For the good of the group? Exploring group-level evolutionary adaptations using Multilevel Selection Theory

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Abstract

In this paper, we present an evolutionary framework, Multilevel Selection Theory (MLS), that is highly amenable to existing social psychological theory and empiricism. MLS provides an interpretation of natural selection that shows how group-beneficial traits can evolve, a prevalent implication of social psychological data. We outline the theory and provide a number of example topics, focusing upon prosociality, policing behavior, gossip, brainstorming, distributed cognition, and social identity. We also show that individual differences can produce important group-level outcomes depending on differential aggregation of individual types and relate this to the evolutionary dynamics underlying group traits. Drawing on existing work, we show how social psychologists can integrate this framework into their research program and we suggest future directions for research.

Keywords: evolution, natural selection, altruism, multilevel selection theory, group selection

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Humans are social animals. It may seem a trite observation, but acknowledging that statement has important implications for how we go about trying to study and understand human behavior. Firstly, it stresses that humans are subject to the biological laws as much as any other organism. Humans evolved from a more ape-like ancestor, shaped by the various selective pressures that came to bear upon our ancestors. Those of us here today owe that fact to the better adapted natures of our ancestors. The second implication, which is the central focus of this manuscript, is that humans operate in groups. Generally, we grow up in families, we have friends and work colleagues, we are members of churches or protest groups or hobby groups, we live in neighborhoods, retire to community homes and may even be laid to rest in groups. It is common in manuscripts focusing on an evolutionary perspective to stress the selective pressures for individuals to be adapted to survive and reproduce, but for humans, as for other social species, living in a group presents an additional means to tackle this problem. Individuals can work together as a group to face the challenges of life.

In this paper we give consideration to an evolutionary framework, Multilevel Selection Theory (MLS, Sober & Wilson, 1998), which offers a bridge between the social psychological and the evolutionary levels, linking the immediate (proximate) psychological mechanisms that produce group-beneficial behavior and the evolutionary (ultimate) reasons for their existence. We explain how MLS integrates with issues that interest social psychologists, outline the key relevant concepts, and review existing use of MLS in social psychology for topics such as personality, prosociality, brainstorming, transactive memory, social exclusion, and social identity.

Group-level adaptations from an evolutionary perspective

MLS posits that natural selection operates at different levels of biological organization. At the lowest level are genes. At higher levels of organization are cells and then organisms. Organisms, in turn, can form groups. In each case, different units within a level function cohesively to maximize fitness (reproductive success) at the higher level. We view chromosomes or cells or even organisms as unified entities because life transitioned long ago from solely comprising of biological organisms organized at the lowest levels (Maynard-Smith & Szathmary, 1995). Just as natural selection produces individuals adapted to their environment, so the same can occur at the group level. To see how this can work, it is important to understand that natural selection simply requires three components to operate: variability in a trait, heritability for that trait, and a relationship between that trait and reproductive success. Ceteris paribus, the trait that is better adapted to the environment will on average out-replicate any alternative variants.

The standard representation of selection is of it acting on individuals, where individuals with one particular trait prove superior to others in some domain that impacts fitness. For example, a trait that enhances an organism's ability to find food will likely spread in the relevant population, depending on other costs (such as metabolic costs), because individuals which possess the trait will be more likely to survive and reproduce, outcompeting rivals and achieving a *relative* fitness advantage (Wilson, 2004). The same process can occur between groups (Sober & Wilson, 1998). Thus, a group of individuals that possess a trait that provides them with a competitive advantage over other groups will tend to translate that into a reproductive advantage, thus resulting in the likely increased presence of the trait in the next generation. Whether it does become more prevalent will depend on factors such as whether others within the group share the trait and how costly the trait is for the actor. Thus, the group-level (between-group) selection must outweigh the individual-level (within-group) selection for a group-beneficial trait to spread.

For example, imagine a hypothetical animal that forages fruit from shrubs. In the area where it lives, there are two types of shrub, one taller than the other. Individuals cannot reach the fruit on the taller shrub alone. There are two types of this fruitivore, of which individuals of one type cooperate by standing beneath the shrub and allowing another to leap on them to reach fruit on the taller shrubs. Which variant is likely to prosper evolutionarily? Well, possibly, the variant that cooperates. Cooperators lose opportunities to forage by allowing others to use them to reach fruit, but groups of such cooperators will gain access to greater amounts of food, raising the benefits all round. If accessing food is critical to survival, then groups with more cooperators will have higher average fitness, though selfish individuals within any such group will have higher fitness again. The balance between the two types will be set by the selection against cooperators within groups versus selection in favor of groups with more cooperators (see Wilson, 2007, for an extended discussion of a related model).

An alternative way to look at the above issues is to see that genes usually have multiple copies in a population and that as long as a particular gene “causes” its carrier organism to behave in a way that increases the copies of that gene, it does not matter if that specific instantiation of a gene is passed on to another generation. Termed *inclusive fitness* (Hamilton, 1964) and popularized as the “selfish gene” approach (Dawkins, 1976), it is fully equivalent to MLS (Hamilton, 1975; West, Griffin, & Gardner, 2007; Wilson, 2008; Wilson & Wilson, 2007). However, in contrast to the gene-centered focus of inclusive fitness, MLS focuses on the phenotypic level (the level on which selection directly acts) and so on *individuals* and *groups*, the level of analysis for social psychologists.

Applying MLS to social psychology

One approach to examine whether a trait contributes to group-level functionality is to partition the adaptive features of various personality dispositions into their within-group and between-group components. For any trait x, thought or known to predict adaptive outcome y, groups of individuals either high or low on the trait might be created (while preserving within-group variability). Within the group setting, participants can then be asked to perform the adaptive task. Depending on the trait of interest, one might specifically place participants into particular groups and set them working together, or, one might let the participants select themselves into groups and let group-members make their own decision about whether to work together. Either way, a zero-order predictive relationship between trait x and outcome y is established. However, we should not stop there or risk committing the *averaging fallacy* (Sober, 1984): averaging across the groups loses important information about the relationship between competing forms of a trait within groups (where interactions actually take place) and the relationship at a metagroup or population level. This issue will be familiar to those who work with multi-level modeling scenarios. Thus, the relationship should be decomposed, via multi-level modeling, into its within and between group components. Considering the balance between these two variance components can reveal much about how various traits work, how much they depend on a group-level component, and how susceptible they are to undermining via free riders within groups.

As a concrete illustration of this research strategy, using constructs familiar to social-personality psychologists, we will briefly consider some work by Sheldon and colleagues. Sheldon and McGregor (2000) assessed participants’ value orientations using Kasser and Ryan’s Aspirations Index (1993, 1996). This measure distinguishes between intrinsic (intimacy, community, personal growth) and extrinsic (money, beauty, popularity) values, and considerable research has shown that those endorsing intrinsic values more strongly than extrinsic values gain emotional and well-being benefits. But do they also gain functional resource benefits, at least in some situations? Sheldon and McGregor tested this idea by creating three types of four-person groups: four extrinsics, four intrinsics, and mixed two intrinsic/two extrinsic groups. Groups engaged in an iterated forest resource dilemma, in which each participant was a timber company making yearly anonymous bids regarding how much timber to cut from a self-replenishing forest. Groups kept bidding until their forest was gone.

As hypothesized, a significant linear association emerged such that intrinsic groups harvested the most, overall, with mixed groups harvesting less and extrinsic groups harvesting still less. That is, “nice groups finished first;” because intrinsic groups were more self-restrained, their forest lasted longer, and their individual members earned more, on average. Intriguingly, however, when group membership was ignored, participants’ scores on the values measure itself did not predict individual harvests. Multi-level modeling indicated that the between-group advantage for those within intrinsic groups was almost completely counter-acted by a within-group vulnerability to free-riding. That is, more extrinsic members of all three groups harvested more within their group than their more intrinsic counterparts, undermining the advantages of intrinsic values. What this means is that the functional benefits of having intrinsic (i.e., cooperative) values depends on what type of group one is embedded within. Critically, biological altruists--individuals who provide fitness benefits to others while incurring fitness costs to themselves--benefit from reducing interactions with free-riders.

This study was instructive because it illustrates how important it can be to separate out the within- and between-group components of a trait. If we had not looked at the group level in the preceding example, we would have thought that values have no relation to social dilemma outcomes, overlooking the important dynamic relation between individuals, values, groups, and social dilemma outcomes. Also, the Sheldon and McGregor research established the conditions under which intrinsics would actually fare better than extrinsics by illustrating that as intrinsic and extrinsic groups become more and more dissimilar, intrinsics gain more and more of an advantage, something that fits with the MLS framework. Finally, the study illustrated that, despite their vulnerability to exploitation, intrinsic participants did no worse in the game than their extrinsic counterparts, because of their group-level advantage. One might as easily say that extrinsic participants were thwarted in their goal of out-profiting the intrinsics, because intrinsic participants were able to benefit from cooperative coalitions. Given a chance to establish within-group communication and develop systems for controlling for extrinsics, as might be the case in temporally extended communities, intrinsics might do even better.

This work illustrates two key points. The first is that group-level selection produces traits that are functional at the group-level but which are likely to be costly at the individual level; that is, biologically altruistic traits. Intrinsics were exploitable by extrinsics but groups of intrinsics outcompeted groups of extrinsics, with a continuum in between. Being nice can work, but the other point to note is that group-selected traits are vulnerable to cheaters, favored at the within-group level. This sets up an arms race between group-level selected and individual-level selected traits. Individuals with selfish traits can exploit group-level traits while this is countered by traits that reduce exploitation. These in turn prompt further selection for psychological capabilities such as the ability to recognize altruists (Brown & Moore, 2000) and cheaters (Cosmides &Tooby, 1992), track others' behavior, a desire for punitive enforcement (Fehr & Gächter, 2002), and a facultative ability to act altruistically. These traits can buttress biological altruism and may have facilitated its evolutionary emergence or been selected as a result of the arms race between individual- and group-level selection.

In this regard, an important limitation of the Sheldon and McGregor (2000) research was that participants were assorted into different groups via experimental assignment. For the intrinsic (cooperative) strategy to work, intrinsic participants would have to be able to assort on their own, excluding the extrinsic participants who would undermine the group. Sheldon, Sheldon, and Osbaldiston (2000) tested this idea by asking participants to draw from their friends and acquaintances to create their own 4-person groups, in order to play a group bidding game with free movie tickets for high scorers. First, both participant and recruited acquaintance values were assessed. A significant intraclass correlation of .17 emerged, indicating that participants did in fact assort by intrinsic (vs. extrinsic) values in the process of forming their groups and suggesting that human altruists aggregate non-randomly.

Sheldon et al. then asked all group members to make bids in an N-person prisoner's dilemma, using a points system in which one could either yield to temptation or rely on the group-level performance in one's quest for movie tickets. The same pattern emerged as in Sheldon and McGregor (2000); although the values measure did not predict game score at a zero-order level, more intrinsic groups scored better than more extrinsic groups, and extrinsic group members scored better, within groups, than intrinsic group members. Intrinsics again mitigated their assumed competitive disadvantage against extrinsics, this time by assorting into groups with other intrinsics. Conversely, extrinsics were undermined by tending to associate with others like themselves, which curtailed their group-level benefits in the study and likely impacts their real-world experiences. Sheldon et al. speculated that given more time to form groups, intrinsics might have had higher assortative levels and reaped even greater benefits.

The conflict between the individual and group levels is no different to what can happen within the body. For example, tumors consist of cells reproducing selfishly at the cost of the organism (the higher-level). Because new mutations are always occurring in evolution, the balance between group- and individual-level selection is likely always shifting. In the case of tumors, the selective advantage of cells functioning cohesively outweighs the gains made by "individualistic" cells. Indeed, the vast majority of multi-celled organisms are so interdependent at the cellular level that tumors very often kill, though this is by no means essential to the theory. Whenever lower-level units have a *shared fate* for specific events—situations where the fitness of units is similarly impacted ('trait-group", Sober & Wilson, 1998)—then group-level selection pressures can occur. Of course, if the group-beneficial trait is not costly at the individual level (no within-group selection) then there is no conflict between levels of selection.

Group-level adaptations

Now that we have outlined the fundamentals of MLS, we can begin to address the question of what kinds of group-level traits might exist in human psychology; that is, for what sorts of psychological mechanisms might have between-group selection been stronger than within-group selection? It is at this point worth noting that the within/between group decomposition research strategy, just described, might be applied to other personality traits. A similar finding was made when Campbell, Bush, Brunell, and Shelton (2005) applied the same kind of modeling approach in an attempt to understand the costs and benefits of trait narcissism. Utilizing a similar "tragedy of the commons" design, they found that narcissists tend to exploit other group-members, accruing personal advantage; however, at the group level their strategy backfired, limiting the benefits of their acquisitive strategy and resulting in a wash, overall. This illustrates why a "society of narcissists" might be an unpleasant group to belong to! Once again, the benefits of being selfish within the group are costly if altruists can exclude you. One could also examine the person-level vs. group-level benefits of various personality traits such as agreeableness, openness, and extraversion. To what extent do these traits yield positive individual outcomes via the contrast between the self and nearby group-members, versus via their contribution to group-level processes that contrast with the performances of other, nearby groups?

Of course, as is well known, humans are highly prosocial and engage in a variety of helping behaviors (Penner et al., 2005), right up to the level of self-sacrificial behavior (Smirnov et al., in press). Some recent work has sought to integrate the psychological literature on prosocial behavior and evolutionary theory (e.g. Penner et al., 2005; Van Vugt & Van Lange, 2006), with a recognition that prosociality is evolutionarily vulnerable leading to a fresh view. Research shows the importance of MLS to understand patterns of prosociality: People tend to be more willing to help those perceived as ingroup than as outgroup (Brewer & Caporael, 2006; Penner et al., 2005; Van Vugt & Hart, 2004). Importantly, prosociality, even one-to-one helping, has its origins in the evolutionarily long-term situation of social living. Indeed, extreme forms such as heroism can impart disproportionate benefits upon the group (Smirnov et al., in press). Recognizing that explicit helping behavior can thrive frees us to consider less obviously altruistic behaviors that nonetheless are group-beneficial.

We already discussed one method for free-riders to be contained, by forming groups with other likeminded individuals. Another method is to regulate group members' behavior by punishing group-harmful behavior. At the genomic and organismal levels, mechanisms exist to constrain cheater genes and cells. And indeed, there is an extensive body of research showing that humans are willing to punish free-riders in public-goods situations (Fehr & Gächter, 2002; Henrich et al., 2006; O'Gorman, Wilson, & Miller, 2005; Wilson & O'Gorman, 2003).

Moreover, it appears that humans will do so, even when the act of punishing is itself costly (Fehr & Gächter, 2002). Such *altruistic punishment* is evoked in controlled lab studies, where participants are anonymous to each other and do not interact more than once with any other participant, avoiding the possibility for reputations to be developed and for signals of future intent (but see Burnham & Johnson, 2005, and Hagen & Hammerstein, 2006).

The function of such punishing behavior appears to be to regulate and police the behavior of other group members to ensure compliance with group interests. Outside the lab setting, such policing may take the form of gossip (Kniffin & Wilson, 2005; Wilson, Wilczynski, Wells, & Weiser, 2000), exclusion and expulsion from groups (Boehm, 1999; Brown, 1991; Spoor & Williams, 2007), and even extending to murder on occasions (Boehm, 1999; Brown, 1991). Although policing takes an institutionalized form in most modern societies, informal sanctioning remains an alternative to legal recourse (Ellickson, 1991) and has been repeatedly documented in non-literate societies (de Waal, 1996; Mahdi, 1986). It is quite likely that humans have been policing themselves for a long time, to the benefit of the group as an adaptive unit.

The power of exclusion is evident from both the reaction people have to negative gossip about them (Ellickson, 1991) and the fear that ostracism can induce (Spoor & Williams, 2007). While gossip consists of a range of functions (Dunbar, 2004) with policing-related content apparently accounting for a small proportion, Kniffin and Wilson (2005) showed that the presence of a free-rider within a group can result in a disproportionate amount of gossip being targeted at the free-rider. However, gossip's power surely lies in the step that it can lead to if no remedy occurs in the target's behavior: With widespread knowledge of apparently wrongful behavior, the group-at-large is able to develop a consensus and coordinate a response, easily imposing some level of exile or expulsion on the target. Spoor and Williams (2007) note the implications of expulsion for survival, and hence, reproduction of expelled individuals. Thus it is not entirely surprising that ostracism can hurt as much as real pain (Eisenberger, Lieberman, & Williams, 2003) although perhaps it is a little surprising that people initially are aversive to being ostracized by groups such as the Ku Klux Klan or from playing a game of "Pass the Bomb" (Spoor & Williams, 2007)! With such a powerful impact on fitness, it is hardly surprising that humans possess a variety of techniques to avoid exclusion (Spoor & Williams, 2007), prompted by the equally unsurprising capability of human groups to use such weapons to rein in otherwise destructive behavior. Gossip therefore serves not just as a warning to free-riders but also as a vital coordinating mechanism for group members by distributing key information, perhaps explaining that urge to gossip that so many of us have experienced!

However, there still remains a group-level decision to be made, involving recognition of the problem, recording transgressions, evaluating the level of punishment and ultimately taking action. Such distributed functioning (Brewer & Caporael, 2006) is not well studied but is a likely result of MLS. One such example is cooperative cognition (Wilson, Timmel, & Miller, 2004). Wilson et al., drawing on MLS, illustrated this with two experiments that pitted groups against individuals. In the initial experiment, they had participants play twenty questions either individually or in a group. This game requires players to determine what topic has been chosen by another individual, of whom the players can ask up to twenty questions which can yield only "yes" or "no" answers. Wilson et al. found that groups performed approximately twice as well as individuals, with the performance discrepancy in favor of groups increasing with harder topics. Wilson et al. followed this up with an experiment in which they manipulated task difficulty, as well as adopting a format that allowed comparison between real and nominal groups. Participants had to come up with as many job titles as possible. The harder version of this task provided seven questions related to jobs that already had been “answered”, thus limiting what jobs could qualify. Real groups outperformed nominal groups on the harder task by 50%.

This result runs contrary to the predominant findings in the brainstorming literature that brainstorming by groups does not work as effectively as nominal groups of individuals brainstorming alone (Mullen, Johnson, & Salas, 1991; Nijstad, Stroebe, & Lodewijkx, 2003). Wilson et al. suggest that, with harder tasks, the advantage of a group tends to emerge. In fact, we can relate this to findings that social loafing decreases with increased task difficulty (Jackson & Williams, 1985) and to the importance of the task, where increased importance of task outcome and self-perceived value of participant contributions enhance engagement (Karau & Williams, 1993). If humans have been members of groups over our hominid evolution and group decision-making has been critical to fitness, then human groups should be effective decision-making machines, but with the caveat that individuals will weigh the value of their contribution against the opportunity to free-ride, with individual differences. High task difficulty or the likelihood of a critical impact on the group should prompt group members to engage with the decision-making process more so than more trivial problems, with the latter offering opportunities to conserve limited time and energy.

This research shows the importance of examining human behavior in the appropriate contextual setting, with relevant task demands. More than this, it suggests that some cognitive functioning may primarily tend to be group-related. Human social behavior is likely to be as fine-tuned as the functioning of our bodies—revealing the mechanisms requires that each feature be studied appropriately. One cannot study the functioning of the circulation system by cutting out a heart. Of course, this is not to suggest that cognitive skills are solely to produce a group-level adaptation; rather, that functionality in individuals may be only part of the story. For social cognition, further research exists that hints at possible group-level functionality. Hutchins (1995), examining cognition "in the wild", has shown the highly coordinated manner in which human groups navigate in such situations as a ship entering harbor, with no one individual centrally coordinating actions. Instead, the outcome results emerge from the team's individual contributions. Liang, Moreland, & Argote (1995) similarly showed that individuals trained together on a task outperformed individuals trained separately, with both enhanced recall of the task and spontaneous specialization for task elements. Such work suggests that humans' aptness for roles may result from selection for group-level functional specialization.

Wegner (1986, 1995), examining "transactive memory"—essentially knowledge distributed across individuals in non-transitory groups—has demonstrated how groups of individuals, such as a relationship-based couple (Wegner, Erber, & Raymond, 1991), can function as a memory unit more effectively than non-familiar equivalent groups. He has also outlined, using an analogy to computer networks, how human groups might operate using distributed cognition (Wegner, 1995). While discussing the analogy without suggesting that groups are *designed* to function as a unit, he does point out that computer networks are designed to achieve such functionality. A framework such as MLS can build on Wegner's work, because while human groups are not attempting to function like computer networks, they may be adapted to be functionally coordinated—to confront the challenges of life. Going further, many cognitive processes such as information acquisition (through perception), evaluation, and inference can be distributed over a group, particularly in the face of ambiguous or anomalous data from the environment (Brewer & Caporael, 2006).

All of this has parallels in other organisms that produce group-functional behavior, such as ants and honey bees. For example, honey bees decide where to move their colony when swarming by scouts returning and performing dances. A decision is reached by an aggregated process in which scouts visiting less desirable destinations stop dancing until the scouts that continue to dance (over a period of time) are all favoring the same site (Seeley & Buhrman, 1999). As a result, a colony can make a decision that is not localized in, nor are all the possible alternative sites experienced by, any one individual. Nor are such processed limited to insect groups, but occur across a range of social animals (Conradt & Roper, 2005). The challenge is in studying appropriately relevant groups in the evolutionarily relevant situations. Indeed, alongside distributed knowledge and roles, a balance of skills may also be an important factor in human group success. Traits such as intelligence (which could be further broken down), physical skills and social skills may be required as a mix to produce maximally effective groups—in long-term groups individuals could afford to specialize in the most appropriate one without necessarily compromises other important attributes such as status.

Underlying all of these processes is an ability to track group memberships, to know, at some cognitive level, who is a part of the task-group to appropriately allocate cognitive resources. This is achieved through social identity, which plays a critical role in knowing who is in our ingroup for any particular event. Both Brewer and Caporael (2006) and Van Vugt and Hart (2004) have emphasized the importance of group identity as a critical form of social glue to unite individuals into higher-level entities. Even a brief conversation within a newly formed group can result in very high cooperation in otherwise anonymous interactions that usually result in little cooperation (Kramer & Brewer, 1984). Someone who is a known member of the group can be trusted by other group members, but this probably necessitates an ongoing display of prosociality toward the group to demonstrate commitment and that one is not exploiting the group. As we have already discussed, there is evidence that individuals with biologically altruistic traits tend to form social networks together. Brewer and Caporael suggest that different types of entities (dyads, task-groups, and larger units they call demes and macrodemes) require different identities and have different functions. Dyads will be units such as parent-child and mating partners; task-groups are larger and focused on specific tasks, which evolutionarily might have been related to foraging, hunting, or security, for example. Demes would perhaps consist of a local community while macrodemes would be the local communities, which would be interrelated and evolutionarily would have shared accent or language, and cultural ties through long-term relationships. Cognitively, these identities have different requirements (Brewer & Caporael, 2006). Dunbar (2003) proposes a similar social structure based on a range of empirical evidence. Importantly, use of social identities should be cut according to the needed cloth and should not be equivalent. Coherent group functioning is essential to successful competition. This may rest on internal harmony, trust and familiarity between group members to optimize behavior, for which group identity plays a crucial role.

Conclusion

There are many areas of social behavior upon which we have not touched in this paper where MLS has relevance, including leadership (Hardy & Van Vugt, 2006), morality and religion (Wilson, 2002), laughter (Van Vugt, Hardy, Stow, & Dunbar, 2007), social norms (O'Gorman, Wilson, & Miller, in press) and culture (Wilson, Van Vugt & O'Gorman, 2007). For each of these topics, there are important group dimensions that may shape how they function at the group level. Wilson (2002) has argued that moral norms and religion provide mechanisms to coordinate group functioning, ensuring that free-riders are controlled. Van Vugt et al. (2007) have shown that laughter can facilitate group bonding, mediated by hormonal changes. Social norms represent a means of reducing within-group behavioral variation, and thus shifting selection primarily to the group level. Meanwhile, culture appears to represent a group-level mechanism for human groups to adapt to environmental challenges (Wilson, Van Vugt & O'Gorman, 2007) and, particularly, changes over time (Richerson & Boyd, 2005). The framework of MLS outlines how different levels of biological organization can contribute differentially to the evolution of a trait and incorporates group-level effects on the fitness of organisms. We do not doubt that there are many other topics in social psychology which could gain from the lens of multi-level selection theory.

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