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Key individuals catalyse intergroup violence

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Intergroup violence is challenging to understand: why do individuals cooperate to harm members of other groups when they themselves may be killed or injured? Despite progress in understanding the evolutionary and proximate mechanisms that underlie violence, we still have little insight into the processes that lead to the *emergence* of coalitionary aggression. We argue that an overlooked component is the presence of individuals who have a crucial role in initiating violence. In instigating intergroup violence, these *key individuals* may expect to face lower costs, receive greater benefits, or garner benefits that have a greater value to them than others. Alternatively, key individuals may be motivated by individual traits such as increased boldness, propensity for aggression or exploratory behaviour. Key individuals catalyse the emergence of coalitionary violence through one of several processes including altering the costs and benefits that accrue to others, paying a greater share of the startup costs, signalling privileged knowledge, or providing coordination, among other factors. Here we integrate diverse lines of empirical research from humans and non-human animals demonstrating that inter-individual variation is an important factor in the emergence of intergroup violence. Focusing on the role of key individuals provides new insights into how and why violence emerges.

This article is part of the theme issue 'Intergroup conflict across taxa'.

1. Introduction

Coalitionary violence creates an especially puzzling form of collective action because of the high costs participants pay through the risk of injury and death, in addition to the time, energy and opportunity costs. Yet a range of social species routinely manage to solve the collective action problem inherent in coalitionary violence including some social insects, chimpanzees, wolves, banded mongoose, western gorillas, spider monkeys and, of course, humans. Understanding the problem of intergroup violence requires insight into the biological, psychological and social factors that lead groups of individuals to harm others.

Most evolutionary approaches to the study of collective violence have focused on identifying the selective constraints that have shaped a species' psychology to be adapted for group-based coalitionary violence. These approaches have involved studying how the potential resources accessed through success in intergroup conflict may create conditions that favour intergroup violence, such as through imbalances of power between groups [1,2]. Empirical research designed to test selection hypotheses has typically assessed the costs and benefits to individuals of participation. Among chimpanzees, for example, members of successful groups take over the territory of their rival groups [3], which may result in increased fecundity [4]. In some human groups, individuals who have been part of successful intergroup violence have increased reproductive success [5–7]. Research focused on collective action in intergroup conflict has usually centred on the question of how violence is sustained once initiated [8,9]. Alternatively, psychologically based approaches have examined

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the psychological mechanisms that may disinhibit aversion to violence or increase the appetite for violence. Such approaches have tended to focus on practices relating to the dehumanization of others, fear suppression or revenge motivation [10–13].

Despite the number of different frameworks for studying intergroup violence, most perspectives have overlooked the initiation of violence in the first place. What are the factors that lead individuals to initiate or join coalitions for violence when other preconditions are met? How does any specific instance of collective violence overcome the collective action problem? Why is there spatio-temporal variability in when and how violence emerges? We argue that inter-individual differences can explain not just why violence varies across time and space but why it may appear or disappear in the first place.

Consider what is involved in initiating intergroup conflict in a social primate species. Upon hearing calls from a neighbouring group of primates, each member of the group faces a choice between approach and avoidance. If any number of individuals choose to approach, there is a high likelihood of intergroup conflict. The outcome of the conflict depends heavily on the number of individuals who approach, the number of individuals in the other group, and the investment each makes in the conflict. Once the group or a sub-group begins to approach, each potential participant can then update their decision, choosing to under-contribute, defect, or to increase their level of participation. To make their decision, each individual assesses the anticipated benefits and costs of each strategy based on factors such as the probability of numerical asymmetry and their own physical and reproductive condition. However, *their anticipated costs and benefits also depend on the behaviour of other group members*. Thus, each potential participant also has to assess the expected behaviour of other group members, which requires having a reasonable expectation about whether others will participate and the degree of their investment (thus making inferences about their own, and others', individual expected costs and benefits). In making such inferences, individuals must be sensitive to cues and signals from each other that indicate their likely behaviour and investment, their resource holding power, and any unique information they may have. They then must integrate this information into their decision to approach or avoid. At the same time, decisions are vulnerable to exploitation and suboptimality through false signals and misinterpreted cues. Thus, successful coalitionary violence involves the alignment of the decisions of multiple individuals, each considering their own anticipated costs and benefits as well as those of other potential participants, all the while knowing that each can also defect. Solving these challenges is significant and may be one reason that collective violence only occurs in a small number of social species, typically eusocial insects who are highly related and gregarious social vertebrates [1].

Given these challenges, individuals who are willing to initiate or coordinate conflict, pay higher costs in the initial investment, possess privileged information about the costs or benefits (or are perceived to), or are well-connected in the social network having numerous allies or friends, may have an outsized influence on whether intergroup conflict occurs. Their influence can serve to motivate or facilitate participation of others. We refer to such individuals as *key individuals* [14,15], though they are sometimes referred to as '*impact*' or '*keystone*' individuals [16,17] or more generally as leaders, though the connotations differ between fields [18–21]. An approach centred on key individuals shifts the focus from studying why aggression may be ultimately adaptive, to viewing the initiation of violence as the product of a set of individual strategic calculations derived from interactions with others. Of course, a vital precondition for violence is an underlying psychology that facilitates coalitionary aggression, but this is not enough to generate instances of coalitionary violence. Instead, the actual initiation of coalitionary violence requires not only psychology designed for aggression but also the right social and ecological conditions.

One of the most critical social conditions involved in potentiating the emergence of collective violence depends on having access to information about the likely behaviour of other potential participants. Key individuals help solve this information problem by signalling commitment, paying transaction costs involved in coordinating others, paying a high share of the costs in intergroup conflict, or having strong social relationships with others who are also likely to participate. By focusing on the preconditions to the emergence of violence—conditions at the meso-level, between individual psychology and evolutionary selection pressures—we can better understand why violence emerges when and where it does, as well as why it fails to emerge when it might otherwise be expected.

2. Key individuals

Most approaches to understanding group behaviour treat individuals as homogeneous and largely interchangeable [22]. But persistent individual differences in traits such as boldness, aggressiveness, cooperativeness and risk-taking commonly occur in many species, including insects such as honeybees [23], harvester ants [24] and even cockroaches [25]. Individual differences have also been robustly demonstrated across a range of vertebrate species, including stickleback fish [26], homing pigeons [27], chimpanzees [28] and, of course, humans [29]. In the past decade, a growing body of research has demonstrated that variation among individuals within a group can have profound consequences at the group level. Particular individuals within a group can have an extraordinarily large influence on the behaviour of others [30,31]. For example, the presence of hyper-aggressive male water striders in a group reduces the mating success of all-male group members, including that of the hyper-aggressive male [32]. Among ants, differences in knowledge or work rate can lead to large improvements in the quality of nests sites and the rate at which nests are moved and constructed [14,33]. Among chimpanzees, the presence of a single motivated individual can drive both intergroup conflict and collective monkey hunting [17,34].

Key individuals may affect the behaviour of others directly through modifying the costs and benefits of various options, or indirectly by providing coordination or reducing the transaction costs for others. Importantly, their impact on others is not inherent to their role in the group, such as being alpha, high status, or a parent—it is due to individual characteristics such as their knowledge or expertise, physical condition, social network capital and so on. Numerous other terms have been used to label influential individuals that often have different connotations depending on the species

and system they are describing. These include leaders, dominants, alphas, impact individuals, superspreaders, among others. Due to the varying connotations across fields, especially with the term 'leader', we use the more general term 'key individual'. A key individual may exert their influence through leadership, such as being a first mover or paying a larger share of the costs [18,35]. However, they may exert their influence through other pathways that are often not typically considered leadership. For example, a key individual may be well-connected in the social network and their mere participation may be sufficient to motivate others to also participate even though they neither move first nor pay any disproportionate costs.

Key individuals may have a long-term influence if they exert a disproportionally large impact on others over an extended period. Alternatively, their influence may be confined to a short duration, such as when the group moves, in which case their influence may cease once the group ceases movement. For example, bolder homing pigeons tend to fly faster and are thus more likely to lead the flock by virtue of their flight speed, but this has an outsized influence on the group only while in flight and does not carry over beyond flight [27]. Similarly, key individuals may have influence over only a single domain or context. Group movement, for example, is often led by knowledgeable individuals but their outsized influence on the group generally does not appear to extend to other domains [33,36,37]. Alternatively, in some species a single key individual may shape a range of group behaviours. Among pigtailed macaques, the removal of individuals who have a key role in conflict resolution influences a range of other behaviours including rates of in-group aggression, levels of play and grooming [38].

(a) Key individuals, collective action and cooperation

In the past decade, a growing body of research has demonstrated that individual variation is especially important in overcoming collective action problems [30,39]. Individuals across a range of species vary in their propensity for cooperation and much of this variation is stable, meaning that an individual likely to cooperate at one point in time will be likely to cooperate at a later point [40–42]. This stability is often so robust across species that it is termed a *cooperative phenotype* [43]. Even in humans, individual differences in cooperation are common and stable. Studies using variations of public good games have found that a minority of players are high cooperators. For example, Kurzban & Houser [44] classified 25% of a sample of participants in public good games as strong cooperators. Cooperative behaviour in games has been shown to be stable between games played over 100 days apart and to correlate with real-world cooperative efforts [43].

Data from a range of species demonstrate that individual differences can be instrumental in promoting cooperation. In experimental conditions among humans, having more cooperators in a group faced with solving social dilemmas leads to other group members contributing larger amounts and making more frequent contributions [45]. A series of experiments among captive and semi-free-ranging chimpanzees tested whether and how they were able to solve a collective action problem through a series of tasks that involved pulling a rope [28]. In the first task, group sizes were small and dominant individuals were more likely to obtain a larger share of the reward than other group members. In this case, the possibility of receiving a larger share of the reward appeared to drive participation in collective action with dominant individuals being much more likely to invest, and subordinates more likely to free-ride. A second experiment was conducted that increased the group size and decreased the likelihood of asymmetric rewards to dominant individuals by dispersing the rewards so they could not be monopolized by any one individual. In this condition, the key factor influencing group success was the presence of individuals highly motivated to act even if they did not receive a larger share. The propensity of some individuals to cooperate by pulling, and motivate others to pull, was so strong as to label these individuals 'impact pullers'. Without the willingness of these 'impact pullers' to initiate collective action, most trials would have resulted in failure [28].

Inter-individual variation even catalyses potentially dangerous collective action activities such as predator deterrence and collective hunting. Predator deterrence in social species is often a collective good reducing the risk of predation for all group members, although only some individuals may risk attempting to deter the predator. To deter predators, individuals harass and threaten them, varying how close they come to the predator while encouraging others to join in creating a mob against the predator. An experimental study among warblers used taxidermized mounts of avian threats (e.g. predators) to study how inter-individual variation could lead to the mobbing of the predator [46]. As expected, individuals who stood to gain more from deterring the predator, such as having the closest nest, invested more in predator deterrence. Stronger responses from the initial individuals led to others joining in thus creating a mob. Thus, a few individuals were able to successfully instigate mobs due to their strong initial response to the mounted threat.

Collective hunting among chimpanzees also appears to be initiated by a few key individuals. Wild chimpanzees opportunistically hunt colobus monkeys in the canopy. Doing so is costly because colobus groups typically contain adult males who mob the attacking chimpanzees, attempting to bite them and, in some cases, successfully deterring their attacks. Using 70 years of data from chimpanzee communities, Gilby *et al*. [17] analysed how hunting is sensitive to the presence of specific individuals who appear to catalyse hunts. For two of the chimpanzee communities, they identified a small number of individuals (five) they call *impact hunters* who had very high rates of hunting participation for their ages. Groups of chimpanzees that encountered colobus monkeys were more likely to hunt if they contained one of the impact hunters. Furthermore, impact hunters were typically the first to hunt when approaching the defending colobus—one impact hunter was the first to hunt in 87% of hunts in which he participated. Initiating the hunt is typically the costliest role because the initiator usually becomes the target of defensive aggression by the adult male colobus monkeys, while the other chimpanzees predate the remaining poorly defended monkeys. These differences explain variation in hunting rates over time and between locations [47]. At the Kanyawara site, after the death of one impact hunter, hunting rates dropped significantly [17,47]. Similarly, one chimpanzee site lacked an impact hunter and there was a much lower rate of hunting despite a similar encounter rate with colobus monkeys. These results suggest that the role of key individuals

may be especially pronounced in high-cost contexts, such as hunting, where the risk of being injured is greater. Without such individuals, high-cost collective activities may fail to emerge.

3. Key individuals in intergroup violence

Key individuals are especially important for the emergence of intergroup conflict in both offensive and defensive aggression because of the chance of injury or death, especially when free riding is a greater possibility. In-group variation in ability, rank or resources can lead individuals who would otherwise monopolize larger shares of in-group resources to act more cooperatively in between-group conflicts, including paying higher costs [48]. The most active contributors in intergroup conflict typically should be those with greater capability or those who are likely to either pay lower costs or reap higher benefits [30]. Accordingly, having such variation in a group can catalyse collective action in intergroup conflict by asymmetrically advantaged individuals—even when it is high cost to them [49].

Across species there are significant differences in how willing individuals are to participate in intergroup conflict [50–52]. Some of this variation points toward a role for key individuals. Among free-ranging dogs, intergroup conflicts sometimes result in injuries to one or more members, especially to the losing group [53]. During intergroup encounters, not only did smaller groups have higher cooperation among their members when compared to larger packs, but a small percentage of dogs across packs were consistently high cooperators—cooperating more in intergroup conflict both when the odds were favourable and unfavourable. These highly cooperative dogs were more likely to be at the front of the pack during a conflict and thus were most likely to be injured in an encounter [53]. Among lions, some group members so regularly lead responses to simulated aggressive territorial intrusions that they have been labelled 'unconditional cooperators' [54]. Other lions, however, regularly lagged behind, and some were conditional cooperators, joining more when they were needed more.

The most comprehensive data from non-humans demonstrating the importance of key individuals in the initiation of intergroup conflict comes from detailed studies of chimpanzee communities. Chimpanzee communities often have lethal coalitionary attacks between groups that can be a major source of mortality [55]. Most lethal encounters between groups result from a border patrol, in which a small group of chimpanzees leaves the core of their home range and travels toward the border of their territory with a neighbouring group. Border patrols consist mainly, but not exclusively, of males and they appear to search for evidence of their neighbours, pausing to listen for sounds from other groups [56]. If they find evidence of another group and appear to outnumber them, they may move rapidly toward the neighbours with the aim of attacking them [57]. Data from 32 years of wild chimpanzee movements indicate the presence of 'impact patrollers', similar to impact hunters [34]. When one of the impact patrollers was present in a group that was near the periphery of its territory, the group was significantly more likely to go on patrol than if they were absent. This suggests that similar to collective hunting, high-stake collective action in the form of chimpanzee patrols requires the presence of exceptionally motivated individuals to catalyse the group.

Although group size is an important component of success in intergroup conflict [58,59], larger groups often have greater difficulty with solving the collective action problem [60,61]. This may be the reason why data from several species reveals that numerically superior groups do not necessarily win intergroup conflicts—factors including the composition of the group and location of the conflict may matter more than numerical superiority alone [62,63]. Among lemurs (*Verreaux sifaka*), analyses of 141 intergroup encounters from five groups found that larger groups were not more likely to win either cumulatively or by sex (i.e. a greater number of males or females) [64]. Playback studies among wild capuchin monkeys showed that group members were more likely to run away from a simulated intrusion when their group was larger than the intruder's group, though the strength of the effect depended on the location of the simulated conflict [65]. Thus, the investment that each individual makes in conflict may matter to whether their group is successful. The presence of individuals who are exceptionally motivated may be decisive to the outcome and may be one reason why smaller groups sometimes defeat larger groups [62].

(a) Human intergroup violence and key individuals

There are surprisingly few studies examining the dynamics of coalitionary violence in real-world conflicts. Much of the best evidence in support of the role of key individuals in human violence comes from experimental studies of intergroup behaviour [66–69] and qualitative accounts of coalitionary violence [70,71]. Experimental studies on intergroup conflicts demonstrate that the willingness to pay a larger share of the costs in conflict or willingness to move first can have a large impact on group outcomes [48,69]. For example, when a group has one member who moves first in intergroup conflict, this increases the participation of other individuals, likely by facilitating their coordination [69]. Alternatively, first movers may pay a larger share of the costs, such as by taking greater risks, thus reducing the costs to other participants and thereby increasing the likelihood of success in conflict [48].

These findings have been well-established qualitatively [72]. Mobs and riots, for example, 'need … an instigator, a leader …' [73, p. 189], while Reicher & Stott [74, p. 38] acknowledge that 'there has to be someone who acts first' and mobilizes the crowd. Riots are hypothesized to require 'entrepreneurs' or a person who 'serves as a catalyst … to get things going' [75, p. 151]. Inter-ethnic violence in state-level societies, for example, almost always has an organizer or instigator [76]. In small-scale decentralized societies the pattern is similar. The Waorani in the Amazonian Ecuador previously experienced some of the highest levels of raiding of any recorded society [77]. However, the vast majority of raids that have been studied were initiated by two men who appeared to be critical for catalyzing many of the raids [78]. Among the Yanomamo of Venezuela, 137 men participated in the killing of another person but of these, 60% participated in only one death [5]. A small group of men (11), however, participated in the deaths of more than 10 individuals.

Detailed data on the initiation of intergroup violence data come from a study of nomadic pastoralists in southwest Ethiopia where intergroup violence takes the form of violent cattle raids in which people are frequently killed [79]. In this

Table 1. Evidence for key individuals in intergroup violence. The study of key individuals has mostly focused on non-aggressive behaviours. Here we highlight studies most directly relevant to intergroup violence.

species	description
chimpanzees	*patrolling catalysts*: when an impact patroller was in a group that was near the periphery of their territory, that group was more likely to go on patrol [53].
lions	*unconditional cooperators*: using playback experiments simulating aggressive territorial intrusions, some individual lions reliably responded to simulated intrusions, while most other lions acted conditionally or lagged behind [48].
free-ranging dogs	*affiliative partnerships*: in intergroup encounters among free-ranging dogs, a small number of dogs reliably approached members of the other pack, cooperated more in conflict, and were more likely to be injured in conflict. These dogs tended to have more affiliative partners [47].
humans	*first movers and leaders*: experimental studies showed that first-movers increase the likelihood of other group members investing in the conflict. Experimental studies also showed that individuals who receive a disproportionate share of the spoils of conflict, or generally have higher motivation for conflict, were more likely to invest in conflict [43,64].
	qualitative studies from mobs and riots showed that typically there is a first mover or instigator who serves as a catalyst to initiate the conflict [69–71].
	studies on raiding parties from small-scale societies revealed that a small number of individuals usually organize raids and motivate others to participate in them [74–77].

context, raids take one of two forms. The first is small-scale stealth raids with usually 4–12 participants that pose low risk for attackers. The second form of raid are battles that involve hundreds of participants who face a much higher chance of being killed or injured. High-risk large battle raids always involve several recognized raid leaders who had extensive experience with warfare and recruit other raiders, secure food for them and plan tactics. These individuals are also more active participants and are much more likely to be killed during the raid compared to other participants [80]. This is similar to patterns in decentralized warfare seen elsewhere in the context of large high-cost battles. For example, among the Kapauku of New Guinea the raid leaders 'did not stay protected in the rear, but one usually saw them in the front line and in the lead of an attacking force' [81, p. 118], while Cheyenne war chiefs had a much higher rate of deaths from conflict [82]. Small stealth raids, on the other hand, involve key individuals who function as informal leaders who recruit other participants and plan the raid. Glowacki *et al*. analysed the network dynamics of stealth raid participation and found that a small number of participants participated with high frequency and catalysed the raid by recruiting others [79]. These results are similar to ethnographic reports from a range of societies indicating that many forms of coalitionary action, including raiding parties, usually had informal leadership [83,84].

Thus diverse lines of evidence from experimental paradigms and naturalistic studies of human societies demonstrate that key individuals often have a significant role in initiating high-cost collective action, including intergroup violence. Without their presence, coalitionary violence may fail to materialize even though the other preconditions are met (table 1).

4. Why be a key individual?

We focus on understanding why some individuals serve as key individuals in intergroup conflict: key individuals often face lower expected costs and/or greater expected benefits motivating them to promote intergroup violence. Alternatively, they may have increased motivation to initiate conflict due to temperament, personality or behavioural syndromes.

(a) Key individuals face lower costs or anticipate greater benefits

Some individuals may expect to asymmetrically benefit from intergroup conflict or to pay fewer costs, thus lowering their threshold for participation and these differences can contribute to their role in instigating intergroup violence. The reasons for these differences can be due to phenotypic variation—such as some individuals being larger, stronger, or otherwise more capable increasing their likelihood of success in conflict. Alternatively, key individuals may have different cost and benefit curves than others due to background features such as wealth, family status or reproductive condition. Evidence from experimental studies in humans shows that men who are judged to be more formidable because they possess greater upper body strength were more likely to support the value of using force to resolve conflict, both in personal as well as international contexts. Notably, such men had an increased history of fighting and also more strongly endorsed aggressive and interventionist foreign policies [85]. Interestingly, humans seem to be able to accurately assess physical strength and fighting ability in males from visual portrayals of the upper body and the voice, showing the influence of background selection pressures on both the value and recognition of physical fighting ability [86,87].

There have been only few studies of the costs and benefits to individuals from their participation in intergroup violence. What data there are indicate that the extent to which costs and benefits shape key individuals depends on the species and context. For example, among banded mongooses, who have extremely high levels of intergroup violence with severe causalities, violence is typically initiated through the

movement of females who asymmetrically benefit from reproductive opportunities gained during the intergroup encounter while most of the costs are borne by her other group members [88]. Among wild vervet monkeys, females have a key role in incentivizing intergroup aggression through selectively grooming males who had participated in aggression and aggressing males who had not. Crucially, the likelihood of selective grooming and aggression to promote intergroup aggression depended on whether high-quality food resources were at stake. In cases where they stood to gain or lose high-quality food resources as a result of the conflict, they were more likely to promote aggression through selective grooming and aggression [52]. However, in a range of species, differential costs and benefits of participation in intergroup conflict (as a proxy for being a key individual) appears to only partly explain variation in conflict participation [34,50,51,53].

Data from humans on the costs and benefits key individuals receive from intergroup violence is meager and mixed. A range of studies suggests that participating in intergroup violence can provide social and reproductive benefits to successful participants [9,89,90]. Among the Yanomamo of Amazonian Venezuela, men who had participated in killing another person on a raid and who went through a ritual post-conflict ceremony had more wives and children than other men [5]. Data from cattle raiders among the Kuria of Tanzania show that raiders are more likely to be men who are sister-poor [91] because sisters generate incoming wealth in the form of livestock that can be used for marriage. Raiding appears to be a way to make the best of a bad situation in this case. However, these cases do not focus on the costs and benefits key individuals face but rather participants at large. An experimental study between groups experiencing real-world violent conflict demonstrated that individuals who were randomly selected to receive a larger share of spoils from conflict were more likely to initiate conflict, even when doing so led to sub-optimal returns for the rest of the group [92].

There are unfortunately few data from real-world conflicts to test the generalizability of these results. Data from the Nyangatom, a group of pastoralists in Ethiopia and South Sudan, present a mixed picture of the costs and benefits for key individuals. A high level of participation in stealth raids was associated with an increased number of wives and children over a lifetime [6]. Increased raiding participation was also strongly associated with being a stealth raid leader, suggesting that stealth raid leaders were more likely to benefit reproductively over a lifetime. But unlike the Kuria, raid leaders did not face more intensive reproductive competition than other men due to being sister poor or brother rich, nor did they generally receive a larger share of the spoils [6]. Battle leaders, on the other hand, tended to be higher status than other men, did not benefit reproductively, and faced a much higher mortality rate than other participants [80].

Taken together, data from non-human animals and human groups suggest that the costs and benefits individuals face, as well as individual differences in various characteristics, have a mixed role in predicting differential investment by key individuals that promotes intergroup violence. Of course, in humans many other social and historical factors can contribute to the emergence, escalation and perpetuation of violence. Cycles of revenge and retaliation come into play within the social dynamics of in-group defense and outgroup discrimination. Furthermore, human leaders often rely on shared aspects of social identity or political ideology to recruit followers and organize collective violence [93]. Thus, assessing costs and benefits alone are inadequate to understanding key individuals in humans.

(b) Personality or behavioural syndromes

Individuals across a wide range of species vary along many dimensions affecting behaviour including their boldness, shyness, aggression, reactivity and exploratory behaviour [94–96]. The sources of these differences are variously called personality, disposition, temperament or behavioural syndromes, though these terms have slightly different meanings. Importantly, these differences are stable or consistent across contexts or over time. For example, individuals who are more aggressive in one context are likely to be more aggressive in other contexts regardless of payoffs. Among funnel-web spiders, aggressive individuals are faster to attack prey *and* members of their own species who intrude on their territory [96]. These differences may be due to genetic, hormonal or developmental experiences that make such behaviour more endogenously rewarding to some individuals than to others. However, these characteristics do not exist in isolation; rather, for some species such as humans, they operate in a social context that rewards or sanctions such behaviour. Thus, the local ecology matters for producing and reinforcing or sanctioning aggressive or violent behaviour. This points to the critical importance of environmental as well as developmental factors in cultivating key individuals who can serve a critical role in catalyzing coalitionary violence.

There is little empirical data on the role of personality or behavioural syndromes for key individuals in intergroup aggression but the data that do exist suggests the importance of individual differences in catalyzing aggression. Just as chimpanzee experimental cooperation and monkey hunting depends on key individuals, chimpanzee patrols are sensitive to the presence of key individuals or 'impact patrollers', who catalyse patrols that search for signs of other chimpanzees [34]. The propensity to be a key individual in chimpanzee patrols and hunting is attributed to variation in personality with some individuals being more predisposed to patrol than others [34]. Intriguingly, key patrollers and impact hunters among chimpanzees are not the same individuals, suggesting that different underlying psychological traits motivate each behaviour.

Personality differences in aggression are consistent with what data there are from human groups as well. The fact that a small percentage of humans seem especially prone to aggression suggests an underlying personality or behavioural syndrome that motivates their aggression rather than a cost/benefit calculation on their part [97]. Abbink *et al.* [66] showed that groups consisting of more cooperators were more aggressive in intergroup contests than groups composed of egoists. Similar results have been found in other studies using intergroup contest paradigms [98,99].

In real-world intergroup conflict, it is unclear whether the underlying personality trait driving key individuals in promoting intergroup aggression is aggression, prosociality, boldness, exploratory behaviour or some combination of these and possibly other factors. Aggression and boldness are often correlated in the same individuals [100]. Individuals

who are more bold or aggressive may be more likely to approach a potential threat or initiate intergroup conflict when confronted with a threat whether from a potential predator or members of other groups. Differences in exploratory behaviour may have an important role for initiating chimpanzee patrols or human raiding parties. If some individuals are more drawn to new environments, their propensity to explore those environments may then affect the behaviour of other individuals who follow them [15].

5. Mechanisms by which key individuals promote collective action

Understanding how key individuals promote intergroup violence is complicated by the fact that there are multiple pathways through which individuals can exert outsized influence on the behaviour of others, including reshaping the social network [24,101], altering the costs and benefits for others [16], positive matching [15] or instigating conflict through bringing groups into contact with each other [88]. We focus on the pathways that are most likely to be important for key individuals in human intergroup violence: reducing the perceived costs and increasing the benefits to others, and social coordination.

Data on participation in intergroup violence among non-human animals demonstrates that for non-key individuals the decision to participate in conflict is strongly influenced by individual costs and benefits—with factors including sex, age and reproductive condition all influencing the likelihood of participation based on the likely outcome of conflict [50,60,102]. Thus, if a key individual can alter the actual or perceived costs and benefits of intergroup violence to potential participants, this will have the effect of decreasing the threshold for others to participate. Although we lack empirical data testing this explicitly in intergroup aggression, data from the role of chimpanzee key individuals in collective hunting support this hypothesis. Key hunters among chimpanzees are typically the first individuals to climb toward the monkeys making them more likely to be victims of defensive mobbing and physical attacks by the monkeys. Their effort disperses the other monkeys, reducing the costs of hunting for the other chimpanzees who can catch them more easily [17]. Although this example is from hunting, not intergroup aggression, we expect that the pattern is often similar in intergroup aggression where key individuals invest a greater amount in the conflict itself, reducing the chances that others might be injured.

Key individuals can also help initiate violence by reducing transaction costs for other participants by helping coordinate and organize conflict. High impact individuals, who often function as first movers in conflict situations, signal to other followers that they will not be alone in their actions. They allow potential followers to anticipate what other actors might do. Key individuals thus provide the behavioural signal around which actor expectations converge [103]. To the extent that the key individual can effectively recruit others, each additional follower will anticipate that they are more likely to emerge victorious because of the increasing number of recruits. This means each individual needs to contribute less, lowering the tipping point where the costs of action outweigh the costs of inaction. Note that such coordinating action serves the purpose of increasing the number of participants whether or not the key individual actually possesses superior fighting or strategic skills; the organizational advantages provided by such key individuals offer coherence as well as coordination. They may also take a more direct role in coordinating the actual instances of aggression by (in humans) planning tactics or solving logistical challenges. This is perhaps one reason why leadership in human intergroup aggression is a near universal [76,83,84].

6. Discussion

We have argued that key individuals are critical to overcoming the collective action problem inherent in intergroup violence. Initiating potentially high-cost coalitionary violence requires some individuals to invest disproportionally—even if just to serve as a first mover or provide a signal around which the expectations of others converge. Our argument, however, applies not just to collective violence but to high-cost collective action generally, including among contemporary industrial societies. Just as collective violence requires key individuals to initiate collective action, many public goods such as civic organizations, relief programmes or social movements also require key individuals. Without some individuals investing disproportionally, it is hard to understand how many kinds of high-cost collective action can be initiated, much less sustained or achieved.

The second implication of our argument is that just as there are key individuals who initiate violence that then spreads, there may be individuals who have a key role in conflict prevention or reconciliation. Among several primate species, specific individuals appear to have a large role in conflict resolution in their group [38,104]. Their removal has the effect of increasing levels of aggression in the group [38]. Among human groups, targeted interventions with prominent individuals may serve to decrease conflict. In an experimental study of 56 American middle schools, randomly selected groups of students were selected for training in anti-conflict intervention [105]. Groups that contained more highly connected individuals, called 'social referents', were more effective at reducing student conflict. A similar approach of identifying individuals who yield a large social influence may be an effective strategy for reducing and preventing intergroup violence across contexts, including urban group-based violence that characterizes much contemporary violent conflict [106].

The study of key individuals is still relatively new and there are several areas of outstanding importance going forward. We explicate significant areas in need of more research in table 2. Ultimately, resolving questions about how key individuals function will require more data on inter-individual participation in intergroup violence, alongside detailed individual level data including life-history data, and measures of personality.

In sum, while most work on intergroup violence focuses on the adaptive significance of violence or psychological mechanisms involved in provoking violence, it has overlooked the social dynamics involved in catalysing collective violence. Hence, a large gap exists between theory and our understanding of when, why and how violence varies over time and between contexts. Focusing on the role of key individuals in the emergence of violence will generate new streams of data and ultimately enrich the theoretical landscape in our understanding of why and how violence occurs.

Table 2. Directions for future research.

cross-species comparisons
There have been few efforts to systematically evaluate whether key individuals exert influence through similar processes across species. For example, are the mechanisms through which impact patrollers in chimpanzees exert influence on their group similar to those in other primates?
developmental trajectory of key individuals
There has been little work on the developmental factors that lead some individuals to become key individuals. Are specific developmental experiences or gene-environment interactions necessary for the emergence of key individuals? Is there a common or shared developmental trajectory for key individuals within or across species? Most human violence is produced by young males. Does this pattern hold for impact individuals?
evolutionary origins of key individuals
To what extent is being a key individual the result of selective processes? What mechanisms would be responsible for maintaining this phenotype, i.e. frequency-dependent selection?
why can personality be so effective at mobilizing others?
In humans, being a key individual appears to require the ability to recruit followers. Doing so effectively may be due to experience, knowledge or skill. Among humans, however, charisma also appears to be important but does not reduce to knowledge, skill or experience [103]. What explains the effects of charisma in catalysing followers for intergroup violence?
variation in types of aggression between individuals
Key individuals catalyse coalitional aggression but are the same individuals involved in different types of aggression, including intergroup, intragroup, offensive and defensive aggression? Are the mechanisms by which they motivate others to participate similar across types of aggression? For example, among chimpanzees, impact patrollers do not appear to be the same individuals as impact hunters, suggesting that key individuals differ between types of aggression.

Data accessibility. This article has no data.

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