurwitz, M. (2018). Exploring distributed leadership: A leader-follower collaborative lens. In N. Chatwani (Ed.). Distributed leadership: The dynamics of balancing leadership with followership. Cham, Switzerland: Palgrave Macmillan.
- Kiyonari, T., & Barclay, P. (2008). Cooperation in social dilemmas: Free riding may be thwarted by second-order reward rather than by punishment. *Journal of Personality & Social Psychology*, 36, 826–842.
- Kurzban, R., & Van Vugt, M. (2007). Cognitive and social adaptations for leadership and followership: Evolutionary game theory and group dynamics. In J. P. Forgas, W.v.

Hippel, & M. G. Haselton (Eds.). Evolution and the social mind: Evolutionary psychology and social cognition (pp. 229–244). UK: Psychology Press.

- Lopez, A., McDermott, R., & Petersen, M. B. (2011). States in mind: Evolution, coalitional psychology, and international politics. *International Security*, 36, 48–83.
- Lorenz, K. (1948/1996). The natural science of the human species: An introduction to comparative behavioral research, the "Russian Manuscript". Cambridge, Mass: MIT Press1944–1948.
- Lukaszewski, A. W., Simmons, Z. L., Anderson, C., & Roney, J. R. (2016). The role of physical formidability in human social status allocation. *Journal of Personality and Social Psychology*, 110, 385–406.
- Marr, D. (1982). Vision: A computational investigation into the human representation and processing of visual information. New York: Henry Holt and Co.
- Minsky, M. (1974). A framework for representing knowledge. Artificial Intelligence Memo, 306.
- Noë, R., & Hammerstein, P. (1995). Biological markets. Trends in Evolution and Ecology, 10, 336–339.
- Olson, M. (1971). The logic of collective action: Public goods and the theory of groups (2nd ed.). Cambridge, Mass: Harvard University Press.
- Panchanathan, K., & Boyd, R. (2004). Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature*, 432, 499–502.
- Patton, J. Q. (1996). Thoughtful warriors: Status, warriorship, and alliances in the Ecuadorian Amazon. PhD dissertationUniversity of California Santa Barbara.
- Patton, J. Q. (2000). Reciprocal altruism and warfare: A case from the Ecuadorian Amazon. In L. Cronk, N. Chagnon, & W. Irons (Eds.). Adaptation and human behavior: An anthropological perspective (pp. 417–436). New York: Aldine de Gruyter.
- Pedersen, E. J., Kurzban, R., & McCullough, M. E. (2013). Do humans really punish altruistically? A closer look. Proceedings of the Royal Society B: Biological Sciences, 280(1758).
- Price, M. E. (2005). Punitive sentiment among the Shuar and in industrialized societies: cross-cultural similarities. *Evolution and Human Behavior*, 26, 279–287.
- Price, M. E., & Van Vugt, M. (2014a). The evolution of leader-follower reciprocity: The theory of service-for-prestige. *Frontiers in Human Neuroscience*, 8. https://doi.org/10. 3389/fnhum 2014.00363.
- Price, M. E., & Van Vugt, M. (2014b). The service-for-prestige theory of leader-follower relations: A review of the evolutionary psychology and anthropology literatures. In S. M. Colarelli, & R. D. Arvey (Eds.). *The biological foundations of organizational behavior* (pp. 169–202). Chicago: University of Chicago Press.
- Raihani, N. J., & Barclay, P. (2016). Exploring the trade-off between quality and fairness in human partner choice. Royal Society Open Science, 3, 160510.
- Sell, A. (2011). The recalibrational theory and violent anger. Aggression and Violent Behavior, 16, 381–389.
- Simon, H. A. (1962). The architecture of complexity. *Proceedings of the American Philosophical Society*, 106, 467–482.

- Simon, H. A. (1969/1996). The sciences of the artificial (3rd ed.). Cambridge, Mass: MIT Press.
- Smith, J. E. (2017). Non-human leadership. In T. K. Shackelford, & V. A. Weekes-Shackelford (Eds.). Encyclopedia of evolutionary social sciencehttps://doi.org/10.1007/ 978-3-319-16999-6\_2714-1.
- Smith, J. E., Gavrilets, S., Borgerhoff Mulder, M., Hooper, P. L., Mouden, C. E., Nettle, D., ... Smith, E. A. (2016). Leadership in mammalian societies: Emergence, distribution, power, and payoff. *Trends in Ecology & Evolution*, 31, 54–66.
- Smith, J. E., Ortiz, C. A., Buhbe, M. T., & van Vugt, M. (2018). Obstacles and opportunities for female leadership in mammalian societies: A comparative perspective. *The Leadership Quarterly*.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. Barkow, L. Cosmides, & J. Tooby (Eds.). The adapted mind: Evolutionary psychology and the generation of culture. New York: Oxford University Press.
- Tooby, J., & Cosmides, L. (2015). Conceptual foundations of evolutionary psychology. In D. M. Buss (Vol. Ed.), (2nd ed.). Foundations: Vol. 1. Hoboken, NJ: John Wiley & Sons.
- Tooby, J., Cosmides, L., & Price, M. E. (2006). Cognitive adaptations for n-person exchange: The evolutionary roots of organizational behavior. *Managerial & Decision Economics*, 27, 103–129.
- Trivers, R. L. (1974). Parent-offspring conflict. Integrative and Comparative Biology, 14, 249–264.
- Turing, A. M. (1950). Computing machinery and intelligence. *Mind*, 49, 433–460. Uhl-Bien, M. (2006). Relational leadership theory: Exploring the social processes of lea-
- dership and organizing. The Leadership Quarterly, 17, 654–676.
  Van Vugt, M. (2006). Evolutionary origins of leadership and followership. Personality and Social Psychology Review, 10, 354–371.
- Van Vugt, M. (2017). Evolutionary, biological, and neuroscience perspectives. In D. V. Day, & J. Antonakis (Eds.). *The nature of leadership* (pp. 189–217). (3rd ed.). Thousand Oaks: Sage.
- Van Vugt, M., Hogan, R., & Kaiser, R. B. (2008). Leadership, followership, and evolution: Some lessons from the past. American Psychologist, 63, 182–196.
- von Rueden, C., Alami, S., Kaplan, H., & Gurven, M. (2018). Sex differences in political leadership in an egalitarian society. *Evolution and Human Behavior, 39*, 402–411.
- von Rueden, C., & Gurven, M. (2012). When the strong punish: Why net costs of punishment are often negligible. *Behavioral and Brain Sciences*, *35*, 43–44.
- von Rueden, C., Gurven, M., Kaplan, H., & Steiglitz, J. (2014). Leadership in an egalitarian society. *Human Nature*, 25, 538–566.
- von Rueden, C., & Van Vugt (2015). Leadership in small-scale societies: Some implications for theory, research, and practice. *The Leadership Quarterly*, *26*, 978–990.
- West, S. A., Griffin, A. S., & Gardner, A. (2007). Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20, 415–432.