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Evolution and Groups

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*Camp 10 Ms. Above the river Plate
Monday July 23rd, 1804.*

“A fair morning—sent out a party of 5 men to look to timber for Ores two other parties to hunt at 11 oClock Sent, G. Drewyer & Peter Cruseett $\frac{1}{2}$ Indn. to the Otteaus Village about 18 ms. West of our Camp, to invite the Chiefs & principal men of that nation to come & talk with us &. & also the panis if they Should meet with any of that nation (also on the S. Side of the Plate 30 ms. higher up). (at this season of the year all the Indians in this quarter are in the Plains hunting the Buffalow from Some Signs Seen by our hunter and the Prairies being on fire in the dereliction of the Village induce a belief that the Nation have returned to get green Corn).

(By William Clark, Co-Captain of the Corps of Discovery
[Nebraska edition of the Lewis & Clark journals
edited by Gary E. Mouton]. All errors are original.)

This quote comes from the journals of William Clark, who together with Meriwether Lewis, led the expedition of the American West from 1804–1806. On the orders of President Jefferson, Lewis and Clark organized an expedition, travelling up the Missouri River to the Rocky Mountains and westward along possible river routes to the Pacific Ocean. The journal of their 3-year journey (along with a crew of 33 men) through unexplored territories in the US provides a vivid example of the many challenges that human groups encounter in natural environments. This list includes problems as diverse as securing food, finding safe shelters, acquiring knowledge about places, animals and plants, protection against predators and hostile outgroups, developing peaceful

intergroup relationships, transmitting useful information, following orders, and executing leadership and followership.

These are remarkably similar to the challenges that groups have faced throughout human evolutionary history. Extrapolating from anthropological and archaeological data, for at least several hundreds of thousands of years our human ancestors lived in small and closely tied groups—much like the Lewis and Clark band yet including men, women and children—in natural environments. Although we can only speculate about life in ancestral environments, there is little doubt that, throughout human evolution, groups have been key to the success of humans.

Applying evolutionary theory, group living can be viewed as an adaptive strategy that increased the survival and reproductive success of ancestral humans. This strategy was so successful that humans are among the most “groupish” animals on the planet and together with the social insects have achieved ecological dominance (Wilson, Van Vugt, & O’Gorman, 2008). Thus, students of group dynamics would be well served to take seriously the role of human evolution in shaping our group psychology. Viewing group processes through the lens of evolutionary theory also enables group psychologists to work together with biologists, anthropologists, economists, neuroscientists, sociologists, and other behavioural scientists in developing an overarching theoretical framework on group dynamics.

Charles Darwin pioneered this new evolutionary science of groups. In his second book, *The Descent of Man*, Darwin wrote: “With those animals which were benefited by living in close association, the individuals which took the greatest pleasure in society would best escape various dangers, while those that cared least for their comrades, and lived solitary, would perish in greater numbers” (1871, p. 105). Essentially, Darwin provided an evolutionary account for the affiliation motive which is subsequently identified as one of the core human needs (Baumeister & Leary, 1995).

For ancestral humans, evolving in hostile natural environments where dangers were common and resources were scarce, group associations provided safety and comfort. Only as group members could our ancestors acquire reproductively relevant resources such as food and water and defend themselves against hostile animals and antagonistic outgroups. The conceptual implication is that humans have an innate group psychology that regulates their group interactions. This yields a practical implication as well. By applying the tools of evolutionary theory and psychology we have the potential to more fully understand real-world group processes and improve the design of teams and organizations.

Take the example of groupthink, the phenomenon that highly cohesive groups under time pressures and directive leadership engage in poor decision-making (Janis, 1972). From an evolutionary perspective, groupthink can be seen as the outcome of a trade-off between two distinct strategies, getting the right information (accuracy) and keeping group unity (cohesion). Under certain conditions, such as an imminent external threat, it can be functional for all group members to form a united front and adhere to a group decision, regardless of

whether the decision is factually correct. This does not necessarily imply that it produces the best outcomes, especially in complex modern environments. The ill-fated invasion of the Falkland Islands and the NASA Challenger disaster suggest that our evolved inclination to strive for group unity may have dire consequences indeed.

In this chapter we first provide a brief introduction to evolutionary psychology and its application to group processes. Second we discuss the diversity of methodological approaches that are used by evolutionary psychologists to find evidence for group-level adaptations. Third we address the various functions of groups in human evolution, and suggest that humans have evolved a host of psychological mechanisms to solve critical challenges in six domains of group life: (a) coordination, (b) social exchange, (c) status, (d) group cohesion (e) collective decision-making, and (f) intergroup relations. Finally we provide short and selective reviews of the current state of knowledge in evolutionary research on each of these six group challenges. We conclude by addressing some conceptual and practical implications of a new evolutionary science of group dynamics.

APPLYING EVOLUTIONARY THINKING TO GROUP PROCESSES

An evolutionary approach to the study of groups starts with the recognition that the physiological, neurological, and psychological processes involved in producing human group behaviour are products of biological evolution. It follows, therefore, that conceptual insights of evolutionary sciences can, when applied with rigour and care, produce novel discoveries about human group psychology (Capra, 1997; Van Vugt & Schaller, 2008). Indeed evolutionary inquiries have not only provided deeper explanations for the origins of already-recognized psychological phenomena such as mate preferences and fears and phobias, they also have produced an impressive array of novel theories, hypotheses, and empirical discoveries about the way humans behave in groups and feel about them (Buss, 2005; Kameda & Tindale, 2006).

Evolutionary theory contains three simple premises based on the three core Darwinian principles which together account for every aspect of living matter: (1) variation, (2) selection, and (3) retention. First, there is variation in traits among individuals—to illustrate with an example, some individuals are loners who prefer a solitary existence, whereas others are joiners who prefer to be in groups. Second, some of these trait variants enable their bearers to compete more successfully for reproductive resources—joiners can share resources and defend themselves better and as a result they have a better chance to produce offspring (selection). Third, these traits are heritable such that offspring resemble parents—joiners (or loners) are more likely to have children with joiner (or loner) genes (retention). Repeated over time, this continuing process of variation, selection, and retention produces organisms and species that are well adapted to the environment in which they live: All modern humans are the descendants of individuals who preferred group life over a solitary existence.

An evolutionary psychology approach to group dynamics has the following core assumptions:

(1) Humans Have Social Brains

As a member of the family of primates, humans have evolved as a group living species and therefore it is likely that many of our cognitive adaptations are social psychological. For early humans, group life formed a buffer against perturbations of the natural environment, so there must have been selection for traits facilitating group formation and group interaction. The social brain hypothesis (Dunbar, 2001) posits that humans have evolved large brains in order to make the most of living in large, complex social groupings. In support of the social brain hypothesis, comparative studies have found a positive correlation between the size of the pre-frontal cortex and average group size, comparing humans with other primates and comparing primates with other mammals. Humans come out on top, having both a relatively large pre-frontal cortex and an associated large average group size. From the brain data, the extrapolated group size for humans is around 150 individuals—also known as Dunbar's number—which corresponds roughly to the size of a small community like a neighbourhood or religious community that can be held together through informal social control. One hundred and fifty is also the median number of recipients on people's Christmas card lists according to a UK study (Hill & Dunbar, 2003).

(2) Selection Forces Operate Together

Selection for groupish traits—traits that enable individuals to enjoy and function well in groups, such as sociability—is called social selection, and this should be seen as a complementary selection force to natural selection which reflects adaptations to the physical (natural) environment (Nesse, 2007). Sexual selection is a specific case of social selection, and some group-level traits may be the result of this selection force. Sexually selected traits evolve because they increase the chances of an organism finding a sexual mate or being chosen as a mate. For instance, some conspicuous group behaviours such as public generosity or the display of humour have been interpreted as sexually selected traits because these acts make individuals more attractive to the opposite sex (Griskevicius, Goldstein, Mortensen, Cialdini, & Kenrick, 2006; Iredale, Van Vugt, & Dunbar, 2008; Miller, 2000).

Most selection models assume that social traits have evolved because they benefit the individual possessing that trait—for instance, empathy enables an individual to assess other people's intentions so that the person can protect himself or herself against possible exploitation. Yet recent theorizing suggests that groupish traits may also have been selected for because they produce benefits to the group to which the individual belongs, thus producing an indirect pay-off to the individual (Caporael, 1997; Wilson et al., 2008). Perhaps empathy evolved in humans not so much to protect against cheaters but to build up cooperative

groups that do better than groups with less empathic members in competing for scarce resources. Darwin was an early proponent of these group selection models and he used group selectionist thinking to account for the evolution of morality:

A tribe including many members who, from possessing [a high degree of] the spirit of patriotism, fidelity, obedience, courage and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.

(Darwin, 1871, p. 203).

After some fierce objection against group selection, evolutionary scientists are increasingly considering it a useful framework for examining human group behaviour although there is an ongoing debate about whether group selection operates on genes, culture or perhaps a combination (Richerson & Boyd, 2006; Wilson et al., 2008). Perhaps the lesson is that for each groupish trait one must look at both the individual and group benefits associated with it, and in many cases there may be multi-level selection forces operating in conjunction. For instance, having a sense of humour may have the function to impress members of the opposite sex (a sexually selected trait) but this trait may have evolved originally because of its function in fostering group cohesion (Gervais & Wilson, 2005).

(3) Evolved Psychological Mechanisms

Group-level adaptations come in many different forms, and many contain physiological, neurological, psychological, and behavioural elements. Adaptive group decision-making is activated by a set of evolved psychological mechanisms that are instantiated in the brain. For instance, human language is a biological adaptation enabling humans to transmit information efficiently. Language requires the presence of both physical structures, such as Broca's area, and psychological mechanisms, such as a theory of mind, that enable humans to communicate effectively. Thus, if humans can talk but chimpanzees (one of our closest living relatives) cannot, it is because these two species differ in their evolved physiology and psychology. (Language may be a group-level adaptation that gave early human groups an edge in the competition for reproductively relevant resources.) Similarly, trust in strangers may be triggered by a psychological mechanism telling us to trust individuals who look familiar. This psychological mechanism might be activated by the secretion of a hormone such as oxytocin which plays a role in forming emotional attachments (De Dreu et al., 2010). The key message is that any group behaviour is regulated by both psychological (emotions, cognitions) and neurophysiological (brain activity, hormones, neurotransmitters) mechanisms that evolved through natural selection.

(4) Automatic "If-Then" Decision Rules

Group-level adaptations can be regarded as a set of heuristics or conditional (if-then) decision rules that are activated in appropriate conditions. Because a

social group is a complex environment it pays for humans to have a broad repertoire of conditional decision rules to make adaptive choices under a variety of conditions. For instance, a conditional decision rule such as “I will only cooperate if my partner cooperates but otherwise I will defect” enables an individual to maximize his or her outcomes in social exchange situations (Axelrod, 1984). Many of these decision rules are likely to be highly automatic, meaning that they require little conscious deliberation to produce adaptive behaviours in a wide range of situations.

(5) Domain Specificity of Mechanisms

Many groupish traits are likely to be domain-specific decision rules. They exist in the form they do because they solved a particular, recurrent group problem in our ancestral environment, such as understanding how to defend the group or climb the group status hierarchy. The primary aim of an evolutionary psychology approach to group dynamics is to identify, analyse, and understand specific adaptive group problems as well as the psychological mechanisms that have evolved to solve them.

For instance, the phenomenon of social exclusion can be described in many different ways—for example, when does it occur and to whom, and what are the consequences for the victims? An evolutionary psychology approach would additionally focus on the different functions of social exclusion in solving adaptive group problems in ancestral environments. This “adaptationist” analysis suggests at least three evolved functions of social exclusion: (1) excluding individuals who are likely to be non-reciprocators; (2) excluding individuals who behave unpredictably, and (3) excluding individuals who constitute a contagion risk or coalitional threat (Kurzban & Leary, 2001). Each of these functions may have a unique underlying psychology which is triggered by different stimuli and which produces different behaviours that can solve the specific problem. For instance, people show aggression towards a free-rider and behavioural avoidance to a person carrying a disease threat (Kerr & Levine, 2008; Van Vugt & Park, 2009).

(6) Adaptations to Past Environments

A sixth assumption is that evolution through natural selection is a painstakingly slow process spanning many generations. The implication is that our evolved group psychology reflects adaptations to past rather than present environments. Because modern humans live in very different environments from their ancestors, some of our evolved psychological mechanisms may not produce behaviours that are currently adaptive. For instance, most of the interactions in ancestral human groups were probably with close kin, and so we may not have evolved psychological machinery that is fine-tuned to interacting with genetic strangers. An implication is that we are more likely to trust strangers if they elicit kinship cues, such as facial resemblance, co-residence, or other “familiar” cues such as

sharing the same surname (Park, Schaller, & Van Vugt, 2008). Thus, it is true that in modern organizations humans still carry around Stone Age brains.

(7) Asking Special Questions

An evolutionary approach to group processes offers a meta-theoretical framework, guided by evolutionary theory, in which a particular group behaviour must be understood at different levels of analysis. From this perspective, it is important to ask four questions about a behaviour, corresponding to (1) its form, (2) its development within individuals, (3) its evolutionary history, and (4) its ultimate functions (Tinbergen, 1963). The first question concerns the proximate causes of a group behaviour, for instance why do people conform to norm X but not to norm Y? Many psychologists are mainly interested in this first level. The second question concerns the developmental (ontogenetic) aspects of a behaviour such as conformity, for instance how do conformity rates vary across the life-time of people, and why is it that adolescents are particularly likely to break societal norms? The third question concerns the evolutionary (phylogenetic) history of a behaviour, for instance do other species also have social norms and are these norms similar or different from those of humans? The answer to this question provides an indication of the origins of a trait (Brosnan, Newton-Fisher, & Van Vugt, 2009). The fourth question concerns the ultimate functions of a behaviour, for instance what might have been the benefits of norm conformity for early humans? The third and fourth question most interest evolutionary-minded group scientists. Ideally one should get answers to each of these questions to draw a complete picture of a particular group behaviour, and this often requires adopting a multi-disciplinary perspective.

(8) Falsifying Evolutionary Theory

Finally, although the theoretical framework we offer is guided by the principles of evolutionary theory, evolutionary-minded group researchers are not seeking to test evolutionary theory per se, because evolution and natural selection are scientific facts. What they are testing are specific predictions derived from hypotheses generated by middle-level evolutionary theories (Buss, 1995). For instance, the theory of indirect reciprocity suggests that individuals cooperate in large groups because doing so benefits their reputations (Nowak, 2006). A hypothesis that follows is that when people's actions are public they will cooperate more. This produces the specific prediction that when people know that they are being watched by another person they become more generous. This prediction has received substantial support in both the laboratory and field (Bateson, Nettle, & Roberts, 2006; Hardy & Van Vugt, 2006). Thus, while evolutionary theory offers a framework that enables researchers to generate new hypotheses and predictions, falsifying them does not cast doubt on the validity of evolutionary theory per se.

METHODOLOGICAL APPROACHES TO STUDYING GROUPS FROM AN EVOLUTIONARY PERSPECTIVE

Evolutionary psychology represents an enormously diverse set of theories, methods, and analytical perspectives (Gangestad & Simpson, 2007; Schaller, Simpson, & Kenrick, 2006; Scher & Rauscher, 2003). This conceptual and methodological diversity results, in part, from the fact that evolutionary psychology attracts contributions from scientists with an unusually diverse range of scholarly backgrounds—not just scholars with different kinds of training within psychology, but scholars from biology, primatology, zoology, anthropology, economics, and various other academic disciplines. In addition, this diversity is a functional response to the high evidentiary standards that are applied to theories and hypotheses in evolutionary psychology (Conway & Schaller, 2002). Truly convincing support for an evolutionary hypothesis about some aspect of group psychology needs not only to document the existence of the predicted psychological phenomenon, but also needs to provide evidence for the alleged evolutionary origins of that phenomenon. The first part is relatively easy. The second part is hard.

It is exceedingly difficult to collect behavioural data in ancestral environments or to empirically track the actual evolution of an alleged psychological adaptation. Instead, evolutionary psychologists must rely on a multitude of other, more indirect sources of evidence to build a nomological network of findings and inter-relate these findings to offer support for an evolutionary hypothesis (Schmitt & Pilcher, 2004).

Evolutionary psychologists frequently begin with general theories—often from the core principles of evolutionary biology—that guide their attention toward potential psychological adaptations. Common theories used by evolutionary psychologists include inclusive fitness theory, parental investment theory, life-history theory, costly signalling theory, and evolutionary game theory. If a hypothesized group adaptation flows directly from a general evolutionary theory, then evolutionary psychologists feel a degree of confidence in the existence of a group-level adaptation. For example, differences in parental investment lead to the hypotheses that men signal their ability to acquire resources to women through public acts of generosity and that women find generous men sexually more attractive (Iredale et al., 2008).

Evolutionary psychologists sometimes apply computer simulations to study the evolution of group processes. In these simulations agents that reflect particular social strategies (such as a cooperative or defective strategy) interact with each other and their fitness outcomes are examined to see if particular patterns emerge over time. For instance, simulation studies show that stable levels of cooperation can evolve in even large groups as long as agents can keep track of the past interactions of other agents (image scoring; Nowak, 2006). Game theory models can be helpful in identifying the conditions under which certain group traits evolve, especially when they are competing with alternative traits. For instance, the Prisoner's Dilemma Game has been used to model the

evolution of cooperation. This model makes clear that mutual defection is the unique equilibrium in a one-shot play—which is the outcome most likely to emerge empirically. Only by making additional assumptions, such as repeated play between the same actors, is there an opportunity for the evolution of cooperation—for instance, through Tit-for-Tat (Axelrod, 1984).

Experimental methods of behavioural economics and social psychology are also increasingly used to find evidence for social adaptations. These methods are used to study interactions between players in games such as the Prisoner's Dilemma Game, the Ultimatum Game, the Dictator Game, and the Public Good Game in which players allocate resources. These methods have produced many interesting findings, for instance by identifying the conditions under which players cooperate with each other to defeat a common outgroup (Van Vugt, De Cremer, & Janssen, 2007).

Methods from experimental cognitive psychology are also often used by evolutionary psychologists to find evidence for social adaptations. For instance, relevant experiments have shown that men typically perform better than women on spatial rotation tasks, whereas women typically perform better than men on spatial memory tasks (Silverman & Eals, 1992). One evolutionary interpretation of this result is that ancestral men—the primary hunters—evolved spatial capacities in order to navigate through an unfamiliar terrain and track moving prey. In contrast, ancestral women—the primary gatherers—evolved memory capacities in order to remember fixed locations where fruits and nuts could be collected.

Psychological surveys can also provide evidence for social adaptations by collecting self-report data about people's experiences in real-world groups. For instance, survey evidence reveals that the most important determinant of people's judgments about ideal group members is their trustworthiness, regardless of the type of group or the nature of the group task (Cottrell, Li, & Neuberg, 2007). This suggests that humans have evolved decision rules to interact with people based upon how much trust they elicit (Simpson, 2007).

Additional evidence for hypothesized group adaptations emerges from recent advances in neuroscience. Brain imaging studies, for instance, have the potential to provide data relevant to specific neural structures associated with group-relevant cognition and behaviour (Adolphs, 1999; Duchaine, Cosmides, & Tooby, 2001). For instance, fMRI research has shown that when people experience social exclusion, there is brain activity in a region that is also activated when people experience physical pain, suggesting that these two kinds of "pain" share the same evolutionary background (Eisenberger, Lieberman, & Williams, 2003). Moreover, hormonal research can help identify the hormonal correlates of particular group-level adaptations, such as the connection between status seeking and testosterone (Josephs, Sellers, Newman, & Metha, 2006).

Behaviour genetics studies may be useful in clarifying whether a particular social adaptation has a substantial genetic component. Generally, when a trait has a low heritability (the degree to which children resemble their parents on this trait) it means that the trait is relatively fixed in a population, which suggests a species-typical biological adaptation. For instance, because every

human is capable of acquiring it, language is a species typical adaptation with low heritability. In contrast, a high heritability index suggests that there may be important individual differences in a trait. This points to the possibility that there has been selection for different versions of the trait in human evolution. For instance, introversion and extraversion are traits with substantial heritable components, and this suggests that they may reflect different evolutionary strategies—e.g., introversion may be functional in stable groups and extraversion in unstable groups (Nettle, 2006).

Anthropological and ethnographic databases can provide additional evidence for an evolutionary hypothesis, testing the extent to which specific kinds of group-relevant phenomena are universal across human cultures. This kind of evidence is necessary to differentiate between phenomena that are evolutionary adaptations and those that are more recent, culture-specific manifestations (Norenzayan, Schaller, & Heine, 2006). For instance, research on Western and Eastern cultures suggests that whereas the tendency for positive self-regard is universal, the specific way it is expressed differs across cultures (Sedikides, Gaertner, & Toguchi, 2003).

Finally, cross-species evidence is instrumental in testing speculations about the evolutionary history of an alleged social adaptation. Both chimpanzees and humans, for instance, form coalitions to engage in intergroup violence—a finding implying that the underlying psychological mechanisms predate the divergence of chimpanzee and hominid lines from their immediate common ancestor (Brosnan et al., 2009).

When considered together, the findings from these diverse lines of inquiry have produced important insights into the evolutionary bases of group processes. Although no single finding tells a definitive story about the evolutionary significance of any specific group behaviour, together they point to the existence of a number of specialized mechanisms for dealing with the key challenges of group life.

KEY ADAPTIVE PROBLEMS OF GROUP LIFE

What were the key adaptive challenges that early humans faced living in groups, and what mechanisms could have evolved to solve these? Based on the literature, we identify six critical group challenges:

1. coordinating group activities (coordination);
2. exchanging resources (social exchange);
3. negotiating group hierarchies (status);
4. keeping groups together (group cohesion);
5. making collective decisions (collective decision-making); and
6. interacting with members of outgroups (intergroup relations).

This list is neither exhaustive nor mutually exclusive yet it is a good starting point for building an adaptationist framework for analysing group processes.

Furthermore, the list corresponds closely to the core themes of group dynamics identified in textbooks such as Forsyth's *Group Dynamics* (2010).

Each adaptive group challenge contains a subset of different problems that all need to be solved to produce a good outcome. For example, coordinating a group activity, such as moving the group from one location to another, requires identifying an appropriate location to move to, deciding when to move and for how long, assessing which individuals possess the specific leadership expertise for the task, motivating individuals to follow, keeping the group together while on the move, replacing ineffective leaders, and setting up contingency plans (Van Vugt et al., 2008).

None of these adaptive group challenges has been fully analysed using an evolutionary framework. Yet various research programs have contributed to developing such analyses by providing evidence for evolved psychological mechanisms that address a particular group challenge. The promise of an evolutionary science of group dynamics lies in the generativity and productivity of this approach in formulating novel hypotheses and providing supportive empirical evidence. To date not many group-level adaptations have been explored fully in terms of their form, function, phylogeny, and ontogeny. In the remainder of the chapter, we offer an illustrative set of findings of evolutionary inspired research programs for each of these core group challenges.

(1) Coordination

As a nomadic group living species, early humans would have had to solve problems associated with coordinating their activities with other individuals in sometimes very large groups. For instance, when moving they would have had to decide where to move to and when and for how long to stay there. It would have been potentially lethal for them to stay in one place for too long. To solve this would have required specialized mechanisms for identifying situations as requiring coordination, developing rules for how to achieve coordination (e.g., turn-taking, leadership), and then carrying it out.

Leadership and Followership One evolved mechanism that has recently been identified as facilitating social coordination is leadership and followership. There are multiple indications that leadership might be a social adaptation. Game-theory models show that leadership—where one individual takes the initiative and others follow—is a powerful solution in coordination games. Consider for instance, Pat and James, who are thirsty and must find a water hole. They must stay together as a form of protection, but how do they decide which waterhole to go to? In such cases it is adaptive for one individual to take the initiative to go to a particular water hole, which leaves the other no option but to follow. Coordinating on the same water hole is the equilibrium solution to this game, which suggests at least the possibility that leadership and followership are evolved strategies (Van Vugt, Hogan, & Kaiser, 2008).

An implication is that leadership–followership interaction emerges

spontaneously and does not require much brain power to achieve. The emergence of leadership has been documented across many different animal species that face functionally important coordination problems, including teaching in ants, selecting foraging sites in honey bees (the famous waggle dance performed by scout bees), movement in stickleback fish, and peace-keeping in nonhuman primates (King, Johnson, & Van Vugt, 2009). Among human beings, similar kinds of coordination problems also result in the emergence of leader–follower relations. This occurs quickly and spontaneously across many different situations and cultures, suggesting adaptation (Brown, 1991).

Of course, the exact leadership structure varies across situations and cultures, and there is evidence for both highly democratic and highly despotic leadership structures in humans (Bass, 1990). They likely represent different adaptive solutions to different local group conditions—for instance, dictatorial leadership might have emerged initially in response to an immediate external crisis that required quick and decisive action (Van Vugt, 2009).

There is ample evidence that leadership emergence is more likely among individuals with a predisposition to take initiatives, for example, because they have extraverted, assertive, ambitious, energetic, or dominant personalities (Bass, 1990). Because many such traits have a moderately strong heritable component, it suggests that the evolutionary reason why there are individual differences in such traits is because they help individuals solve coordination problems (Nettle, 2006; Van Vugt, 2006).

The underlying evolutionary logic of leadership also yields hypotheses about the psychological mechanisms underlying followership and leader emergence. An evolutionary approach hypothesizes that humans possess specialized mechanisms for identifying people who are most appropriate for solving a given adaptive problem such as warfare or peacekeeping between groups. Recent studies suggest that warfare elicits a masculine leader prototype, whereas peace elicits a feminine leader prototype (Little, Burris, Jones, & Roberts, 2007; Van Vugt & Spisak, 2008; cf. Lord, DeVader, & Alliger, 1986).

Transactive Memory Another coordination device that may have evolved to support group coordination is a transactive memory system which enhances the capacity of groups to store and quickly access information by dividing cognitive tasks among group members. Cognitive cooperation is common in social insects and one famous example is the waggle dance of the honey bee, a group decision making device for selecting foraging sites (Seeley, 1995). Research on humans also suggests that members working in the same group often specialize in different areas and group members are very quick at recognizing and using each other's expertise (Littlepage, Hollingshead, Drake, & Littlepage, 2008). People who are expert in a particular domain not only have more information on a given topic but they are also the ones who are responsible for storing new information in their area of expertise. A set of experiments showed that teams performed better on a group task to the extent that the team members divided their cognitive tasks more efficiently. Furthermore, members of teams with

better transactive memory systems also trusted each other's expertise more (Moreland, Argote & Krishnan, 1996). Not surprising, considering that—especially at more complex cognitive tasks—groups outperform individuals (Wilson, Timmel, & Miller, 2004).

Mimicry and Behavioural Synchrony Another evolved mechanism for social coordination is mimicry whereby individuals imitate each other in terms of their actions, expressions, or postures. Mimicry is a highly automated process—it is sometimes referred to as the chameleon effect (Bargh & Chartrand, 1999)—and its main function is to smooth coordination between interaction partners. Mimicry is possible in humans because of the evolution of sophisticated cognitive capacities such as theory of mind and empathy that likely emerged late in human evolution (around 50,000 years ago). Research suggests that mimicry and other forms of behavioural synchrony (such as making the same moves while dancing) increases people's liking for each other and their willingness to share: If people are being mimicked they become more generous (Van Baaren, Holland, Kawakami, & van Knippenberg, 2004). Finally, synchrony of emotions, both positive and negative, facilitates group performance.

(2) Social Exchange

Social exchange—cooperation for mutual benefit—is a pervasive and cross-culturally universal feature of human group life. Exchanging vital resources with others is fundamental for any gregarious species, yet humans are unique in being able to establish large-scale cooperation with genetically-unrelated individuals.

Cheater Detection Evolutionary models suggest that for social exchanges with non-kin members to persist stably, individuals must be able to detect "cheaters" who do not reciprocate resources (Axelrod, 1984; Trivers, 1971). Cosmides (1989) argued that humans have an evolved cognitive mechanism specialized for cheater detection. A brain-imaging study with a patient who had bilateral limbic system damage provided some evidence for this thesis. Using the Wason's four-card selection task paradigm, Stone, Cosmides, Tooby, Kroll, and Knight (2002) showed that, compared to normal controls, the patient's performance was impaired only when the logical reasoning task was framed as detecting violators of social contracts. The performance remained intact when the task was framed as detecting violators of non-contractual rules. This dissociation suggests that cheating (violations of social contracts) may be processed separately from other types of social violations by our brains.

Cooperation Norms Human collective action is often governed by a norm of "conditional cooperation" (Fehr & Fischbacher, 2004). This norm dictates that an individual should cooperate if other group members cooperate, whereas he or she is allowed to not cooperate if the others defect. Fischbacher, Gächter,

and Fehr (2001) examined participant's willingness to contribute in a one-shot public-goods experiment as a function of the average contribution of the other group members. Despite the economic incentives to free-ride (contribute nothing), 50% of the participants matched their contributions with the average contribution of other members. Furthermore, when participants simply observed the interaction of two players in a Prisoner's Dilemma Game, they spent their own endowment to punish players who defected unilaterally but not players who defected bilaterally (Fehr & Fischbacher, 2004). This pattern indicates that the norm of conditional cooperation ("unilateral defection is not acceptable"; Axelrod, 1984) is enforced by neutral observers ("third parties").

The evolutionary perspective suggests a novel hypothesis about the psychological mechanisms underlying enforcement of cooperation norms. Given that exchanges of valuable resources occur mainly within ingroups, violation of cooperation norms should be more serious to one's survival if committed by another ingroup member than if committed by an outgroup member. If so, then non-cooperative behaviour by ingroup members should be punished more severely than non-cooperative behaviour by outgroup members. Using the third-party punishment paradigm, Shinada, Yamagishi, and Ohmura (2004) confirmed this prediction. Such selective sanctioning includes not only physical punishment but also social exclusion, collectively denying the violator's access to interpersonal relations in a group. Research reveals that interpersonal exclusion can provoke strong negative emotional responses in the targeted individuals, including intense anger, pain and depression (Eisenberger et al., 2003). People are highly sensitive to interpersonal exclusion because of its adaptive significance (Kerr & Levine, 2008; Van Vugt & Park, 2009).

Distribution Norms Distribution norms refer to a set of shared beliefs that prescribes how resources should be distributed among group members. Evidence suggests that motives for egalitarian sharing often operate strongly in resource distribution (Fehr & Schmidt, 1999; Kameda, Takezawa, Ohtsubo, & Hastie, 2010). For example, results from numerous one-shot Ultimatum Game experiments indicate that modal offers by a proposer for a responder's share are around 40–50% and that offers in this range are rarely rejected (Camerer, 2003). Although there are some cultural differences, extremely small offers (1–10%) are rarely seen in ultimatum bargaining experiments conducted in a wide range of societies including primordial as well as industrialized ones (Henrich, Boyd, Bowles, Gintis, & Fehr, 2004).

Indeed, egalitarian sharing of hunted meat constitutes a core feature of hunter-gatherer life. Compared to collected resources (e.g., cassava), hunted meat is often the target of communal sharing. Kaplan and Hill (1985) argued that the sharing system functions as a collective risk-reduction device. While acquisition of collected resources is relatively stable and dependable, acquisition of meat is a highly variable, uncertain event. By including many individuals in the sharing group, the variance in meat supply decreases exponentially (Gurven, 2004). Kameda, Takezawa, and Hastie (2003) conducted a series of

evolutionary computer simulations to test the robustness of communal sharing as a risk-pooling system. They argued that free-riders who enjoy sharing of meat that other members have acquired but refuse to share their own acquisitions can potentially destroy the egalitarian-sharing system, which is a public good (“social insurance”) sustained only by members’ cooperation. Surprisingly, the simulation results showed that egalitarian sharing norm can evolve robustly under uncertainty while overcoming the free-rider problem. This implies that our minds are built to be highly sensitive to cues of uncertainty in resource acquisition. Kameda, Takezawa, Tindale, and Smith (2002) showed that such uncertainty cues promoted people’s willingness to share with others beyond their personal distributive ideologies.

(3) Status

Our ancestors lived in increasingly large and complex social groups over evolutionary time and as a result there would have been intense competition for scarce resources such as food, water, and sexual mates (Dunbar, 2004). This competition paved the way for the emergence of status hierarchies whereby people’s status would determine their access to reproductively relevant resources. To negotiate one’s position in the group hierarchy would require specialized mechanisms for assessing one’s relative status as well as mechanisms for climbing the group hierarchy and for maintaining a high status position (once obtained).

Status Signalling Humans have likely evolved a set of adaptations to signal their relative status to others. For instance, they display non-verbal signals such as a firm handshake or a poised posture to let others know that they hold a high status position and deserve respect. High status individuals also walk faster (Schmitt & Atzwanger, 1995) and are more likely to tell other people what to do (Forsyth, 2010). When people seek status they speak clearly and loudly, take more initiatives in conversations, and focus attention on their personal achievements. Just like their primate cousins, high status humans have attention holding power, meaning that they are the focus of attention in groups (Keltner, Gruenfeld, & Anderson, 2000). Along with other primates humans also have differentiated behavioural patterns for interacting with other individuals of higher or lower status than they possess. High status competitors are treated with respect, whereas low status competitors are treated in submissive ways (Brosnan et al., 2009).

Status Emotions Humans have also likely evolved a set of specific status-related emotions. When people experience a status gain—for example, winning an award—they tend to feel pride, and when they experience a loss in status—for example, making a stupid remark—they tend to feel shame (Tracy & Robbins, 2004). Similarly people can feel a vicarious sense of pride or shame when the group or team that they identify with experiences a status gain or loss—for example winning or losing a sports competition. Such emotional experiences

are likely to be accompanied by hormonal fluctuations in testosterone, a physiological status marker. In a study with chess players, the winners experienced an increase in testosterone whereas the losers experienced a decrease (Mazur, Booth, & Dabbs, 1992).

Self-Esteem Humans are also likely to have evolved mechanisms for monitoring their status position, and self-esteem may be an internal gauge of an individual's relative status. When people feel valued by their peers their self-esteem goes up, and when they feel devalued or ostracized their self-esteem goes down (Williams, 2009). Self-esteem likely functions as a "sociometer" that monitors people's standing in a group and motivates action when people feel their status is being threatened (Leary, 1999). When people find themselves in a low status position without having the resources to climb the hierarchy, they may become depressed. Depression can be thought of as an adaptive response to avoid status competitions with peers.

From an evolutionary perspective it would be useful to draw a distinction between different forms of self-esteem which reflect different status problems (Kirkpatrick & Ellis, 2004). For example, concerns about one's standing as a potential sexual mate might be quite independent from concerns about being a respected group member or concerns about the standing of one's group (cf. individual vs. collective self-esteem).

Competitive Altruism It has been suggested that humans are helpful toward each other because by doing so they receive status benefits. This phenomenon is called competitive altruism (Hardy & Van Vugt, 2006; Roberts, 1998). Experimental research suggests that generous individuals receive more status than nongenerous individuals and are preferred as group leaders (Hardy & Van Vugt, 2006). Computer simulations show that when agents can freely interact with each other and each individual gets a status score (an image score)—which indicates whether he or she cooperated or defected in previous interactions—cooperation becomes the norm (Nowak, 2006). Evidence for competitive altruism has been found in several other primate species as well (Brosnan et al., 2009).

Competitive altruism requires psychological mechanisms for monitoring one's relative status and mechanisms for improving it. Research suggests that when people think they are being watched by others (i.e., their status is being assessed), they become more generous (Bateson, 2006; Hardy & Van Vugt, 2006)—even a pair of eyes on the computer screen makes people behave more generously (Haley & Fessler, 2005). In addition, status concerns an increase people's willingness to preserve the environment and engage in bystander helping (Griskevicius et al., 2010). Men become especially generous when they are being observed by an attractive female (Iredale et al., 2008).

(4) Group Cohesion

No doubt one of the main problems for ancestral human groups was to maintain cohesion (Dunbar, 2004). Cohesion has been defined as "the resultant of all

the forces acting on people to remain in their group" (Festinger, 1950). In light of the importance of staying together as a unit in a hostile savannah environment, our ancestors (as well as other social species) had to evolve mechanisms to preserve social cohesion. Furthermore, as human social networks increased in size over the course of human evolution, we would expect these bonding mechanisms to have become increasingly sophisticated. To maintain group cohesion would require specialized mechanisms to recognize oneself and others as belonging to the same group as well as mechanisms to feel emotionally connected with others in increasingly large groups. Here we discuss a few such adaptive mechanisms.

Social Identity Thinking of people who are not necessarily around all the time as belonging to the same group as you requires the capacity for symbolic thought whereby symbols such as language or rituals become markers of shared group membership. A symbolic social identity allowed our ancestors to connect with a large network of individuals who were spread around a particular area, and this may have been quite helpful in sharing resources as well as in competing with other groups. Research shows that human social identity is highly group based and that people spontaneously make us vs. them categorizations (Tajfel & Turner, 1979). Groups with highly identifying members are also more cohesive (Jetten, Spears, & Manstead, 1996).

Preserving group cohesion also requires a sense of group loyalty whereby individuals are prepared to forego attractive alternatives in favour of staying with their current group. A sense of loyalty is deeply ingrained in human psychology. When individuals highly identify with a group, they develop strong feelings of group loyalty which increases the attractiveness of their group membership relative to alternative memberships (Van Vugt & Hart, 2004).

Religion, Music, Dance and Laughter Humans have many specialized behavioural mechanisms for fostering group cohesion, which may have deep evolutionary roots. Religion, for instance, is an effective method to promote cohesion between strangers and mobilize them for joint action on behalf of a group (Atran, 2002). Similarly, dance and music may have ancient roots. According to evolutionary anthropologists dance and music may have evolved as adaptations for connecting large networks of genetic strangers (Dunbar, 2004). Another possible evolved mechanism for fostering group cohesion is laughter. Laughter is a highly automatic and contagious phenomenon that quickly spreads positive emotions through a crowd. It is known to increase endorphine level and promote trust among strangers (Dunbar, Van Leeuwen, & Van Vugt, 2011).

(5) Group Decision Making

Utilizing group members' various cognitive as well as physical resources efficiently by careful coordination is a core feature of group life, supported by the language faculty. Group decision making is a good example of such coordination.

Animal Group Decision Making Recent evidence in behavioural ecology suggests that “group decision making” is not exclusively human (Conradt & List, 2009). Seeley (1995) provides a review of honey-bee “group decision making.” In late spring or early summer when a colony of bees divides to find a new nest, several hundred bees fly out as “scouts” to inspect potential nest sites. Upon returning to the current nest, these scout bees perform waggle dances to advertise any good sites they have discovered and their locations; the duration of the dance depends on the scouts’ perception of the site’s quality (the better the site, the longer the dance). Because other bees are more likely to visit and inspect the sites advertised by scout bees, high-quality sites receive more subsequent visits and advertisements. Such a positive feedback loop eventually leads to a “group consensus” about the best site.

Although honey-bee “group decision making” may look more like an automated self-organization than a deliberate coordination, the social-aggregation processes (advertising a favourable site through waggle dances to recruit more fellow searchers) are in fact highly coordinated. Even though honey bees do not rely on language or formal voting for aggregation, they can achieve a group-level “consensus” efficiently. And, most importantly, the bees usually can choose the best site, a phenomenon called the “wisdom of the hive” (Seeley, 1995). Evidently, some well-structured social-coordination mechanisms that yield collective wisdom are an outcome of natural selection.

Despotism vs. Democracy What is the key evolved decisional structure that enables collective wisdom in honey bees and in some other animals? Conradt and Roper (2003) compared two contrasting structures, “despotism” and “democracy”, in the animal kingdom (cf. Van Vugt, 2009). Using a stochastic model, they showed that democratic decisions usually yield better fitness outcomes to group members than despotism—even when the despot is the most experienced group member, it pays other members to accept the despot’s decision only when group size is small and the difference between their own and the despot’s information is large. Conradt and Roper (2003) argued that democratic decisions are more beneficial “primarily because they tend to produce less extreme decisions, rather than because each individual has an influence on the decision per se” (p. 155).

Hastie and Kameda (2005) extended these ideas to human group decision making. Most naturally occurring environments for humans as well as animals are characterized by large statistical uncertainties. These uncertainties affect many key decisions, including choice of foraging/nest sites, choice of travel routes, monitoring of predators, and so on (Kameda & Nakanishi, 2002, 2003). Given that no single individual (despot) can handle these uncertainties alone even though he/she is highly experienced, the more viable and reliable (“less extreme”, Conradt & Roper, 2003) decisional structure in the long run is to use groups as an aggregation device. By aggregating members’ opinions, random errors in individual perceptions under uncertainty are cancelled collectively, as implied by the law of large numbers in statistics (Surowiecki, 2004). Hastie and

Kameda (2005) compared several decision rules, which differed in computational loads, in terms of their net efficiencies under uncertainty. These included the Best Member (“despotism”) rule and the Majority/Plurality (“democracy”) rule. Results from both computer simulations and laboratory experiments showed that the Majority/Plurality rule fared quite well, performing at levels comparable to much more computationally-taxing rules. Furthermore, the Majority/Plurality rule outperformed the despotic Best Member rule, even when members were not forced to cooperate for group endeavour and free-riding was possible (Kameda, Tsukasaki, Hastie, & Berg, 2011).

The Robust Beauty of Majority Rules These results indicate that, despite its computational simplicity, the Majority/Plurality rule can achieve surprisingly high levels of performance. Such observations may explain the popularity of the Majority/Plurality rule across the full spectrum of human groups from hunter-gatherer and tribal societies (Boehm, 1996) to modern industrial democracies (Davis, 1973; Devine, Clayton, Dunford, Sneyd, & Pryce, 2001; Kerr & Tindale, 2004), as well as the animal cases in which democratic decisions are often more beneficial than despotism (Conradt & List, 2009; Conradt & Roper, 2003). Of course, phylogenetically, humans are quite distantly related to honey-bees and other “lower” species. Yet, the striking similarities in decision styles between the two most social species on the earth suggest that humans and honey-bees have evolved structurally similar group aggregation mechanisms (i.e., utilizing the law of large numbers) to solve similar adaptive problems (e.g., foraging). Dealing with uncertainty is the key challenge underlying the evolution and use of these mechanisms.

(6) Intergroup Relations

A final problem that our ancestors faced was how to deal with members of other groups. As population densities increased in human evolution so did the competition for scarce resources, and early human groups increasingly came into contact with members of rival groups. On the one hand, relations with outgroups provided opportunities for sharing resources such as food, mates, and information. On the other hand, intergroup relations could be a source of tension and conflict over scarce resources. As a consequence, humans likely possess highly specialized mechanisms that enable them to reap the benefits of intergroup relations while avoiding the costs.

Fear of Strangers As part of this evolved intergroup psychology, humans are relatively suspicious and even fearful of strangers. Fear of strangers is an innate response which is seen among young children. Fear is strongest toward outgroup males presumably because they constituted a considerable physical threat in ancestral times (McDonald, Navarrete, & Van Vugt, 2012). Outgroups not only posed a significant physical threat in ancestral environments but also a disease threat (think of the spread of contagious diseases). Hence, fear of

strangers might also serve the function of avoiding pathogens. A recent study showed that ethnocentrism is strongest among women who are in the early stage of pregnancy presumably because they (and their foetus) are most at risk of catching a disease (Navarrete, Fessler, & Eng, 2007).

Intergroup Aggression and Warfare An adaptive solution to intergroup competition is engaging in organized violence against members of outgroups. Intergroup aggression is common in humans, and it also found in other primates, including chimpanzees (Brosnan et al., 2009). Humans and chimpanzees use coalitional aggression to gain access to reproductively relevant resources such as territories and sexual mates. In both species such coalitions usually consist of males, arguably because males have more to gain from participating in intergroup conflict—what has been dubbed the “male warrior hypothesis” (Van Vugt, 2009). Research on the male warrior hypothesis shows that men are more “tribal” than women: They are more aggressive in intergroup encounters and have a stronger inclination to infrathumanize outgroup members. Men are also more likely to make sacrifices on behalf of their group during intergroup conflict (Van Vugt et al., 2007). Consistent with the male warrior hypothesis, a recent study suggests that physically formidable men have a stronger preference for intergroup aggression and warfare than do less formidable men (Sell, Cosmides, & Tooby, 2009).

Peacemaking and Reconciliation In past environments intergroup relations also provided opportunities for trading, and so it is likely that humans also evolved mechanisms for engaging in peaceful interactions with outgroups provided that they did not pose a physical or disease threat. For instance, members of high status groups readily offer help to members of low status outgroups when intergroup helping reaffirms the status difference between the groups (dependency vs. autonomy helping: Nadler, 2002). People also tend to be more forgiving of moral transgressions from outgroup members than ingroup members. Finally, even after a lethal intergroup conflict such as the Rwandan genocide, reconciliation efforts between the groups seem to bear fruit (Paluck, 2009). From an evolutionary perspective, we expect that women have a particularly important role in peacekeeping between groups because they are less tribal and possess superior empathic skills (Van Vugt, 2006).

THE PROMISE OF AN EVOLUTIONARY SCIENCE OF GROUP DYNAMICS

An evolutionary approach to group dynamics can be fruitful in at least four different ways. First, an evolutionary perspective can provide a more complete understanding of particular group processes by asking fundamental questions about the functions, origins and evolution of these phenomena. A more complete account inevitably follows from rigorous attempts to establish conceptual linkages between evolutionary processes operating on ancestral populations and psychological processes operating within contemporary groups.

Second, an evolutionary perspective can help overcome biases and blind spots in the study of groups. It strikes us as odd that the social psychological literature on group decision-making often focuses on what is wrong with groups, disregarding the fact that the group is the natural environment for humans (Caporael, 1997; Wilson et al., 2008). Examples include research on groupthink, brainstorming, group polarization, and information sharing. A cursory reading of these literatures all too easily suggests that people are poor collective decision-makers (Wilson et al., 2008). Any such conclusion, however, is inaccurate (or, at the very least, overly simplistic), and we believe that an evolutionary perspective can produce more sophisticated and accurate conclusions about group decision-making (Kameda & Tindale, 2006).

Third, an evolutionary approach is useful in yielding novel hypotheses about traditional group phenomena. For example, Kenrick, Griskevicius, and colleagues have applied evolutionary reasoning to produce a number of new hypotheses about group phenomena such as status, conformity, and social influence that are unlikely to have been stimulated by other theoretical frameworks (Griskevicius et al., 2007; Kenrick, Li, & Butner, 2003; Sundie, Cialdini, Griskevicius, & Kenrick, 2006).

Finally, an evolutionary approach can expand the boundaries of scientific inquiry on group dynamics by suggesting important group phenomena that have previously received little if any attention from group researchers. Laughter, language, gossip, dance, music, sports, culture, and religion are increasingly being understood as group-level adaptations, that is, as manifestations of psychological processes that connect individuals to each other in large and diverse groups, and these insights have benefited from evolutionarily-informed inquiry (Atran & Norenzayan, 2004; Dunbar, 2004; Van Vugt & Schaller, 2008).

In short, an evolutionary perspective reinforces our awareness that group dynamics are fundamental to the study of human nature. Furthermore, it provides a set of conceptual and empirical tools that can be used to understand and describe group processes more completely and accurately.

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