The Nature of Followership:

Evolutionary Analysis and Review

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Abstract

From an evolutionary perspective, followership is puzzling because it is not clear why individuals would relinquish their autonomy and set aside their personal goals to follow those of another individual, the leader. This paper analyzes followership from an evolutionary perspective and advances three main conclusions that are not yet part of the leadership literature. First, followership evolved as a strategy to solve a range of cooperation and coordination problems in groups (e.g., collective movement, peacekeeping). Second, individuals who lack the physical, psychological, or social capital to be leaders themselves are more likely to emerge as followers. Third, followership styles, behaviors, and engagement result from (a) variations in the relative pay-offs that accrue to followers vis-à-vis their leader, (b) the adaptive goals pursued by followers, (c) the adaptive challenges that select for different followership styles, and (d) the prevailing leadership style. Together, these conclusions have several implications for followership theory, research, and practice.

Introduction

Why should we bother about followers when a single leader can achieve great deeds? It is a truism that there can be no leaders without followers; there are many more followers than there are leaders, and most of the time you and us are followers rather than leaders. History is filled with examples of followers who helped leaders achieve their goals, good or bad. Consider the Nazis: Whereas Hitler's closest followers (e.g., Goebbels, Göring, Röhm) were actively colluding with him and completely dedicated to the cause of the Third Reich, a majority of German individuals stood by and did nothing to prevent the prosecution and mass killings of millions of individuals. Some followers actively stood up against the Nazi leadership by showing incredible courage to defy the regime (such as party member Oskar Schindler who put his life at risk to save the lives of his Jewish employees), while others played opportunistically by the Nazis rules because it granted them power and influence that they would have never achieved under normal circumstances.

This example demonstrates both the impact of followers on the course of human history and the richness and diversity in followership behaviors, styles and engagement levels. In this review, we use an evolutionary perspective to study followership. We analyze why individuals follow leaders, and how they do so, addressing various ultimate and proximate questions regarding the psychology of followership: Why would individuals voluntarily give up their autonomy to defer to a leader? Why would anyone want to follow when leading is associated with greater rewards (e.g., money, status)? Which traits, cognitions, and motivations predict whether someone will emerge as follower in a certain context? How can we explain differences in followership styles, behaviors, and engagement? We believe these questions are currently underexplored in the literature and hope to spark some new ideas for followership researchers.

Based on insights from the evolutionary, biological and psychological sciences, we review studies suggesting that humans have an adaptive followership psychology that enables

them to (swiftly) coordinate their actions with other individuals when it is advantageous to do so (cf. evolutionary leadership theory; Van Vugt & Ahuja, 2011). We do not imply that evolution has produced a population of individuals with either fixed leader or follower traits (i.e., genotypes), but rather we suggest that humans have a flexible followership psychology that enables them to select and follow the right kind of leaders under the right conditions, determine an appropriate engagement level, and switch from being a follower to a leader whenever appropriate. Our review also attempts to build bridges with previous writings on followership (e.g., Chaleff, 2009; Kellerman, 2008). Doing so will hopefully open up new theoretical and empirical investigations into solving the puzzle of followership.

Our manuscript intends to make several contributions. First, we shift the focal point away from the analysis of leaders to followers, a much-needed shift for a field that has been heavily taxed with being "leader-centric" (Day, 2014; Hollander, 1992; Yukl, 2002). For all articles published in *The Leadership Quarterly* at the end of 2017, only 8% used the term "follower" (or a derivative) in their title, compared to 83% that used the term "leader" (if we count just the abstract then 22% of articles referred to followership and 94% to leadership)[1]. Yet, followership is arguably the default setting in our brain and on any occasion, we are much more likely to be followers than leaders. As followership scholars have suggested (Carsten, Uhl-Bien, West, Patera, & McGregor, 2010; Riggio, Chaleff, & Lipman-Blumen, 2008), followers are not a monolithic group. These are individuals with different motivations, values, and abilities. Therefore we embrace Shamir's (2007) suggestion to "shift the lens" by understanding the deeper roots of followership. Understanding what motivates people to be followers is crucial if we want to understand the very essence of the leadership process.

Our second contribution concerns the use of evolutionary theory that, in our view, provides a compelling integrative theoretical model to analyze followership. Leadership

[1] Retrieved from Web of Science on September 9, 2018.

science tends to be a highly fragmented discipline, because there is no unifying theory such as is the case in biology, physics, or chemistry (Antonakis, 2017b). By adhering to an evolutionary perspective, we offer a parsimonious model to study followership through integrating literature and data from various fields including evolutionary biology, animal behavior, anthropology, and applied psychology. This allows us to come up with a set of propositions that can be tested through experiments, simulations, and field case studies (see Schmitt & Pilcher, 2004).

The review proceeds as follow. We first define followership and theorize about its origins. Using game theory as bedrock, we suggest that followership emerged as an evolutionary stable strategy. We then go back to human evolutionary history and argue why humans have evolved an adaptive followership psychology and what the psychological mechanisms underlying followership are. We then review literature on followership across various disciplines and come up with a number of propositions about followers' behaviors, styles and engagement levels. In the discussion we address contemporary questions such as: Is following still always an adaptive choice? Why are there gender differences in leading and following? What makes a bad follower? What are the neural correlates of followership? We conclude by offering ideas for followership research and practice.

Understanding Followership

To ensure a common understanding, we first need to clarify what we mean by followership. Following previous evolutionary work, we consider leadership and followership as adaptive solutions to various kinds of organizational challenges associated with group living (King, Johnson, & Van Vugt, 2009; Van Vugt, 2006; Van Vugt, Hogan, & Kaiser, 2008a). The vast majority of primate species live in groups, and so do humans, although our groups tend to be larger and socially more complex (Dunbar, 1993). One way to reap the benefits of group life is for humans to cooperate with each other and coordinate their actions in the pursuit of joint activities, such as collective movement, hunting, foraging, teaching, conflict management,

group defense and warfare. Leaders can be defined as individuals who have a *differential influence* on the initiation, direction, and coordination of group activities (Shamir, 2007; Smith et al., 2016; Von Rueden, Gurven, Kaplan, & Stieglitz, 2014). In turn, we define followers as individuals who adopt the leader's goals temporally (e.g., following someone's directions to a restaurant) or structurally (e.g., accepting the authority of a parent, manager or president) and *freely accept the influence* of leaders (cf., Antonakis, Bastardoz, Jacquart, & Shamir, 2016). Followers will generally freely accept influence because it is the optimal strategy among a set of potential other alternatives, but at times, individuals will freely follow dominant, despotic leaders because they lack credible alternative options (King, Douglas, Huchard, Isaac, & Cowlishaw, 2008). Because coordination failures can be costly (think of a poorly organized army), groups will benefit from coordinated group action which they can achieve by forming leader-follower relationships.

These definitions require distinguishing leadership from dominance and followership from coercion. When individuals are not freely conferring influence to another individual, a dominance hierarchy ensues. As currently operationalized in the evolutionary literature, a dominance strategy implies that other group members do not freely confer influence, or leadership, to the individual (Maner & Case, 2016), and we argue that this situation does not reflect followership because following implies voluntarily deference. Although coercing or intimidating others can be an effective strategy to attain high-status positions in some societies, these individuals are not leaders according to our definition. However, as long as followers freely defer influence, leaders can use "dominance-based" tactics such as the use of rewards or the threat of sanctions. Followers may also select leaders with dominance characteristics due to their functionalities in certain tasks – because they enforce coordination more quickly or efficiently – which is not the same as saying that individuals made their way to leadership roles by coercing or intimidating their followers (Van Vugt, 2006; Von Rueden, Alami, Kaplan, &

Gurven, 2018). Our definition also departs from a role-based perspective that operationalizes leadership and followership based on people's formal positions in an organizational hierarchy (e.g., manager, worker; Baker, 2007; Carsten et al., 2010). Viewing followership as a voluntary deference process is conceptually precise, allows for developing clean hypotheses as to why individuals accept to follow particular individuals, and is aligned with previous writings on the nature of followership (e.g., DeRue & Ashford, 2010; Shamir, 2007).

Why Follow?

An intriguing question from an evolutionary perspective is why anyone would want to be a follower if this means giving up some autonomy to another person. Given the benefits usually associated with leadership, following seems at first sight an irrational choice. When leaders obtain greater rewards in terms of status, wealth, and reproductive benefits (Buss, 2005; Von Rueden & Jaeggi, 2016), the selfish gene view of evolution would contend that anyone ought to have a strong motivation to lead (Dawkins, 1976). In a review of leadership in small-scale societies, Von Rueden and colleagues (2014; see also von Rueden & Van Vugt, 2015) identified various incentives for individuals to compete for leadership positions: (1) leaders grasp a higher share of resources seized from collective action for them and their kin; (2) leaders impose a tax to all members of the group for coordinating activities (Gavrilets & Fortunato, 2014; Hooper, Kaplan, & Boone, 2010); (3) leaders have preferential access to mates; (4) through their actions, leaders signal personal qualities to the group that benefit leaders in recruiting allies or sexual partners (Gintis, Smith, & Bowles, 2001); and (5) leaders are being reciprocated by getting priority access to food or receiving support when they hit upon difficult times (Boone & Kessler, 1999; Price & Van Vugt, 2014). Based on these incentives, natural selection should favor all individuals to adopt a strategy to become a leader rather than a follower, because it enables them ultimately to be more successful in passing on their genes to future generations.

However, following is probably less surprising and irrational if we consider the following situation. Imagine a group of individuals who go out hunting, with three possible outcomes: Individuals can (a) hunt alone, (b) lead a join hunt, or (c) follow a hunt leader. Hunting alone is less efficient, offering an incentive to hunt together; being in a group offers safety by numbers and an increased chance to obtain surplus food (such as through killing big game; see the Stag-Hunt game discussed in the following section). Then, individuals must be willing to initiate an action and able to attract followers to emerge as leader; successful coordination happens only if followers grant leadership to the individual. Without individuals being willing to follow, there is no followership and thus no leadership (DeRue & Ashford, 2010). So, only when individuals are motivated to lead and able to attract followers will they emerge as leaders. In all other cases, followership is the only reasonable option (see Figure 1).

Insert Figure 1 about here

Evolutionary insights can account for why so many of us emerge as followers most of the time. First, humans are a social species that survived and thrived living in groups with social exclusion implying a certain death (Tooby & Cosmides, 1992). As a result humans place an inherent value on being in a group and have a strong need for belongingness (Baumeister & Leary, 1995) that trumps the risks of going alone or failing to secure leadership. Second, even if leaders fare relatively better, being a follower in a coordinated group can get you more resources than going alone. Followers can collectively bargain the outcomes of collaboration with the leader (Boehm, 1993), dilute predation risks by staying together when foraging (Rands, Cowlishaw, Pettifor, Rowcliffe, & Johnstone, 2003), or generate a surplus of resources (Powers & Lehmann, 2014), thus making them better off than individuals acting alone.

Third, there are also situations in which following actually offers a better outcome (in terms of relative fitness benefits) than leading. In certain cases, the leader at the front of a group

movement may incur a large cost such as a higher risk to be attacked by predators (Bumann, Krause, & Rubenstein, 1997) or a lower access to food when they monitor the environment for potential predators while followers eat (Smith et al., 2016). Furthermore, a leader who needs to resolve a conflict may be dragged into conflict and experience physical or social costs. Fourth, following can be a reasonable option for someone with a motivation to lead but no ability to attract followers – a way to make the best out of a bad situation (Dawkins, 1976). Humans are able to accurately assess their competencies to produce coordination benefits vis-à-vis others in the group (Van Vugt et al., 2008a), and when a leadership position is unattainable, following remains the best strategy to obtain more resources (Gangestad & Simpson, 2000). Fifth, followership may just be a temporary role. Following can be profitable for anyone who wants to find out what it takes to be a leader, because following enables observation and learning from leaders before claiming these roles later for themselves (Henrich & Gil-White, 2001). Some companies, like Procter & Gamble, have their high potentials start as lower-level managers. This organizational design offers future top managers both a hands-on approach to understand the business and they can learn appropriate behaviors and norms from higher-placed managers who act as role models in an apprentice-master relationship.

Sixth, there can be no leaders without followers and this is also true from an evolutionary game perspective. An appropriate ratio of followers to leaders is necessary for these strategies to co-exist in the population (cf., frequency-dependence; Maynard-Smith, 1982). Having many individuals compete for a few leadership positions generates excessive costs for individuals claiming leadership, making a followership strategy more attractive. Biologists Johnstone and Manica (2011) used computer simulations to show that an increase in the number of individuals with a fixed leader trait reduces the benefits associated with this strategy as a result of coordination failure. Psychological experiments confirm that group performance suffers when too many individuals compete for leadership (Groysberg, Polzer, &

Elfenbein, 2011; Ronay, Greenaway, Anicich, & Galinsky, 2012).

Insights from Game Theory

The emergence of followership can be formally modeled using basic evolutionary game theory (Maynard-Smith, 1982). Game theory uses social games with fitness consequences associated to certain individual actions. It offers powerful insights regarding why leadership and followership emerged by clarifying not only the benefits and costs linked to each strategy, but also the potential conflicts of interests that each player faces (Van Vugt, 2006; Van Vugt & Kurzban, 2007). We focus on common coordination games – the stag hunt, battle of the sex, and game of leader – because they are representative of the coordination challenges observed in nature and are thus especially relevant to address leader-follower relationships.

We start with the Stag Hunt game (see Table 1a). In this two-player game, individuals can choose between two strategies: Hunt a stag or a hare. An important feature is that a stag can only be hunted successfully if both players choose this strategy, whereas hunting a hare is an individual and sure strategy. If both players coordinate their actions and decide to hunt the stag, they reap the benefits of coordination and both receive a high payoff (upper-left quadrant, 'stag-stag' strategy). If they both go for the safe option and decide not to cooperate, that is, to hunt a hare alone, they receive a small positive payoff (down-right quadrant, 'hare-hare' strategy). If one individual decides to hunt a stag while the other chases a hare, the former is left with nothing – because one cannot successfully hunt a stag alone – whereas the latter receives the assured payoff that chasing a hare provides ('hare-stag' and 'stag-hare'). Although hunting the stag is beneficial for both parties, chasing the hare is independent of the other player's action. Thus, coordination on the stag strategy may not so easily be achieved. When individuals play simultaneously, individuals often fail to coordinate and get inefficient outcomes. However, when the game is played sequentially (i.e., one individual at the time) and communication between the individual before taking a decision is allowed, coordination is more

likely to arise (Cartwright, Gillet, & Van Vugt, 2013). If the first player, the leader, can persuade the second player, the follower, to coordinate and credibly signal a commitment to this course of action by choosing the 'risky', cooperative strategy, the second player has no risk of being exploited; thus, pairs of players are more likely to coordinate their actions and a leader-follower structure generally ensues (Grabo, Spisak, & Van Vugt, 2017).

Insert Table 1a about here

A second coordination game is called the Battle of the Sexes (see Table 1a). Here, the two players have diverging individual preferences, but they still benefit from coordinating their actions. Imagine that Lucy and Jon are the two players: Lucy would really want to watch a movie whereas Jon would enjoy watching a football game. If Lucy could lead by influencing Jon to watch a movie, she would benefit the most (and vice versa). However, Lucy would be less satisfied if she chose to watch a movie while Jon watches football (i.e., by failing to lead). In this game, players benefit from coordination although to different degrees depending on their own preferences. Again, when this game is played sequentially, in a leader-follower kind of way, coordination emerges more frequently (Van Vugt & Kurzban, 2007).

To understand followership more fully, we can use a third coordination game called the Leader game (see Table 1a). In this game, players face two options: They can either claim to lead or choose to follow. If both players aim to lead, coordination fails and both receive negative payoffs (assuming there is a cost to claim leadership, but this feature can be removed). If both players choose to follow, coordination fails again and both players are left with nothing. If one player decides to lead and the other chooses to follow, and by doing so they reach a leader-follower structure, both players benefit from coordination. Using the logic of this simple game and slight variations in the payoff associated with the different strategies, we model three basic followership strategies that could have evolved in nature (see Table 1b):

1. "Mutualistic" followership: Leaders and followers have the same payoffs. Individuals have incentives to coordinate on a leader-follower structure regardless of who leads or follows.
2. "Coordinating" followership: Leaders receive higher payoffs than followers. Both strategies benefit from coordination.
3. "Opportunistic" followership: Followers receive higher payoffs than leaders. Both strategies benefit from coordination.

Insert Table 1b about here

These different versions account for different kinds of followership and followership engagement. Mutualistic followership suggests that both players are indifferent regarding who is the leader and who is the follower. Individuals share the benefits of coordination equally. Due to a lack of conflict of interest, this followership strategy is highly prevalent in nature and across species (Smith et al., 2016). Examples of mutualism include groups that have an interest to stick together in their movement, but no individual has a strong interest in the group direction or destination (e.g., a flock of sparrows, a shoal of fish).

Evolutionarily speaking, opportunistic followership is the easiest strategy to explain because following offers the highest payoff and evolution should thus favor it. One could then wonder: Why would anyone emerge as an altruistic (servant) leader in situations in which leading is relatively costly or dangerous? Various evolutionary theories can explain such costly leading behavior. First, Hamilton's (1964) kin selection theory suggests that individuals can behave in an altruistic manner if it helps their kin to survive. Hamilton's formula ($r*b > c$) shows that an action may be evolutionary adaptive if the benefits b for the recipient (i.e., the follower) outweigh the costs c for the helper (i.e., the leader), given a certain degree of gene relatedness r between the recipient and the helper (Hamilton, 1964). Parents investing time and

resources in raising their children represent good examples of this kind of servant leadership. Second, costly signaling theory suggests that individuals may be willing to bear costs associated with a leading strategy if they can signal personal attributes that could otherwise not be credibly signaled (Bliege Bird & Smith, 2005; Gintis et al., 2001; Spence, 2002). For instance, low-ranked employees may volunteer to replace a manager who has fallen ill to signal their ambition and competence. If the signal is hard to fake and credible, individuals may obtain benefits at a later stage (e.g., getting a promotion or a pay rise). Relatedly, there may be indirect rewards for leaders, like prestige conferred by followers, to compensate for the costly leader behaviors (Price & Van Vugt, 2014). If individuals can anticipate and ex-ante expect the prestige premium associated with leading, this leader strategy may become the best strategy in the long run. Because such computation probably requires sophisticated cognitive mechanisms, humans may be among a handful of species in which service-for-prestige leadership could have evolved (Tooby, Cosmides, & Price, 2006).

From an evolutionary perspective, coordinating followership is probably hardest to explain because a following strategy is relatively less favorable than a leading strategy. Still, a following strategy is adaptive because followers grasp the benefits of group coordination and do better than lone individuals. In a later section ("Who will follow"), we will discuss what personal and situational characteristics predict what kind of followership emerges. We first discuss features of our evolved followership psychology.

Psychology of Followership

Having made some theoretical progress in explaining why followership could be adaptive (and thus could have emerged across species), we focus now on followership in humans. To understand the nature of our followership psychology, it is necessary to understand the premise of evolutionary psychology. Evolutionary psychology argues that our brains, like our bodies (as well as the brains and bodies of other species), are the result of a long process of

biological evolution through natural selection (Buss, 2005; Tooby & Cosmides, 1992). Natural selection operates via three simple mechanisms: Variation, selection and retention. First, there is variation in the physical and behavioral properties of individuals. Second, certain traits do better than others in some environments. Third, to the extent that these traits are heritable, they are passed on to next generations at the cost of traits that are doing relatively worse in these environments. Evolutionary psychology assumes that our brain consists of many different psychological mechanisms that evolved because they allowed our ancestors to solve critical problems related to survival and reproduction. For instance, humans have an innate fear of snakes, strangers, and heights because it enables them to avoid potentially costly and dangerous situations (Buss, 2005).

As group-living species, humans also have many adaptive social-psychological mechanisms that enable them to function effectively in groups. Mechanisms such as language, empathy, and cheater detection facilitate humans' coordination and cooperation (Buss, 2005). We argue that followership is part of an adaptive psychological system to coordinate actions with others. Like any psychological mechanisms, followership is triggered by certain cues or inputs (e.g., a threat or opportunity in the environment) and responds by showing certain adaptive outputs (e.g., coordinating with a leader who seems able to manage the threat or opportunity in the environment). Figure 2 below exemplifies this process. Followership mechanisms operate via "if-then" algorithms, working in a similar fashion as schemas, scripts, or heuristics. An example of such a follower algorithm may be: "When in danger, follow a physically strong leader." It is easy to argue that this algorithm offers a better pay-off than alternative heuristics such as "when in danger, follow any individual" or "when in danger, fend for yourself." Over time, by virtue of producing better outcomes than alternatives, these follower algorithms have become part of our followership mind (and the inferior alternative algorithms disappeared).

Insert Figure 2 about here

Proposition 1: Followership emerges when coordination or cooperation is beneficial.

Proposition 2: Followership is underpinned by various evolved psychological mechanisms (mental algorithms) for coordination.

A Brief History of Followership

To understand how potential followership mechanisms may operate in humans, we need to understand the environment in which humans evolved. The hominid line originated several millions year ago by separating from the last common ancestor that humans shared with the bonobos and chimpanzees. Humans appeared at the start of the last Pleistocene, a period lasting from about 2 million years ago until around 10-15 thousand years ago. During the majority of this period, humans lived in small, egalitarian semi-nomadic tribes in the African savannah. These tribes were composed of about 100-150 individuals, bound together by kinship and reciprocity ties. As the human ecologic niche became more skill intensive (e.g., hunting big game, digging up tubers) and risks of predation was high, humans faced adaptive pressures to pool risks by coordinating their actions on critical tasks, including defense and hunting, and cooperate via sharing food or exchange in collective actions (Kaplan, Hill, Lancaster, & Hurtado, 2000). To survive, the human species evolved unique characteristics such as language, theory of mind, or shared intentionality that allowed humans to coordinate their activities and cooperate on mutually beneficial opportunities (Tomasello, Carpenter, Call, Behne, & Moll, 2005). Interestingly, cooperative arrangements were obtained without formal hierarchies and institutions meaning that leadership was neither powerful nor permanent (Van Vugt et al., 2008a; von Rueden & Van Vugt, 2015). Some individuals, the so-called Big Men and often the best hunters or warriors, exerted influence on the activities of their tribe, but their influence was restrained to their areas of expertise and contingent on their reputation of trust (cf., Van Vugt

et al., 2008a).

In general, decision-making was fiercely egalitarian among tribe members (i.e., equal rights and privileges), meaning that influential individuals had no coercive power over other individuals (reverse dominance hierarchy; Boehm, 1993). To ensure that no leader dominated the group, followers formed coalitions and monitored leader decisions with scrutiny (von Rueden & Van Vugt, 2015). Thus, egalitarianism was maintained through norms and social contracts, and reputation – a reliable proxy for indirect reciprocity – served as a regulating mechanism to achieve coordination in groups (Von Rueden, 2014). Followers granted leaders with differential influence based on the latter ability in helping groups achieve their goals, and could revoke their influence anytime. Thus, leadership was mostly situational and contextual, easily disposable, and highly functional. Societies could remain highly egalitarian because there was no opportunity to store food or accumulate wealth, preventing power disparities between individuals (von Rueden & Van Vugt, 2015).

The environment dramatically changed with the development of agriculture some 12 thousand years ago, which fundamentally changed the relationship between leaders and followers (Van Vugt & Ahuja, 2011). Agriculture led to a sedentary life style, possibilities to store surplus resources, and dramatic increases in population sizes, marking a turning point in our evolutionary history (Harari & Perkins, 2017). Anonymity, mobility, and social inequality characterize large-scale societies, undermining the pillars on which ancestral cooperation was based and paving the way for formalized and institutionalized leader-follower structures as ways to maintain coordination and cooperation (Van Schaik, 2016). Although this last period marked impressive changes in how our societies were organized (e.g., chiefdoms, nation states, multinationals), it is probably too short in evolutionary terms to have persistently affected our followership psychology that evolved during the several millions of years before.

To sum up the evolution of followership, we can identify five major phases underpinned

by different conditions (King et al., 2009; Van Vugt et al., 2008a): (1) Followers emerged in many social species to solve basic coordination challenges such as group movement; (2) situations of conflict of interest gave rise to socially dominant "leaders" in non-human primates that constrained followers; (3) followers regained control over dominant leaders in egalitarian hunter-gatherer societies through the ability to form coalitions; (4) followers selected pro-social and prestigious leaders whom they could trust and culturally learn from, and (5) followers invested power in formal leaders and institutions (e.g., kings, presidents, CEOs) to successfully manage the complexity of large-scale cooperation[2].

Who Will Follow?

In the "Coordinating" followership strategy, payoffs are symmetric for both players (i.e., Player 1 payoff from leading when Player 2 follows is similar to Player 2 payoff from leading when Player 1 follows; see Table 1b). This assumption is probably unrealistic because individuals have heterogeneous payoff structures as a result of different cost-benefit functions linked with leading and following (Balliet, Tybur, & Van Lange, 2017; Sell, Tooby, & Cosmides, 2009; West, El Mouden, & Gardner, 2011). By investigating the source of this heterogeneity in payoff structures, we can gain some insights as to why some individual characteristics increase the probability of followership emergence. Thus, an evolutionary psychology perspective suggests that individuals are more likely to emerge as followers if: (1) benefits associated with leading are relatively low; (2) costs of leading are relatively high; (3) individuals lack the ability to lead and attract followers.

Gains from leading

First, some individuals benefit more from leading than others and so have a higher motivation to lead. Individuals who stand to gain relatively little from leading will emerge as

[2] One could even argue that we are currently in a sixth phase where formal leaders tend to abuse the power invested in them to privilege themselves and their kin at the detriment of exploited followers.

indifferent or reluctant followers who can still extract benefits from coordination. In egalitarian small-scale societies, individuals who stand to gain more from coordination emerge as leaders more often in coordinating activities such as collective fishing (Von Rueden et al., 2014). Experiments with animals show that hungrier individuals are more likely to lead group movement (Krause, 1993; Krause, Bumann, & Todt, 1992). Biological models suggest that leader-follower structures emerge based on need differential (Conradt, Krause, Couzin, & Roper, 2009; Rands et al., 2003). In humans, differences in ambition, power, or achievement motives (McClelland, 1975), motivation to lead (Kirkpatrick & Locke, 1991), or in status drive will predict followership emergence. Finally, individuals low in autonomy or high in need to belong (Baumeister & Leary, 1995) are more likely to become followers because they attach relatively more value to group cohesion. We suggest that followers are individuals who benefit relatively less from initiating joint actions compared to leaders.

Proposition 3: Individuals will emerge as followers if they lack the motivation to be a leader.

Second, the cost to lead may be so high for certain individuals that claiming a leadership role is simply too costly. Even if someone could benefit greatly from leading, prohibitively high costs associated with a leading strategy may prevent someone from emerging as a leader. Using a simple formal model, Zehnder, Herz, and Bonardi (2017) show that leadership emergence is negatively related to the cost of leading. Inversely, an individual may emerge as leader simply because the cost of leading is negligible for this person (Tooby et al., 2006). Hooper et al. (2010) model shows that individuals who incur a relatively low cost in punishing free-riders emerge as leaders. Examples of qualities reducing the cost of leading include physical prowess and dominance, because individuals can more easily enforce coordination in group activities (von Rueden & Gurven, 2012). On the contrary, individuals with high anxiety or low self-esteem (Ensari, Riggio, Christian, & Carslaw, 2011) have cost functions that prevent them from emerging as a leader, and so these traits will predict followership emergence.

Proposition 4: Individuals will emerge as followers if the costs of leading outweigh the benefits.

Third, individuals are more likely to emerge as followers whenever they think they are unable to take on the leader role. These individuals have incentives to persuade capable individuals to lead the group. Although the characteristics necessary to provide benefits to followers depend on contextual factors, we suggest that individuals will emerge as followers if they lack (a) physical, (b) psychological, or (c) social capital to be leaders.

Physical capital refers to qualities such as height, strength and formidability. Studies in small-scale egalitarian societies show that physical qualities are attributes desired in a leader. Individuals high on physical capital are effective leaders not only in physically demanding activities (such as hunting a prey), but also in social activities (such as dealing with neighboring tribes, resolving conflicts, or persuading and influencing group members; Von Rueden, 2014; Von Rueden et al., 2018; Von Rueden et al., 2014). In ancestral times, taller leaders were probably functional in enforcing cooperation for hunts or raids, and currently still emerge more often as leaders (Blaker et al., 2013; Gawley, Perks, & Curtis, 2009; Judge & Cable, 2004). Even young infants use height as a cue to determine the outcome of social interactions (Thomsen, Frankenhuis, Ingold-Smith, & Carey, 2011). Similarly, small fishes follow larger informed fishes whereas large fishes are less likely to follow small informed fishes (Reebs, 2001). Yet, the relevance of physical capital differs across situations. For instance, in a sport team context, Elgar (2016) found that age (part of social capital, see below), rather than height, best predicts who emerges as team captain.

Psychological capital includes both personality and knowledge. Personality capital refers to characteristics making someone likely to signal interest in leading or with desirable properties in the eyes of followers. For example, introverted individuals are more likely to emerge as followers (Judge, Bono, Ilies, & Gerhardt, 2002), because individuals low on assertiveness makes for less effective leaders (Ames & Flynn, 2007). The animal literature is

replete with studies showing how differences in temperament predict followership. For example, shy or less active fishes are more likely to follow (Beauchamp, 2000; Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009; Ward, Thomas, Hart, & Krause, 2004). Personality capital also refers to benevolent characteristics because followers fear to be exploited by untrustworthy individuals. For instance, agreeableness predicts results of political elections probably because followers perceive agreeable candidates as more altruistic or willing to listen (Wyatt & Silvester, 2018). GLOBE studies find that universally desirable characteristics of leaders include traits related to benevolence, such as fairness, trustworthiness or integrity (Den Hartog, House, Hanges, Ruiz-Quintanilla, & Dorfman, 1999), a finding echoed in egalitarian small-scale societies (Von Rueden et al., 2014).

Knowledge capital refers to information, intelligence, or expertise; these qualities help group members attain their goal. More intelligent and skilled individuals can identify coordination challenges, offer successful strategies to achieve cooperation, and influence others regarding the quality of their strategy. Having knowledge capital renders individuals more likely to emerge as leaders (Judge, Colbert, & Ilies, 2004), an attribute desirable universally (Den Hartog et al., 1999). Experimental data and simulated models indicate that informed individuals emerge as leaders to coordinate actions in small and large groups (Couzin, Krause, Franks, & Levin, 2005; Dyer, Johansson, Helbing, Couzin, & Krause, 2009). In a review of anthropological studies focusing on egalitarian small-scale societies, Von Rueden (2014) found that social status, a proxy of leadership, is correlated in many tribes with expertise in healing or having supernatural powers. In small-scale societies, skilled storytellers who signal messages related to cooperation in group activities emerge as preferred social partners and have more reproductive success (Smith et al., 2017). Less informed individuals follow individuals who have more information in various animal species, including ravens (Wright, Stone, & Brown,

2003), elephants (Foley, Pettorelli, & Foley, 2008) and bees (Riley, Greggers, Smith, Reynolds, & Menzel, 2005).

Finally, social capital refers to characteristics making someone embodying the values and identity of the group. Individuals that are older, group-prototypical, or positioned more centrally in their network are more likely to emerge as leader (Van Knippenberg, 2011). Older individuals are likely to have more allies and a bigger social network; young individuals tend to have accrued less knowledge, expertise and wisdom, disqualifying them to exert leadership (Spisak, Grabo, Arvey, & van Vugt, 2014). Anthropological studies in egalitarian small-scale societies show that followers have generally smaller coalition sizes, as indicated by the size of their family and social network (Von Rueden et al., 2018; Von Rueden et al., 2014). This idea is corroborated in the animal literature where younger individuals emerge as followers in nomadic species migrating (Maransky & Bildstein, 2001).

Altogether, our review suggests that individuals emerge as followers if they lack the capital to successfully lead a group.

Proposition 5: Individuals will emerge as followers if they lack physical, psychological, and/or social capital.

To summarize, our review indicates that followership is more likely when the benefits of claiming leadership are low (*Proposition 3*), the costs of leading are high (*Proposition 4*) or when individuals are unable to attract followers (*Proposition 5*). Rather than making complex cost-benefit computations each time they face a coordination challenge, we suggest that individuals rely on evolved mental algorithms to quickly assess themselves and others in their respective abilities and motivations to lead (Grabo et al., 2017).

Task Analysis of Followership

A computational task analysis suggests that once individuals have identified a need for coordination, different follower mechanisms are being activated. Our adaptive followership

system likely contains mechanisms to (a) select an appropriate leader given certain environmental constraints or opportunities, (b) encourage these individuals to take on leadership roles; (c) monitor their effectiveness, and (d) switch leaders when needed (cf., evolutionary leadership theory; Van Vugt & Grabo, 2015).

Selecting Leaders. What are informative inputs followers can use to select appropriate leaders? Life in ancestral time was harsh and the environment could be threatening, so choosing a wrong leader had tremendous consequences on the survival of the group. Because group living posed various adaptive challenges (e.g., finding food, defending the tribe) requiring different skill sets, an adaptive strategy for followers was to select different situational leaders that would maximize the benefits of coordination (Van Vugt, 2006). This process results in followers deferring to leaders who have the best abilities to solve the coordination problem in a particular context. Thus, cues referring to the physical, psychological and social capital of would-be leaders should matter.

One example of an evolved followership mechanism is a reliance on facial cues to make inferences about other individuals, a process known as face-ism (Antonakis & Eubanks, 2017; Todorov, Olivola, Dotsch, & Mende-Siedlecki, 2015). These inferences are made extremely quickly (Willis & Todorov, 2006) and operate mostly at an implicit level not accessible to consciousness (Bargh & Chartrand, 1999; Kenrick, Li, & Butner, 2003). Face-ism suggests that followers rely on facial attributes to guide who they select as leader. The social psychology and leadership literatures are replete with empirical studies showing that followers make inferences about leaders based on facial cues, especially when it comes to distant leaders such as politicians or CEOs (because followers often lack more relevant information), and these inferences correlate strongly with actual followers' decisions. Empirical evidence points towards facial cues of attractiveness, dominance, competence, and trustworthiness serving as inputs into an adaptive followership psychology (e.g., Antonakis & Eubanks, 2017; Berggren, Jordahl, &

Poutvaara, 2010; Fruhen, Watkins, & Jones, 2015; Linke, Saribay, & Kleisner, 2016; Rule & Ambady, 2008).

Situational cues also matter as inputs into an adaptive followership psychology. One context that calls for particular leadership abilities is intergroup conflict. Empirical studies show that when intergroup conflict arises, followers favor masculine, dominant leaders whereas in times of peace, more feminine, trustworthy leaders are preferred (Laustsen & Petersen, 2015; Little, 2014; Little, Burriss, Jones, & Roberts, 2007; Spisak, Dekker, Krüger, & Van Vugt, 2012). Individual with physical capital are particularly functional in conflicts: They look threatening and frightening to opponents, and they reduce free-riding and coordination failures within the group (Bøggild & Laustsen, 2016; Sell et al., 2009; Von Rueden et al., 2018; von Rueden & Van Vugt, 2015). Concurrently, in peacetime, individuals with a warm personality or social capital will be preferred as leaders (Spisak et al., 2012). Their functionality lies in encouraging coordination and minimizing conflict, thus ensuring the respect of the social order (Little et al., 2007). The stability of the environment is another relevant contextual cue, linked with a preference for younger or older leaders. Younger leaders tend to be favored in times of change, instability, or exploration, whereas older leaders are selected in stable contexts encouraging exploitation (Spisak et al., 2014). A stable environment may select for leaders with past records of performance in similar contexts or knowledge of the particular situation, favoring older leaders. An unstable environment may select for skills such as physical ability, cognitive agility, or flexibility in the information and schema employed, thus favoring younger leaders (von Rueden & Van Vugt, 2015).

Proposition 6: An evolved followership psychology relies on personal and situational cues to select leaders.

Encouraging and Monitoring Leaders. Once followers have selected their leader, further adaptive tasks relate to encouraging the chosen individual to take up the leader role and

monitor their actions. To encourage an individual into a leader role, followers and leaders can negotiate over the distribution of the coordination benefits as long as the distribution remains beneficial to both parties (Hooper et al., 2010). When leadership is granted, an adaptive followership task is to ensure leaders are being monitored and kept in check in order to correct for deviant, selfish, or irrational leader behaviors. Due to their differential influence, leaders have leeway to exploit their followers. Leaders often have more information than followers do which they can leverage by conveying inaccurate information (e.g., about the benefits of cooperation) or favoring their kin in the allocation of tasks or cooperation benefits. Leaders can also preferentially benefit from coordination by taxing followers (Bøggild & Petersen, 2016). In essence, the leader-follower relationship is "inherently ambivalent" (Van Vugt et al., 2008a; p.182) because leaders and followers have conflicting interests. Take, as an example, a war situation where coordination failure can be lethal. Leaders with a strong physique may be preferred because the situation requires an individual that has the potential to enforce coordination or resolve intergroup conflict aggressively. Yet, these leaders are also the ones more likely to exploit their own followers (Laustsen & Petersen, 2015; von Rueden & Van Vugt, 2015). Thus, followership involves trade-offs and requires mechanisms to prevent exploitation from leaders.

As discussed before, the human ability to form coalitions "reversed" the dominance hierarchy and paved the way for the emergence of small-scale egalitarian societies in early humans. Anthropologist Chris Boehm (1993) found that a shared characteristic of these societies is their reliance on "leveling" mechanisms to suppress leaders' dominance and exploitation. These mechanisms include the use of public opinion, criticism, ridicule, disobedience, and extreme sanctions such as removal or even assassination of overbearing leaders. Computer simulations indeed confirm that agents with the ability to form coalitions can keep leaders in check (Gavrilets, 2012; Gavrilets, Duenez-Guzman, & Vose, 2008).

Proposition 7: An adaptive followership psychology contains mechanisms to detect and manage exploitation risks of leaders.

Followership Styles

In order to ensure smooth coordination and maximize the benefits of collective action, it is also important that the styles of following match the styles of leading. Thus, there are pressures on followers to adapt their behavioral styles to those of their leaders (and vice versa). The evolutionary literature suggests that there are, by and large, three major strategies for individuals to achieve leadership positions in human groups, reflecting their behavioral style: Dominance, prestige, and charisma (Grabo et al., 2017; Henrich & Gil-White, 2001; Maner, 2017). Dominance-based leaders use coercion, intimidation, and fear to ensure coordination. Prestige-based leaders rely on individual skills, competencies, and knowledge to get individuals to coordinate with them. Finally, charisma-based leaders rely on the signaling of appropriate values, emotions, and identities to attract followers and coordinate group action (Antonakis et al., 2016). Whereas dominance-based leadership is found across many species, prestige- and charisma-based leadership are probably more unique to humans because the role of language is especially instrumental. In the absence of language, signaling charisma would be inherently difficult; yet, enthusiasm or symbolism could still be expressed through non-verbal means, and as such, we would not dismiss the possibility that other forms of charisma exist. Applying French and Raven (1968) bases of social power, dominance-based leadership reflects reward and coercive powers, prestige-based leadership echoes expert and informational powers (e.g., skills, access to and control of information), and charisma-based leadership is akin to referent power (e.g., identification, attraction). These three different styles – dominance, prestige, and charisma – approximate transactional, instrumental, and charismatic/transformational leadership styles (cf., Antonakis, 2017a).

To ensure smooth and efficient group coordination, followership styles should match

these different leadership styles. Followers seeking protection from their leader may accept the influence of a dominance-based leader, because these leaders require people to comply to sanctions and rewards. As a result, dominance-based leadership encourages passive, conformist or even submissive followership styles. Non-verbal studies show that individuals react indeed with submissive bodily postures to physically dominant leader behaviors (Tiedens & Fragale, 2003). In order to benefit from their skill and abilities, followers will want to closely and actively follow prestige-based leaders. A prestige-based leadership style will thus create active and inquisitive followers who are keen to use these leaders as their role models from which they can learn. Finally, charismatic leaders pop up in cases when coordination failures are potentially lethal and quick coordinated group action is required such as in a crisis. Emerging from urgent group needs, a charisma-based leadership style produces enthusiastic, identified, and emotionally aroused followers who open up themselves to the leader's influence. Although individual differences in followership style exists, we argue that followership styles will ensue from the interaction with particular leadership styles.

Proposition 8: Followership styles result from the match with particular leadership styles.

It is good to realize that followers face trade-offs when they interact with particular leadership styles. Dominance-based leaders may abuse their position in a self-serving way, favoring their own interests or those of their kin at the detriment of followers. Their grip over rewards and sanctions give them tremendous power over followers' fate. Prestige-based leaders may possess unrelated skills or outdated knowledge for the task at hand, but mislead followers into believing that they possess the appropriate characteristic to successfully lead. Charisma-based leaders may profit from followers' emotional arousal and strong group identification by using their influence in a selfish, narcissistic manner – this is commonly referred as the dark side of charisma (Howell & Shamir, 2005). Using verbal and nonverbal strategies, charismatic leaders may exploit followers to do things that help their leader or the group at large, but go

against their best interests (e.g., suicide attacks).

Followership Engagement

A final interesting question that an evolutionary perspective informs pertains to the commitment or engagement of followers with leaders and their goals. Commitment, an individual identification with and involvement in the group and its goal (Mowday, Steers, & Porter, 1979), is negatively correlated with followers' turnover and positively predicts satisfaction with the leader and the organization (Meyer, Stanley, Herscovitch, & Topolnytsky, 2002). Our evolutionary approach suggests that followers will consider their satisfaction with outcomes and procedures, the availability of alternatives, and their investment in the relationship to inform their levels of engagement with the leader. These factors may contribute to understand different followership types such as diehards, activists, participants, bystanders, and isolates (cf., Kellerman, 2008).

Satisfaction with Outcomes. Individuals can decide to no longer follow if they are unhappy with the outcomes they receive from coordination, compared to their inputs. Equity theory (Adams, 1963, 1965) suggests that individuals are motivated to reduce inequity whenever what they receive compared to what they provide is lower than this ratio for a referent individual. If the difference in pay-offs between leaders and followers, or between different followers, is deemed unfair, followers will likely lower their engagement as a consequence. Meta-analyses indicate that individuals' perception of distributive justice (Cohen-Charash & Spector, 2001; Colquitt, Conlon, Wesson, Porter, & Ng, 2001; Colquitt et al., 2013) and satisfaction with their pay (Mathieu & Zajac, 1990) significantly correlate with individuals' commitment to the leader and the organization. Also, leaders who reward followers contingent on their performance have more committed followers (Jackson, Meyer, & Wang, 2013; Podsakoff, Bommer, Podsakoff, & MacKenzie, 2006). Note that followers' payoff does not have to be material, but can also be social or psychological (e.g., Peterson & Luthans, 2006).

Fairness of Procedures. Procedural fairness – the idea that leader decisions were arrived at in a just and fair manner – will also influence followers' engagement, especially when outcomes are unfavorable (Brockner & Wiesenfeld, 1996). To avoid being exploited, followers look for cues of fairness in a leader whenever they are uncertain about their outcomes (Van den Bos & Lind, 2002). Bøggild and Petersen (2016) argue that procedural fairness evolved as a followership mechanism that serve two primary functions: (a) A diagnostic function to ensure followers' interests are taken care of; and (b) a bargaining function to broadly communicate a leader's breach of rules. Acting as a mental algorithm, a leader's violation of procedural fairness indicates a potential risk of exploitation to which followers should respond by exiting the relationship (Bøggild & Petersen, 2016). Indeed, leaders' procedural fairness, often operationalized by giving followers "voice" in the leadership process, relates positively to followers' engagement and relationship continuance (see Van Knippenberg, De Cremer, & van Knippenberg, 2007 for a review).

Quality of Alternatives. Followers' cost of leaving the group and the absence of alternative leaders also predict followers' engagement with their current leader (Pfeffer & Lawler, 1980; Rusbult, Farrell, Rogers, & Mainous, 1988). Evolutionary insights indicates that the availability of attractive exit options affects the bargaining power of followers which in turn predicts how the benefits of coordination will be shared and who will claim most of the benefits of coordination (Debove, Baumard, & André, 2015; Gangestad & Simpson, 2000; Noë & Hammerstein, 1994). Powers and Lehmann (2014) used simulations to show that followers' exit costs and the absence of alternative leaders positively correlate with the capacity of a leader to seize a bigger share of the coordination benefits. In contrast, when the opportunity cost of switching groups is low, followers will tend to get a bigger share of outcome.

Investments. A final predictor of follower engagement relates to followers' investments – physical and psychological – in the relationship (Becker, 1960; Meyer & Allen, 1984). Any

resource (e.g., time, effort, money) invested that would be lost if the relationship with the leader was discontinued increases the commitment of individuals. Imagine a follower who has made a considerable effort to support a particular political party candidate. Even if the candidate turns out to be a poor leader, engaged followers may have difficulty in terminating their support. Generally, followers will be more engaged with their leader whenever sunk costs are high (Rusbult & Farrell, 1983). An indicator of followers' investment is the order in which they decide to follow a leader. First followers are more invested and therefore will probably be more engaged than second, third, or the n-th followers. Because early following is a risky yet credible signal of commitment to the leader, first followers are also more likely to obtain a larger share of coordination benefits (e.g., think of US presidential candidate donors who are rewarded with an Ambassador post after their candidate wins the election).

Proposition 9: Followers' engagement results from (a) followers' satisfaction with the coordination outcomes; (b) the fairness of leader procedures; (c) the presence of alternative options; (d) and followers' investments in the leader-follower relationship.

Discussion and Implications

Based on an evolutionary approach, our review has shown that followership is not a scientific puzzle. It is a logical, inevitable consequence of the evolutionary need to live in groups and benefit from coordinated actions with other individuals. Followership is a voluntary deference process and it is not the same as being submissive in a dominance hierarchy. Reviewing different streams of literature, we have proposed that emergent followers are relatively more likely to lack the motivation to lead and/or the ability to attract followers. Our review also indicates that humans have an adaptive followership psychology deeply rooted in our ancestral past, consisting of various psychological mechanisms to recruit and select appropriate leaders, monitor their effectiveness, and replace them whenever needed. Finally, our review suggests that followers match their styles to those of their leaders – to ensure smooth

coordination – and that their engagement results from a combination of satisfaction with outcomes, fairness of leader procedures, consideration of alternative leaders, and investments in the relationship. In the following, we address interesting questions about followership that result from our evolutionary analysis and review, and that could offer fresh insights to followership research.

Is Followership Still Adaptive?

First, if natural selection has produced perfectly adapted followership mechanisms, why do modern people (sometimes) follow the wrong kind of leader? We argue that this may be the consequence of an evolutionary mismatch. Human followership psychology evolved in small-scale societies, yet we currently live and work in large, complex organizations that are evolutionarily novel (Van Vugt & Ahuja, 2011; Van Vugt, Johnson, Kaiser, & O'Gorman, 2008b). Humans have a small-scale followership psychology making certain mechanisms no longer appropriate and even mismatched to current contexts, such as our over-reliance on physical cues to make inferences regarding a leader's competence. Although it may have been adaptive to follow physically formidable leaders in ancestral environments, the functional benefit of this algorithm may be limited in a modern, complex society where leaders often lead from the back rather than the front. Because our inferences remain anchored in first impressions that have a deeper evolutionary functionality, it may result today in irrational follower decisions. Organizations should be aware that individuals are biased towards particular facial and physical cues of potential leaders, and train members of selection panels to avoid such biases. This issue is even more crucial if organizations use social media (e.g., Linkedin, Facebook) to obtain information about potential candidates for a leadership position.

A second mismatch is that modern organizations have structures in place that de facto reduce followers' engagement with their leaders. Leaders are not elected bottom-up by the group but often top-down and appointed by people outside the relevant group. A bottom-up

approach to leader selection increases cooperation levels and leader success (Baldassarri & Grossman, 2011; Rivas & Sutter, 2011), because followers consider the leader as legitimate, prototypical, and identify with their actions (Hollander, 1992). Outside leaders may be competent but may have a style of leadership not favored by followers and their priorities may more likely lie with their superiors rather than their subordinates (Van Vugt, Jepson, Hart, & De Cremer, 2004). Followers should ideally be consulted and have a say in leader selection if organizations are willing to increase followers' engagement.

Third, effective leveling mechanisms are often missing in contemporary organizations. These mechanisms act as safeguards against exploitation and their absence allows ineffective or even corrupt leaders to remain in place. The use of leveling mechanisms like gossip, satire, and public criticism is illegal in particular countries, resulting in potentially toxic leadership cultures. Although in most modern work organizations followers can criticize their bosses when they are unsatisfied with them, followers usually have no authority to dismiss them. Knowing this power imbalance, leaders can easily abuse their position. Organizations could benefit from a culture that gives followers mechanisms to monitor, regulate, and eventually sanction bad leadership (e.g., using followers' feedback as an input in promotion decisions).

Another source of evolutionary mismatch pertains to the lack of direct personal experience with the personal qualities of potential leaders in modern organizations. Information deficits facilitate the emergence of leaders with dark triad personalities. Ancestral cooperation was obtained in small groups with kinship ties and deep personal connections between leaders and followers. Followers knew the personality and values of leaders based on years of close interactions, creating strong reciprocity and reputational norms. In rapidly-changing environments, toxic individuals can easily highjack followers' psychology. Because would-be leaders are not tested over years of personal interactions, narcissistic or over-confident individuals have extant opportunities to make good first impressions without being checked.

Furthermore, toxic leaders can very easily escape a bad reputation and switch to a new group. When selecting leaders, organizations should thus pay more attention to leaders' reputations and their past actions rather than simply focusing on "cheap" signals like a smooth job talk.

A reward system that disproportionally favors leaders over followers is another probable source of evolutionary mismatch. Before the rise of agriculture, leaders and followers shared the benefits of coordination more or less equally (although leaders likely had more reproductive opportunities; Von Rueden et al., 2014). Nowadays, some CEO's get paid astronomical salaries compared to average workers, resulting in large power imbalance. This inequality will affect followers' engagement, reduce their cooperation with leaders, and boost cynicism targeted against high level managers and the organization. A business case could probably be made for a more equitable redistribution of outcomes.

Altogether, these different sources of evolutionary mismatch create what we could refer as reluctant, alienated, disengaged, or destructive followers. In this vein, Schein (2015, p.10) argues that "(t)here is a certain irony that we alienate employees and then spend a lot of effort with surveys and consultants to figure out how to engage them." Organizational decision makers would thus benefit to understand that our followership psychology evolved in small, cooperative groups if they want to increase followers' engagement.

Why Are There Gender Differences in Leading and Following?

An evolutionary perspective can inform why we observe relatively fewer women in formal leadership roles in society. From a biological perspective, women bear children and invest more in parenting. This state of affairs may have led to a sexual division of labor in hunter-gatherer societies and prevented women from taking on tasks involving physical risks (Buss, 1995; Van Schaik, 2016). Warfare and hunting – activities performed mostly by males – required leaders with coalition-building skills or the capacity to coordinate actions within large networks of individuals and followers who accept the hierarchy and defer to the leader

(Von Rueden et al., 2018). Gathering and child rearing – activities performed mostly by women – selected for other characteristics including relationship-building or the capacity to lead communally and with empathy. To perform their task effectively, men and women have thus probably evolved different psychologies, abilities, and preferences (Pinker, 2002), allowing for different leadership and followership styles (Eagly, Johannesen-Schmidt, & Van Engen, 2003; Eagly & Johnson, 1990). Whereas men tend to form more hierarchical leader-follower relationships with each other, women leader-follower interactions will be more egalitarian and consensus-based (Benenson & Markovits, 2014).

A different explanation for male-biased leadership lies in the reproductive benefits associated with a leader strategy. In comparison to women, men have greater variance in reproductive outcomes related to status competitions. That is, men have relatively more to gain by competing for high status leadership roles, such as greater access to resources and sexual mates (Betzig, 2012). Men have thus probably evolved to actively and aggressively pursue such leadership roles. In turn, women prefer men who have obtained high status positions. Empirical evidence indeed suggests that women find socially dominant men to be more attractive (Jensen-Campbell, Graziano, & West, 1995) and men actively signal social dominance in mixed-sex interactions (Campbell, Simpson, Stewart, & Manning, 2002).

A third reason is that leadership in small-scale societies was often directly linked to physical dominance such as hunting or leading a raid (Von Rueden et al., 2018; Von Rueden et al., 2014). This may explain why still today we observe a greater fit between our prototype of a leader and being male, and our prototype of a follower and being female (Braun, Stegmann, Hernandez Bark, Junker, & van Dick, 2017). Some contexts are nonetheless more conducive to the emergence of women leaders, such as peacekeeping, conflict resolution (Van Vugt, 2006), or informal leadership in community affairs (Low, 1992). As organizations continue to move towards flatter hierarchies and self-organizing teams, they need more interpersonal, informal,

and communal leadership skills that will likely open up more leadership positions for women.

What Makes a Bad Follower?

What is a bad follower? From our definition, a bad follower is an individual who does not coordinate well with the leader and/or with other followers. Examples of bad followership behaviors include free-riding, cheating, or social loafing which may produce coordination failure. Bad followership also results from behaviors that are self-serving rather than aimed at improving coordination, such as when followers (a) accept bribes and support bad leaders, (b) undermine the leadership position (e.g., an extroverted individual competing for status at the leader and group expense), or (c) are unpredictable in their actions. To be clear, we do not make a moral statement. Bad followers can be morally good people, but by undermining group coordination they produce suboptimal outcomes for their leader, their group, and ultimately, themselves.

Bad followership can also occur when leaders exploit followers. A failure to use leveling mechanisms against exploitative leaders would be considered bad followership. Examples include followers who do not report deficient or unethical leader behaviors, or do not vote if they get the opportunity to replace an exploitative leader. When leaders are biased in their decisions or abuse their influential position, or when other followers under-contribute, bad followership originates from a failure to act. This perspective on bad followership resonates with leadership practitioners who operationalize good followership in terms of courage (Chaleff, 2009), engagement to the common good (Kellerman, 2008), or critical thinking (Kelley, 1992).

Why Are There So Few Good Leaders?

Leadership failure is common in modern organizations and climate surveys show that a majority of workers find interactions with their direct bosses the most stressful part of their job (Van Vugt et al., 2008a). Why is poor leadership so common? The answer may have partly to

do with the distribution of leaders and followers in the population. Leader-follower ratios have changed from say a 1:5 ratio (hunting parties) in ancestral groups to 1:1,000 or even 1:1,000,000 in large, modern organizations (nation states are led by just a few leaders)[3]. This transition suggests that current groups need fewer leaders, but many more followers to function effectively than in the past. As the ratio of followers to leaders has increased, so has the competition to be the leader, resulting in a winner-takes-all competition, with extreme inequalities in power and pay-offs as a consequence (e.g., a CEO in a US listed company earn on average 354 times the average salary of unskilled workers, which very few believes is fair; Norton, 2014). In turn, as fewer leaders are needed, there has probably been cultural selection on followership traits, favoring more conformist, docile, and passive individuals. Consistent with this line of reasoning is the human domestication hypothesis which suggests that we tamed ourselves as a species to be extremely good cooperators. The result is that humans are good followers (see the classic Milgram and Asch studies in social psychology) but that our leadership skills are underdeveloped. If we culturally evolved to be good followers, this raises interesting questions. For example, how do humans adapt to modern individualistic societies prescribing that individuals should be their own leaders and "never be a sheep" or "never follow"? Also, as we train our kids to be excellent compliers, are there still enough individuals with leadership qualities who are worthy of following?

Naturally, part of our adaptive followership psychology is to be flexible in terms of the roles we take in coordination activities. Being able to follow or lead depending on conditions allows us to create super organizations with many different hierarchical layers, where

[3] As suggested by one reviewer, large organizations contain multiple tiers of formal leadership, so counting only top-level leaders may be misleading. We would however argue that middle-level leaders report to leaders higher up in the hierarchy, removing the formers from their responsibility and discretion in decision making. Potential outcomes may include widespread conformity, alienation, and diffusion of responsibility, which in turn would partly explain why poor leadership is so common.

individuals have to navigate between different identities: To be a leader in one meeting but a follower in another requires cognitive flexibility. In this respect, layered organizations fit our human minds by keeping group sizes within our evolved cognitive limits (Dunbar, 1993). This capacity to operate both as leaders and as followers is probably uniquely human and may have contributed to our species success.

A final issue concerning group size is that the prevailing leadership style probably affects the number of followers per leader (i.e., leader's span of control). In order to be effective, dominance-based leadership requires a small span of control because it involves close monitoring of followers (e.g., dominance hierarchies in great apes point to group sizes of 5-8). Beyond a few followers, it may become difficult to manage free-riders though this may have changed with the development of recent communication technologies (like observation cameras). Prestige-based leaders allow for an expansion of the number of followers. However, because followers want to be near prestige leaders to copy and learn from them, group size could probably not extend beyond 10-15 individuals, the tribe size of small clans. For charismatic leaders, group size has theoretically no limit as long as followers can share emotions and identify with their leader. Because charisma relies mostly on verbal communications, charismatic leaders could probably expand group sizes up to 100-150 individuals. Again, these constraints on group size were lifted with the rise of current communication technologies (e.g., TV, social media), allowing charismatic leaders such as Hitler and Mandela to mobilize much larger groups of followers.

Connections with the Followership Literature

Our perspective takes a "reversing the lens" approach to leadership (Uhl-Bien, Riggio, Lowe, & Carsten, 2014) by focusing on follower motivations, behaviors and outcomes. Our review fits both a role-based approach and a constructionist perspective to followership (Uhl-Bien et al., 2014) although we depart substantially from these approaches. Our review is aligned

with a role-based approach insofar as the substantive amount of studies or meta-analyses included in our review have considered managers to be leaders and subordinates to be followers (i.e., leadership and followership are organizational ranks; Carsten et al., 2010; Kellerman, 2008). This interpretation makes some sense because managers are supposed to lead their subordinates. Yet, these studies mix freely conferred leadership influence with influence stemming from formal authority or hierarchy (Collinson, 2006; Shamir & Eilam-Shamir, 2017). In work relationships bound by contracts and inequality in payoffs between roles, leadership will tend to be primarily based on dominance rather than prestige or charisma. As discussed earlier, dominance-based relationships produce passive, conformist followers with low engagement levels. Furthermore, managers are oftentimes followers themselves; think of a software developer working on a new app and reporting to a manager who has no expertise in app development. Role approaches thus neglect that humans have a flexible followership psychology, allowing us to be in a leader role in some situations but in a follower role in others, and this regardless of the formal hierarchical positions. Our review also fits a constructionist approach towards followership, at least in definitional terms, as we construe leader-follower interactions based on the relational process of granting and claiming leadership (DeRue & Ashford, 2010). That being said, a relational view of followership could be studied using positivist epistemological approaches that complement a socio-constructionist perspective.

Our evolutionary perspective suggests that followership styles result from an interaction between follower goals, leadership styles, and environmental challenges. We do not argue against the idea of individual differences in follower styles, with some individuals being inherently more proactive, enthusiast or critically thinking. Yet, our review suggests that followership styles do not vary exogenously within leader-follower interactions; rather, how a leader behaves as well as the context and its associated followership goals all affect followership styles. When researchers estimate regression models, endogeneity may creep in

because these omitted factors will correlate with outcomes (e.g., a particular coordination task making someone both active and committed) or because the causality may be reversed (e.g., the amount of voice managers grant affects both followers' engagement and voice behaviors). Thus, we would exercise caution in interpreting findings stemming from studies that measure followership styles (Blanchard, Welbourne, Gilmore, & Bullock, 2009), co-production belief (Carsten & Uhl-Bien, 2015), or leader-member exchange with attitudinal scales and use scores as predictors in regression analyses. For these reasons, and others explained elsewhere (see Antonakis, Bendahan, Jacquart, & Lalive, 2010), the effects of followership styles on outcomes have to be purged from endogeneity bias. Potential solutions include the use of stable trait measures (e.g., personality dimensions, intelligence) or experimental inductions of followership (e.g., manipulating leadership styles or the task) as instrumental variables. Another possibility is to measure individual characteristics before they enter in a leader-follower relationship, so that followers' perception of their role does not become tainted by how the leader behaves or the contextual requirement (see for example Dvir & Shamir, 2003).

Finally, our evolutionary perspective provides some theoretical support for previous taxonomies of followership such as motivational differences in followers' engagement, creating followers who are diehards or bystanders (Kellerman, 2008), the active-passive and submissive-dominant follower dimensions (Kelley, 1992), as well as degrees of support for leaders among followers (Chaleff, 2009). Our review also concurs with Kelley (1992)'s notion that individuals follow leaders for specific reasons – prestige-based leaders attract apprentice followers, dominance-based leaders entice submissive followers, and charisma-based leaders appeal to loyal (fan) followers.

Future Research Directions

We invite researchers to bring the propositions advanced by our evolutionary theory perspective to test. For example, we encourage experiments designed to test whether followers

receive greater rewards from coordination when they possess leveling mechanisms and whether more egalitarian leader behaviors mediate this relationship. Similarly, studies investigating the impact of conflict versus cooperative contexts on follower engagement could help advance our understanding of followership, and so does the impact of prevailing leadership styles on followership styles. Work aimed at understanding what traits or situational characteristics make good followers – individuals who coordinate better with leaders – and the order in which they prefer to follow could inform organizational policies on employee selection. Do traits of good followers differ in organizations with steep, formal hierarchies (such as large corporations) compared to organizations with flatter hierarchies (such as start-ups or leisure clubs)? Does the type of coordination task predict what makes an effective follower? More research is also needed that examines how organizational structures and job design affect followership engagement.

Insert Table 2 about here

Another area for future explorations are situations in which cooperation can be obtained without having central coordination (e.g., Kerr & Jermier, 1978), requiring individuals who coordinate without formal leaders as in self-organizing teams. Substitutes for leadership – including rules, norms, or shared motives (Howell, Dorfman, & Kerr, 1986) – reduce the need for the emergence of a leader-follower structure. Formal leadership may not be necessary, or even resented, when the benefit of collective action is small, the group is small, the coordination problem is relatively simple or routine, and/or when there is little risk of defection and free-riding (Hooper et al., 2010). In other words, individuals can still follow rules or norms even if there are no appointed leaders. Appointing a leader when individuals already voluntarily share leadership (Pearce & Conger, 2003) may have adverse consequences on followers' motivations and induce stress or role conflict (de Vries, Roe, & Taillieu, 2002). Individuals' need for

autonomy also suggests that followers could be more motivated without a hierarchical structure in place. More research is needed to understand when formal leadership structures may be detrimental to the needs of followers and the efficient functioning of organizations. Looking to the future, self-organizing teams and sophisticated communication technologies will reduce the need for central coordination through central leadership and promote a more active role for engaged followers.

We would also encourage research on the neuroscience of followership. An evolutionary approach suggests that certain neural mechanisms may be involved when individuals decide to give up their autonomy to follow another individual. One prediction is that there will be a noticeable deactivation in the prefrontal regions of the brain when people follow the lead of another individual. An fMRI experiment measured the brain activity of individuals who listened to speeches of religious leaders and those followers that were religious themselves showed a reduced activity in the executive areas of the brain when they listened to particular charismatic leaders – a similar effect occurs when people are brought in a hypnotic state (Schjoedt, Stødkilde-Jørgensen, Geertz, Lund, & Roepstorff, 2010). In addition, we expect hormonal profile differences between leaders and followers (cf., Arvey, Wang, Song, Li, & Day, 2014). For instance, basal testosterone levels are likely to be lower, structurally, among followers than leaders especially when leaders wield more power (Van der Meij, Schaveling, & van Vugt, 2016). An experiment examined the performance of high and low testosterone individuals when they were randomly assigned to the position of leader or follower. Better performance was obtained for high testosterone individuals in high power positions, and low testosterone individuals in low power positions (Josephs, Sellers, Newman, & Mehta, 2006). In addition, follower personalities may show a great spike in cortisol levels when put in a position of leadership. Finally, we can expect charisma-based leadership to raise endorphin and possibly oxytocin levels in followers, enhancing their engagement levels with their leader and the group

they identify with.

We would encourage studies aiming at the evolutionary underpinning of implicit theories about followers (IFTs; Sy, 2010) and leaders (ILTs; Junker & van Dick, 2014; Lord, Foti, & De Vader, 1984). An evolutionary perspective implies that humans have evolved cognitive mechanisms that guide who they categorize as good or ideal leaders in specific contexts (e.g., war, famine, diplomacy). Our approach helps explain why we observe cross-cultural consistency in leadership prototypes among followers (Den Hartog et al., 1999) or why very young children make inferences similar to adults regarding leader traits and selection (Antonakis & Dalgas, 2009; Cogsdill, Todorov, Spelke, & Banaji, 2014). Yet, this does not necessarily mean ILTs or IFTs are fully operational when people are born. Rather it implies that humans are born with certain templates of good leaders and followers that are further shaped through local cultural and socialization experiences. We thus need to understand both our evolved followership mechanisms and the effect of culture if we want to grasp how individual's ILTs and IFTs are formed. This area is ripe for longitudinal research projects studying how ILTs or IFTs develop over the life span of individuals.

Another important mechanism affecting follower and group decisions at work relates to dynamics originating between followers, especially when certain followers copy the behaviors and decisions of other followers (Asch, 1956; Place, Todd, Penke, & Asendorpf, 2010). This copying process may lead to a cascading effect where the last followers do not necessarily follow the leader, but simply copy the followers prior to them (who in turn act as leaders for these last followers). This "follower cascade effect" suggests that a large group of individuals may steer completely in the wrong direction simply because certain individuals copy other followers rather than decide for themselves. Future research may build on previous social psychological research on conformity and groupthink (Janis, 1971) to uncover when this copying effect will be likely (e.g., when not following others may be individually costly) or to

design organizational structures preventing this bias (e.g., selecting leaders using anonymous voting).

Finally, studying the developmental phases of followership may be a worthy avenue for future research (Van Vugt, 2014). We know that human babies are already capable of following their parents through mimicking their facial expression; nine months old children already follow the eye gaze of their parents (Tomasello et al., 2005). This probably suggests that followership is a default setting in our brain and babies need to be capable of following in order to survive. When children are able to talk, followership emerges through verbal instructions of parents and teachers; much later in their developmental phase, humans are able to follow abstract cultural and moral norms. Through these developmental stages, humans turn into good followers allowing for the smooth coordination of large, complex societies. That being said, critical problems may emerge at any developmental stage that may prevent people from turning into good followers (e.g., losing a parent, failing to achieve a grade at school, a war experience).

Conclusion

The sportswear company Adidas started a recent advertising campaign encouraging individuals to "never follow." It wants everyone to unleash their leader instincts and create history. Yet, human history is ultimately made by followers who supported their leaders to achieve great deeds (e.g., ANC's fight against apartheid) or commit great atrocities (e.g., Nazi Germany). We tend to forget that followership has been the default strategy across human evolution, shaping our minds, and allowing our species to thrive in increasingly large, well-coordinated groups (which our non-human primate cousins have failed to do). To reap the benefits of coordinated action, following the right leaders under the right conditions has been one secret of our success as a species. Many outstanding questions regarding followership remain, but we hope that this review will encourage scholars to lead the study of followership.

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Table 1: Game-theoretic payoffs

Table 1A: Cooperation games

1) **Stag Hunt (Assurance) Game**

		Player 2	
		Stag	Hare
Player 1	Stag	(5;5)	(0;3)
	Hare	(3;0)	(3;3)

2) **Battles of the Sexes**

		Player 2	
		Football	Movie
Player 1	Football	(5;3)	(0;0)
	Movie	(0;0)	(3;5)

3) **Leader Game**

		Player 2	
		Leader	Follower
Player 1	Leader	(-1;-1)	(3;1)
	Follower	(1;3)	(0;0)

Table 1B: Following strategies

I. **Mutualistic followership**

		Player 2	
		Leader	Follower
Player 1	Leader	(0;0)	(1;1)
	Follower	(1;1)	(0;0)

II. **Coordinating followership**

		Player 2	
		Leader	Follower
Player 1	Leader	(0;0)	(3;1)
	Follower	(1;3)	(0;0)

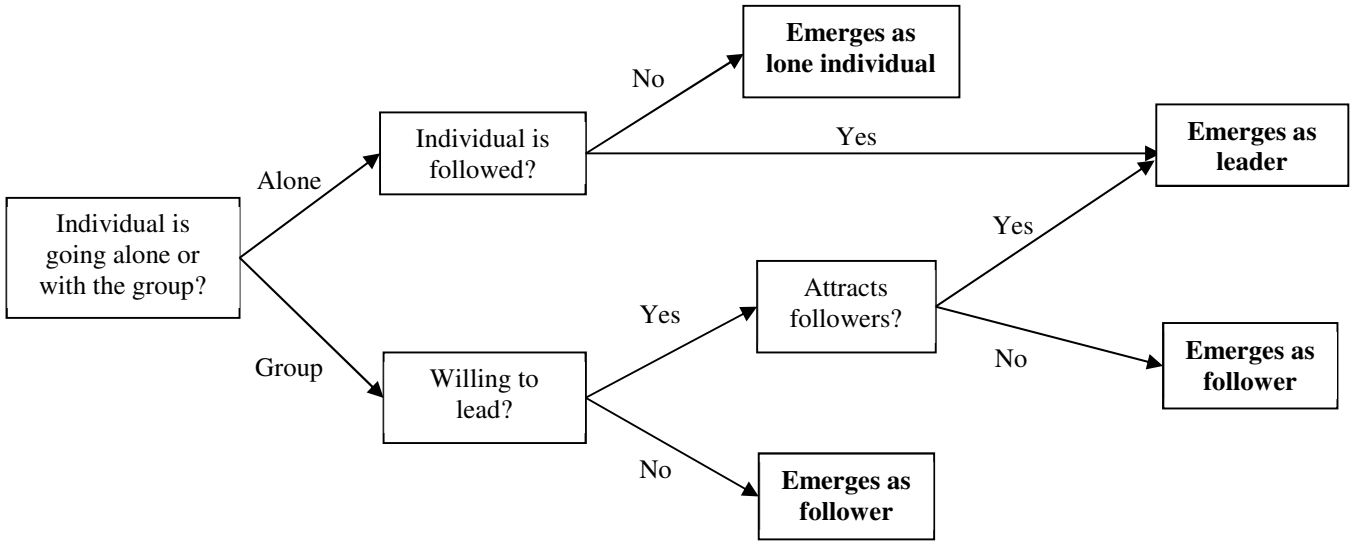
III. **Opportunistic followership**

		Player 2	
		Leader	Follower
Player 1	Leader	(0;0)	(1;3)
	Follower	(3;1)	(0;0)

Table 2: Summary of propositions

Propositions		Ways to test the propositions
1	Followership emerges when coordination or cooperation is beneficial.	• Examine in which situations leader-follower structures emerge, conditional on the level of cooperation or coordination required. • Study individual reactions when leader-follower structures are endogenously imposed without it being required for coordination or cooperation.
2	Followership is underpinned by various evolved psychological mechanisms (mental algorithms) for coordination.	• Neuroscience studies investigating the neural pathways of followership. • Take a developmental approach to the emergence of implicit leadership and followership theories.
3	Individuals will emerge as followers if they lack the motivation to be a leader.	• Experimentally manipulate the incentives linked with adopting a leadership strategy. • Expand research on personality traits and states as predictors of followership.
4	Individuals will emerge as followers if the costs of leading outweigh the benefits.	• Connect personality and physical traits with high costs of leading to infer followership. • Study how individuals across different organizations evaluate the different costs associated with leading.
5	Individuals will emerge as followers if they lack physical, psychological, and/or social capital	• Link bundles of social capital with followership emergence in different contexts. • Use a social network approach to study the "follower cascade effect."
6	An evolved followership psychology relies on personal and situational cues to select leaders.	• Analyze individual and contextual moderators of face-ism. • Examine ways to forestall physical biases in selection and promotion decisions.
7	An adaptive followership psychology contains mechanisms to detect and manage exploitation risks of leaders.	• Develop organizational policies aimed at keeping leaders in check based on leveling mechanisms found in small-scale societies. • Analyze the psychological and behavioral consequences when followers detect exploitation by their leader.
8	Followership styles result from the match with particular leadership styles.	• Experimentally manipulate (e.g., using virtual reality) different followership and leadership styles and study how their match improves coordination. • Explore the consequences of a mismatch in leadership and followership styles.
9	Followers' engagement results from (a) followers' satisfaction with the coordination outcomes; (b) the fairness of leader procedures; (c) the presence of alternative options; (d) and followers' investments in the leader-follower relationship.	• Investigate followers' engagement with their leader across different kinds of organizations. • Examine how the presence or absence of exit options affects followers' engagement with their leader.

Figure 1: Individual decision tree when in need of coordination



Note: Individuals may emerge as leaders without claiming leadership but because followers grant them a leadership role.

Figure 2: Example of an evolved followership mechanism

Dangerous environment
Require self-protection

Following a leader is good
Select an individual that
can protect me

Endorse a physically strong leader