



Introduction

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Solving the puzzle of collective action through inter-individual differences

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Models of collective action infrequently account for differences across individuals beyond a limited set of strategies, ignoring variation in endowment (e.g. physical condition, wealth, knowledge, personality, support), individual costs of effort, or expected gains from cooperation. However, behavioural research indicates these inter-individual differences can have significant effects on the dynamics of collective action. The papers contributed to this theme issue evaluate how individual differences affect the propensity to cooperate, and how they can catalyse others' likelihood of cooperation (e.g. via leadership). Many of the papers emphasize the relationship between individual decisions and socio-ecological context, particularly the effect of group size. All together, the papers in this theme issue provide a more complete picture of collective action, by embracing the reality of inter-individual variation and its multiple roles in the success or failure of collective action.

1. Introduction

Natural selection frequently results in cooperation, from helping relatives to mutualistic interactions between plants and pollinators to the emergence of higher-level evolutionary units, such as eukaryotic cells, multicellular organisms or social groups [1]. Yet explaining the evolution of cooperation is a challenge. If selection is a competitive process, how can cooperation emerge and stabilize in the presence of a selfish strategy? When cooperators pay costs to produce a collective good, cooperation can be undermined by selfish cells or individuals who under-contribute or over-consume the collective good [2,3]. Examples of such collective action problems span the domains of life and include cancers, reproduction by worker ants and over-harvesting of natural resources by humans.

Darwin conjectured that selection at levels other than the individual could explain cooperation [4,5], anticipating inclusive fitness theory and multi-level selection theory a century later. These and other theories have provided tremendous insight into how organisms solve collective action problems. Cooperative individuals, who tailor their cooperation based on relatedness or reciprocity or threat of punishment, can out-compete non-cooperators under favourable conditions [6–9]. Cooperative strategies can also spread in structured populations via inter-group competition [5,10,11].

In models of collective action, cooperative equilibria sometimes involve inter-individual differences in strategy, but models infrequently account for differences across individuals beyond a limited set of strategies, ignoring variation in endowment (e.g. physical condition, wealth, knowledge, personality, support), individual costs of effort, or expected gains from cooperation. Likewise, experimental economics research on collective action tends to control for inter-individual differences rather than focus on their effects. Participants often are unaware of each other's characteristics, receive equal material endowments and are provided equal financial incentives for their decisions. However, emerging evidence from the field of animal behaviour indicates that inter-individual differences can have significant implications for the dynamics of

collective action. For example, inter-individual differences within groups can generate leader–follower relationships that are integral to successful collective action [12–15].

This theme issue investigates a broad range of inter-individual differences as they relate to the resolution of collective action problems in humans and non-human primates. These inter-individual differences include genetic, neuroendocrine and personality variation, differences in physical, material and social endowment, opportunity costs and anticipated benefits from cooperation. Several of the papers in this issue consider how individual differences affect the propensity to cooperate. Other papers consider how inter-individual differences catalyse others' likelihood of cooperation (e.g. via leadership). Many of the papers emphasize the relationship between individual decisions and socio-ecological context, particularly the effect of group size. In this introduction, we review the papers in this issue which, together, provide a more complete picture of collective action by embracing the reality of inter-individual variation and its multiple roles in the success or failure of collective action.

2. Recent modelling

The idea that inter-individual differences can be critical for solving collective action problems is not new. For example, in the 1960s, Olson [3] and Salisbury [16] described how differences in endowment or anticipated benefits may motivate some individuals to unilaterally provide a collective good. Gintis *et al.* [17] extended Zahavi's ideas on signaling [18] to the context of public goods, in which cooperation is an advertisement of quality to attract better mates and/or allies. However, these concepts have received relatively little formal development in evolutionary biology. Gavrillets [19] reviews and develops models that incorporate Olson's insights. In the context of collective actions against 'nature' (e.g. group foraging) and against other groups (e.g. inter-group warfare), he shows that the largest contributors are those with the largest endowment, who anticipate the largest share of the collective good, or who can contribute at least cost. In some cases, however, the largest contributors end up with smaller net pay-offs. The latter effect, described first for a specific case in Gavrillets & Fortunato [20], appears to be a general property of models with multifarious groups. Greater inter-individual differences boost contributions when there is weak (but not strong) nonlinearity in the benefits and costs of contribution. These theoretical observations have implications for the current debates on the origins of human egalitarian preferences [21,22] and the effects of within-group inequality on cooperation in human groups at different levels [23–25].

Variation in cooperativeness itself can promote matching and successful cooperation, via the evolution of choosiness over cooperative partners [26,27]. McAuliffe *et al.* [28] describe behavioural evidence of positive matching of cooperative contributions in various animal societies, such as in cooperative breeding or joint resource production. This 'cooperative matching' is sometimes facilitated by key individuals. The authors discuss how cooperative matching can be generated via information-seeking on the part of co-contributors, the ability to advertise quality and coercion. They also suggest that more productive models of cooperative matching consider how the costs and benefits to individual contributors are influenced by others' contributions.

3. Genes, hormones and personality

Mutation, selection and developmental processes produce a constant source of individual variation related to cooperativeness, including personality differences. Heritable variation in cooperativeness can arise from fluctuating (including frequency-dependent) selection, mutation–selection balance or as a result of selection for polymorphisms that affect cooperativeness as a by-product, such as in the context of pathogen–host coevolution [29,30]. Another possibility is that cooperativeness may be 'reactively heritable', by developing over ontogeny as an adaptive response to genetic variation in other traits that affect the costs and benefits of cooperativeness [31]. Consistent with the reactive heritability model, a recent human study found that heritable variation in personality traits related to gregarious sociality is explained in part by heritable variation in physical size and skill [32]. However, these latter effects leave much variance unexplained, and the extent to which heritable personality variation is adaptive remains unclear [33].

Dawes *et al.* [34] test the heritability of cooperativeness in humans in terms of civic engagement, using data from a longitudinal twin study. They assess civic engagement based on voting in elections, volunteering for community service and contributing to charitable causes, which all involve an incentive to free-ride on the cooperativeness of others. Civic engagement is moderately heritable in their twin population and correlates with verbal IQ and personality traits related to positive emotionality. Furthermore, they argue that genetic factors largely account for these correlations, which is consistent with models in which variation in cooperativeness results (adaptively or as a by-product) from heritable variation in other traits.

The physiology underlying differences in cooperativeness include endocrine mechanisms. Trumble *et al.* [35] review shared and derived endocrine mechanisms that facilitate the unique levels of cooperation in primates relative to other vertebrates. Intra- and interspecific differences in cooperativeness are shaped by baseline hormone concentrations, binding proteins, and receptor sensitivity and specificity, which all can evolve independently and respond over ontogeny to individuals' condition and socio-ecology. The authors focus on the roles of oxytocin and testosterone in contexts of collective action including pair-bonding, food sharing and territorial defence. Individual differences in these hormones, in part, reflect different adaptive strategies that affect and are affected by contributions to collective action.

How personality affects cooperativeness can depend on the context of cooperation. Schroeder *et al.* [36] argue that reward and punishment institutions modify the associations between personality traits and contributions to a collective good in humans. In public goods experiments, they show that extraversion is associated with a strategic shift from free-riding to cooperation when punishment is possible. This follows from the prediction that extraversion reflects variation in sensitivity to social rewards. They show that agreeableness associates with higher initial contributions independent of opportunity for punishment, and contrary to prediction, neuroticism is unassociated with a shift in cooperation in the presence of punishment. The authors encourage future experiments to simulate the institutions that regulate cooperative behaviour outside the laboratory, and they call for greater attention to how

personality and socio-economic background affect participants' decision-making.

4. Ecology, group size and anticipated benefits

Collective action has received little systematic cross-species comparison. Van Belle & Scarry [37] and Willems *et al.* [38] analyse collective action in the context of communal range defence across non-human primate species. Hooper *et al.* [39] analyse foraging groups in two small-scale human societies. These papers make similar claims that individual decisions to participate in collective action are a function of socio-ecology (including group size) and individual differences in efficiency and anticipated benefits of cooperation.

Van Belle & Scarry [37] observed communal defence in wild black howler (*Alouatta pigra*) and tufted capuchin monkeys (*Sapajus nigritus*). They find that both species rely on assessment of numerical asymmetry in male group size (rather than total group size) when deciding to participate in communal defence. As females of both species participate in communal defence, their motivation may be to catalyse male participation more than increase their group's competitive ability. Participating males can be motivated by mating opportunity in black howlers, though this was not evident in tufted capuchins because many participants were subordinates. While the tufted capuchins increased participation in communal defence with increasing relative male group size, black howlers increased their participation when male group sizes were equal. The authors argue that this variation arises from an absence of dominance relationships among black howler groups, unlike among tufted capuchins, which motivates individuals to closely assess rival groups with matching competitive abilities.

The extent to which communal defence presents a collective action problem depends on species' socio-ecology, including the mating system and foraging range. Willems *et al.* [38] argue that for primates who are cooperative breeders or live in pairs, communal defence is mutualistic. For primates who live in large groups with overlapping foraging ranges, participation in communal defence tends to be variable and can suffer from a collective action problem. Among vervet monkeys (*Chlorocebus*), the authors describe significant variation in communal defence across species, between populations of one species and across individuals. They ascribe this variation to communal defence being structured like a Volunteer's Dilemma, in which the public good is only produced if a minimum number of individuals contribute. Among the vervets they observe, individuals who are most likely to contribute are dominants of either sex, who anticipate greater benefits from communal defence.

Humans show considerable variation in social organization and the scope of collective action, including within the same society. Hooper *et al.* [39] analyse the size, composition and productivity of foraging groups in two small-scale human societies. They attribute variation in group size and composition to the dependence of collective action on three factors: the sexual division of labour, the intergenerational division of labour, and economies of scale in production. They show that individual decisions to join foraging groups are based on the individual's sex and age-based comparative advantage within the particular foraging activity. The authors observe economies of scale for activities that benefit

from complementary roles, such as hunting large game and collecting honey from large stinging bees. The authors propose that a general theory of economic group formation (and individual roles within groups) can account for the size and structure of groups in both small- and large-scale societies with substantially greater economies of scale and economic specialization.

5. Leadership and prestige

Inter-individual differences in endowment or expected gains from cooperation can contribute to the emergence of leaders and followers. Leadership may involve the active coordination and motivation of group members, or involve more passive influence. Gilby *et al.* [40] argue that group hunting in wild chimpanzees (*Pan troglodytes*) is catalysed by 'impact hunters' who initiate hunts but do not actively coordinate other hunters. Using long-term data from three populations of wild chimpanzees they show that certain individuals initiate hunts more often than chance, and without them hunting is less likely to occur. When these impact hunters initiate a hunt, they appear to dilute prey defences, which lowers the costs of hunting for other chimpanzees. The kill rates of impact hunters do not tend to be higher than other hunters of the same age, which suggests other factors motivate impact hunters to initiate hunts.

Acquiring a reputation for delivering benefits to others (i.e. prestige) is a principal motivation of human leaders. Individuals compete for prestigious reputations because they gain access to greater social support or mating opportunity, as in competitive altruism models [41,42]. Macfarlan & Lyle [43] use ethnographic data from two small-scale societies to evaluate how reputations for prosociality and competency affect social support. In both societies, a reputation for prosociality is associated with receiving greater help, particularly in contexts of collective labour. Somewhat surprisingly, they find that a reputation for competency is more likely to attract cooperative partners than a reputation for prosociality across several contexts. One explanation for the importance of competency over prosociality is that highly competent individuals may produce goods at a higher rate or produce goods of greater quality than less competent but more prosocial individuals. Macfarlan & Lyle [43] offer one of the first ethnographic studies of effects of multiple types of reputations on collective action.

Henrich *et al.* [44] show that a psychology for copying the prestigious can facilitate collective action. They develop a formal model, in which prestigious leaders act prosocially with some probability, and group members decide whether to cooperate or defect based in part on their propensity to copy the leader. The emergence and stability of collective action depend on how likely followers are to learn cooperative behaviour from leaders, followers' retention of cooperative behaviour over time and the transmission of cooperative behaviour via social learning to subsequent generations. Based on their model, Henrich *et al.* [44] argue that leaders can facilitate collective action independent of any special role in coordination, monitoring or sanctioning of group members, as a result of prestige-biased cultural learning. Following this process of cultural evolution, they then show that natural selection can promote even greater prosociality in prestigious individuals (though the effects of selection depend on group size). Henrich *et al.* [44] suggest that in non-human

primates, a relative lack of prestige-biased cultural transmission contributes to an absence of leader-driven collective action.

Glowacki & von Rueden [45] use ethnographic data to argue that leadership in small-scale human societies can solve collective action problems by facilitating coordination and reducing the transaction costs of cooperation. Leaders are able to lead because they commonly have a larger endowment, such as size, strength, age-related experience or more social connections. They argue that the nature of leadership in small-scale societies provides insights into the origins of socio-political complexity. Leadership in small-scale societies is usually informal and situational. However, leadership becomes more institutional in domains of collective action, such as resolution of intragroup conflict, where collective action failure threatens group integrity.

6. Conclusion

Advances in collective action research in evolutionary biology will involve linking inter-individual differences to known mechanisms of cooperation, including mutualism, relatedness, reciprocity and punishment. Modelling and experimental work has often ignored individual differences, such as in endowment and anticipated gains from cooperation, despite their importance for resolving collective action problems. Many of the authors of this special issue also

emphasize the socio-ecological and institutional contexts of collective action, which interact with inter-individual differences at both proximate and ultimate levels of explanation. By incorporating inter-individual differences and their dependence on context, the various theoretical and experimental approaches developed for studying the evolution of collective action gain explanatory power, and they may also gain greater influence within and outside academia, where inter-individual differences and contextual factors are common considerations in the study and design of collective action. The complementary perspectives provided by the papers in this issue provide a more encompassing micro foundation for understanding the macro phenomenon of cooperation in groups.

Competing interests. We declare we have no competing interests.

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