In-Group Defense, Out-Group Aggression, and Coordination Failures in Intergroup Conflict

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Intergroup conflict persist when and because individuals make costly contributions to their group's fighting capacity, but how groups organize contributions into effective collective action remains poorly understood. Here we distinguish between contributions aimed at subordinating out-groups (out-group aggression) from those aimed at defending the in-group against possible out-group aggression (in-group defense). We conducted two experiments in which three-person aggressor groups confronted three-person defender groups in a multi-round contest game (*N*=276; 92 aggressor-defender contests). Individuals received an endowment from which they could contribute to their group's fighting capacity. Contributions were always wasted, but when the aggressor group's fighting capacity exceeded that of their defender group, the aggressor group acquired the defender group's remaining resources (otherwise, individuals on both sides were left with the remainders of their endowment). In-group defense appeared stronger and better coordinated than out-group aggression, and defender groups survived roughly 70% of the attacks. This low success-rate for aggressor groups mirrored that of group-hunting predators such as wolves and chimpanzees (*N*=1,382 cases), hostile takeovers in industry (*N*=1,637 cases) and interstate conflicts (*N*=2,586). Furthermore, whereas peer punishment increased out-group aggression more than in-group defense without affecting success-rates (Exp. 1), sequential (versus simultaneous) decision-making increased coordination of collective action for out-group aggression, doubling the aggressor's success-rate (Exp. 2). The relatively high success rate of in-group defense suggests that evolutionary and cultural pressures may have favored capacities for cooperation and coordination when the group goal is to defend, rather than to expand, dominate, and exploit.

competition | parochial altruism | coordination | collective action | intergroup relations

Human history is marked by intergroup conflict. From tribal warfare in the Holocene to Viking raids in medieval times, to terrorist attacks in current times, small groups of often no more than a handful of individuals organize for collective violence and aggression. Individuals within such groups contribute, at sometimes exceedingly high personal cost, to their group's capacity to fight other groups [*1—5*]. And in doing so, individuals and their groups waste resources and people, and create imprints on collective memories that affect intergroup relations for generations to come [*6—10*].

Given the risk of injury and death, and the collective wastefulness of intergroup conflict, it may seem puzzling that people self-sacrifice and make costly contributions to their group's fighting capacity. However, by contributing to intergroup aggression individuals enable their groups to subordinate rivaling out-groups and absorb its resources [*3,4*], something from which individual group members benefits too. Indeed, groups that most effectively elicit contributions from its members are most likely to be victorious and, perhaps, intergroup competition and conflict pressures individuals to contribute to intergroup violence [*1,3,5,11,12*] and its supporting institutions [*8,9,13,14*].

That intergroup conflict elicits self-sacrificial contributions to one's group's fighting capacity has been robustly revealed in experiments using *N*-person (intergroup) prisoner's dilemma [*4,5,15—17*] or price-contest games [*18—21*]. What cannot be derived from these setups, however, is whether individuals self-sacrifice to defend their in-group against out-group aggression, to aggressively exploit and subordinate the out-group, or because of some combination of both reasons [*5,9,10,22,23*]. In addition, it is unclear how the willingness to defend the in-group relates to the willingness to aggress out-groups. These issues are non-trivial because tendencies for in-group defense and out-group aggression are often differentially dispersed between opposing groups. From group-hunting by lions, wolves, or killer whales [*24,25*], to groups of chimpanzee raiding on their neighbors [*11*], to hostile take-overs in the marketplace [*26*] and territorial conflicts within and between nation states [*27*], intergroup conflict is often a clash between the antagonist's out-group aggression and the opponent's in-group defense [*23,28*]. Second, in-group defense and out-group aggression appear to have distinct neurobiological origins [*5,29—31*] and may thus recruit different within-group dynamics [*4,28*]. Whereas self-defense is impulsive and relies on brain structures involved in threat signaling and emotion regulation, offensive aggression is more instrumental and conditioned by executive control [*29—31*]. Third, the motivation to avoid loss is stronger than the search for gain [*32,33*], suggesting that individuals more readily contribute to defensive rather than offensive aggression. Finally, self-sacrifice in combat

Significance

Across a range of domains—group-hunting predators, laboratory groups, companies and nation states—we find that out-group aggression is less successful because it is more difficult to coordinate than in-group defense. This finding explains why appeals for defending the in-group may be more persuasive than appeals to aggress a rivalling out-group, and suggests that (third) parties seeking to regulate intergroup conflict should, in addition to reducing willingness to contribute to one's group's fighting capacity, undermine arrangements for coordinating out-group aggression—like leadership, communication, and infrastructure.

Reserved for Publication Footnotes

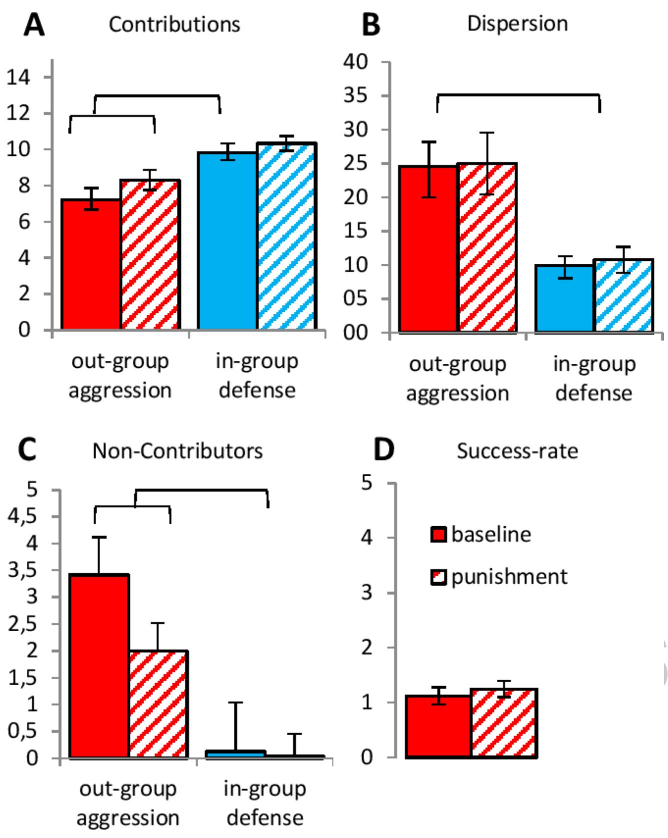

Fig. 1. Peer punishment in intergroup aggressor-defender conflict (displayed Mean±1SE); Connectors indicate difference at $p≤0.05$. **(A)** Contributions (range 0—20). **(B)** Within-group variance (dispersion). **(C)** Number of non-contributors per group across conflict episodes (range 0—5); **(D)** Aggressor success (range 0–5).

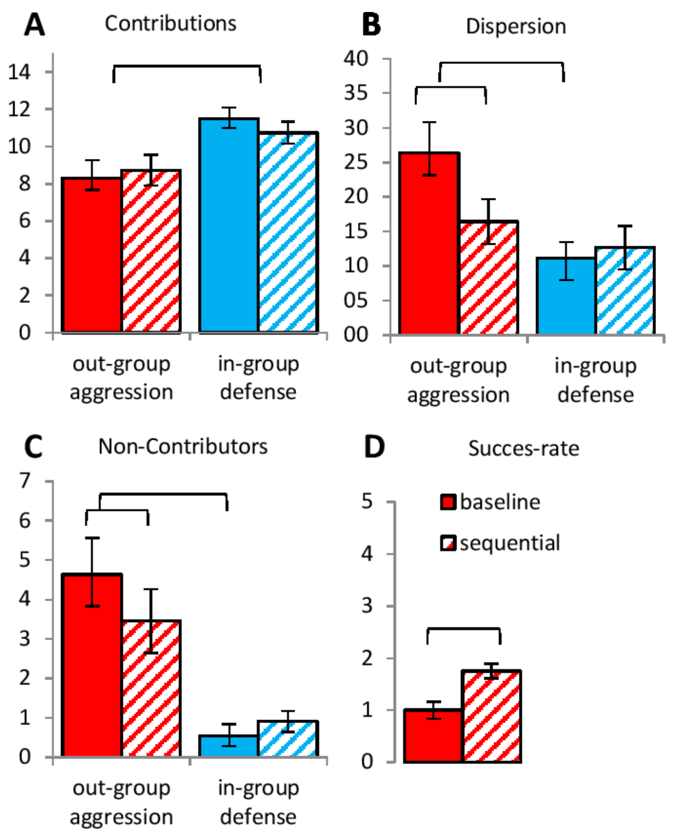

Fig. 2. Sequential decision-making in intergroup aggressor-defender conflict (displayed Mean±1SE); Connectors indicate difference at $p≤0.05$. **(A)** Contributions (range 0—20). **(B)** Within-group variance (dispersion). **(C)** Number of non-contributors per group across conflict episodes (range 0—5). **(D)** Aggressor success (range 0–5).

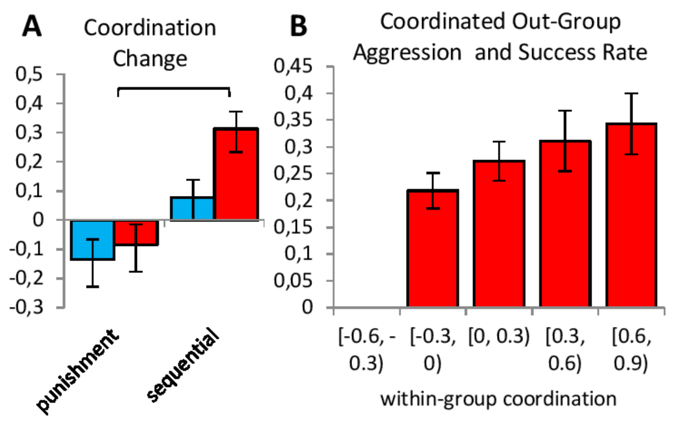

Fig. 3. Coordination in intergroup aggressor-defender conflict (displayed Mean intraclass-correlation±1SE); Connectors indicate difference at $p≤0.05$. **(A)** Change from baseline when punishment or sequential decision-making is introduced. **(B)** Aggressor success as a function of aggressor's within-group coordination.

is publicly rewarded more (e.g., with a Medal of Honor) when it served in-group defense rather than out-group aggression [34]. Accordingly, in-group defense may emerge more spontaneously, and individuals may be more intrinsically motivated to contribute to in-group defense than to out-group aggression.

If in-group defense is indeed more intrinsically motivating and spontaneous, groups preparing for in-group defense should face fewer non-contributors than groups preparing for out-group aggression. Aggressor groups should thus have higher within-group dispersion in contributions and may have greater difficulty organizing adequate out-group aggression. This collective action problem in aggressor groups may emerge because of motivation failure—individuals are less willing to contribute to out-group aggression than to in-group defense—or it may be the result of poor coordination—it is more difficult to coordinate and align individual contributions to effectively aggress a rivaling group, than it is to raise proper in-group defense.

We examined these possibilities, and their consequences for conflict trajectories and resolution by pitting out-group aggression against in-group defense. Because existing models of intergroup conflict such as *N*-person prisoners' dilemmas and intergroup contest games are ill-fitted to distinguish between out-group aggression and in-group defense, we developed a novel intergroup aggressor-defender conflict (IADC) game. Six individuals randomly divided in 3-person aggressor and defender groups each received 20 Experimental Euros from which they could contribute g ($0≤g_i≤20$) to their group's pool C ($0≤C≤60$). Individual contributions to the pool were wasted, but when $C_{aggressor}>C_{defender}$, the aggressor won the remaining resources of the defenders ($60–C_{defender}$), which was divided equally among aggressor group members and added to their remaining endowments (20-g_i). Defenders thus earned 0 when aggressors won. However, when $C_{aggressor} ≤ C_{defender}$, defenders survived, and individuals on both sides kept their (20-g_i). Thus, individual contributions in aggressor (defender) groups reflect out-group aggression (in-group defense). We used the game to (i) test whether individual contributions to out-group aggression are weaker than those to in-group defense, (ii) examine how this translates into

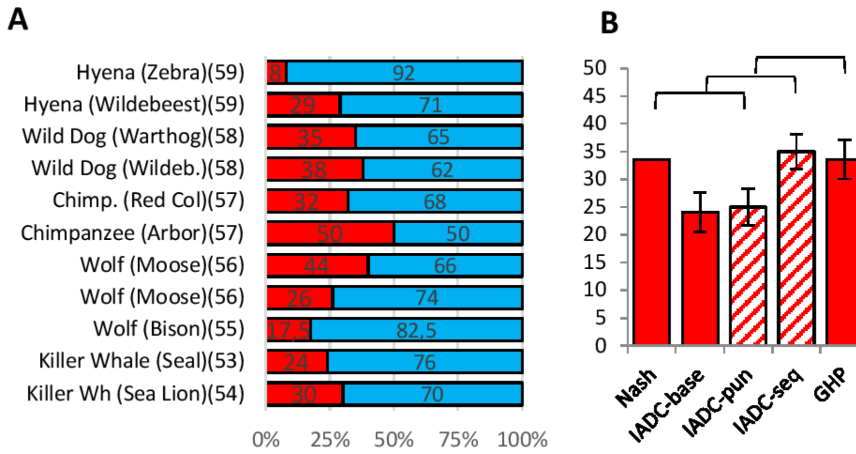

Fig. 4. Aggressor-defender success-rates. (**A**) percentage of successful attacks by group-hunting animals (and their prey). Black (grey) bars are predator (prey). Numbers in bars are observed cases; bracketed numbers in Y-axis are source references. (**B**) Nash-estimate for aggressor's success in the IADC (Nash), observed aggressor success in baseline treatments of Experiment 1 and 2 (IADC-base), punishment (IADC-pun) and sequential decision-making (IADC-seq), and sample-size weighted average success-rate in group hunting predators (GHP) (displayed percentage±1SE); connectors indicate difference at $p \leq 0.05$.

aggressor's success in subordinating its defender, and (iii) determine whether possible failures to subordinate defender groups are due to a lack of motivation to contribute to out-group aggression and/or to a failure to align and coordinate individual contributions to out-group aggression.

Method Summary

The IADC was implemented in two experiments. In Exp. 1, $N=144$ subjects participated (106 female; Median age=21). In Exp. 2, $N=132$ subjects participated (78 females; Median age=22). In each experiment, one session involved six subjects divided at random in a 3-person aggressor and a 3-person defender group; Exp. 1 thus has 144/6=24 IADC sessions and Exp. 2 had 132/6=22 IADC sessions. In both experiments, the six individuals invited for one IADC session were randomly assigned to one of two laboratory rooms and one of three individual cubicles within that room. Subjects were unaware of who else was in either laboratory room and, once seated, signed informed consent and read instructions for the IADC [*Materials and Method*]. Thereafter, subjects indicated their contribution g ($0 \leq g_i \leq 20$) to their group's pool C, were informed about the total contribution their group made to C ($0 \leq C \leq 60$), the total contribution C made by the other group, and the resulting earnings to the members of their own group, themselves included. This concluded one IADC episode. In total, subjects engaged in one block of five baseline episodes, and one block of five treatment episodes (i.e., allowing for peer punishment in Exp. 1; and for sequential decision-making in Exp. 2; further detail below). Order in which blocks were presented was counter-balanced and found not to qualify conclusions drawn below.

Investments were always wasted and, from a social welfare perspective, it thus is optimal for all individuals on both sides not to contribute anything. This contrasts with both individual and group welfare considerations. Specifically, the IADC has mixed-strategy Nash equilibria in which individuals contribute to out-group aggression (in-group defense) on average 10.15 (9.77), and aggressors (defenders) win (survive) 32.45% (67.55%) of the episodes [*35; Materials and Methods*]. We examined these estimates against the data from the five baseline episodes of the two experiments combined ($N=276$ individuals in 46 IADCs). Out-group aggression fell below ($M=-2.401$, $SE=0.567$) and in-group defense exceeded ($M=0.858$, $SE=0.400$) the Nash-equilibrium ($t[45]= -9.231$, $p \leq 0.001$ and $t[45]=2.146$, $p=0.037$); Aggressors defeated defenders in 22.5% of their attacks, which is below the Nash success-rate ($M=-0.679$, $SE=0.154$; $t[45]=-4.405$, $p \leq 0.001$).

Experiment 1

As noted, a first possible explanation for the relatively low success-rate for out-group aggression is a relative low willingness to contribute to the aggressor's fighting capacity. If true, sanctioning arrangements that are known to increase contributions to public goods should (i) increase contributions more in aggressor groups than in defender groups (in which contributions are already high). If sanctions indeed affect contributions especially in aggressor groups, and if relatively low willingness to invest is a cause for the aggressor's low success-rate, sanctions also and therefore may (ii) increase the aggressor group's success-rate.

One sanctioning arrangement that can increase costly contributions is peer punishment. Individuals, after they see their group members' contributions, can execute a punishment that is costly to themselves but more costly to the punished group member(s) [*13,19,36—39*]. Experiments have shown that individuals punish to motivate others to contribute more, that individuals respond to (the threat of) punishment by increasing subsequent contributions in public good provision [*36—39*] and intergroup contests [*13,18,19*]. Accordingly, Exp. 1 examined whether relative to baseline episodes in which peer punishment was absent, (i) the presence of peer punishment increased contributions to the group's fighting capacity especially in aggressor groups and (ii) whether such relative increase in out-group aggression translates in higher success-rates for aggressor groups. The experiment involved five baseline episodes and five consecutive episodes in which individuals could assign costly punishment within groups. In episodes with peer punishment each player i received 10 "decrement points" and could assign s ($0 \leq s_{i;j} \leq 5$) to any other player j in their group, with each point assigned reducing 1 from the punisher i's EE, and 3 from the punished player j's EE (punishment across groups was not possible). As in baseline episodes resulting earnings were then shown, which ended the episode (on each round, we randomly reshuffled the letter by which group members were identified, so that within the group [expecting] punishment was decoupled from reputation and reciprocity considerations).

Data were aggregated to the group-level and submitted to a 2(role: aggressor/defender) x 2(punishment: present/absent) ANOVA. Contributions to in-group defense were higher than to out-group aggression ($F[1,23]=41.97$, $p=0.0001$). Importantly, punishment increased contributions to out-group aggression ($F[1,23]=4.49$, $p=0.046$) but not to in-group defense ($F[1,23]=1.18$, $p=0.289$) (Fig 1A). Reflecting less coordination in aggressor groups, we observed that within-group dispersion in a conflict episode was larger for out-group aggression than for in-group defense, $F[1,23]=14.52$, $p=0.001$; dispersion was not influenced by punishment (Fig 1B; role x punishment: $F[1,23]=1.26$, $p=0.276$). Zooming in on non-contributors (individuals who invested zero, within groups and across episodes), ANOVA revealed effects for role, $F[1,23]=21.22$, $p=0.001$, punishment, $F[1,23]=9.25$, $p=9.25$, $p=0.006$, and role x punishment, $F[1,23]=8.60$, $p=0.008$ (Fig 1C). Punishment did not affect the (very low) number of people not contributing to in-group defense, but reduced the higher number of people not contributing to out-group aggression from 23% to 13%. Thus, peer punishment increased out-group aggression more than in-group defense. This notwithstanding, punishment failed to increase success: aggressor groups only won 23.75% of all episodes, a success-rate not conditioned by punishment (F[1,23]≤0.35, all p≥0.588) (Fig 1D).

In Exp. 1 peer punishment increased contributions more in aggressor than defender groups, but the increased fighting capacity in aggressor groups did not increase success (and reduced individual wealth; *Materials and Methods*). The relatively low success-rate for out-group aggression cannot be simply elevated by increasing the contributions. Exp. 2 targeted the alternative possibility, that out-group aggression fails because of poor coordination. If true, arrangements that enable groups to align its members' contributions into coordinated fighting should be particularly effective in aggressor groups, and increase their success-rate. One such arrangement is sequential decision-making [*52.40,41*], which has been shown to solve collective action problems in public goods provision [*40—43*]. In such a procedure, one individual moves first, allowing the rest of the group to adapt and follow the first-mover's lead [*40,41,43*]. It is seen in group-hunting carnivores like wolves—upon encircling their prey, the group waits until the most senior wolf leads by launching the first attack [*25,44*]—and has been identified as a minimal form of leadership with voluntary followers [*45,46*].

Experiment 2

In addition to the five baseline (simultaneous decision-making) episodes, Exp. 2 included five episodes of sequential decision-making: one member in each group was randomly selected to move first, then the randomly selected second player made its decision, and then the remaining third player made its decision [*43*]. Each decision was shown to the other two group members. The episode ended with back-reporting earnings.

Data were submitted to a 2(role: aggressor/defender) x 2(decision-making procedure: simultaneous/sequential) mixed-model ANOVA. Contributions to in-group defense were higher than to out-group aggression (F[1,21]=29.30, p≤0.001) and not affected by decision-making procedure (F[1,21]=0.07, p=0.799) or the role x procedure interaction (F[1,21]=2.71, p=0.115) (Fig 2A). As in Experiment 1, dispersion was larger for out-group aggression than for in-group defense, F[1,21]=5.42, p=0.030. However, a role x procedure interaction (F[1,21]=5.04, p=0.036) showed that sequential decision-making reduced within-episode dispersion for out-group aggression but not for in-group defense (Fig 2B). Zooming in on non-contributors, ANOVA revealed effects for role, F[1,21]=17.52, p≤0.001 and role x procedure (F[1,21]=6.36, p=0.020 (Fig 2C). Sequential decision-making did not affect the (low) number of people not contributing to in-group defense; in aggressor groups, however, sequential decision-making reduced the (higher) number of people not contributing to out-group aggression from 31% to 23%. Crucially, sequential decision-making almost doubled aggressor's success, from 20% under simultaneous decision-making to 35% under sequential decision-making (F[1,21]=6.05, p=0.023)(Fig 2D).

Conclusions and Discussion

The experiments together showed that (i) individual contributions to out-group aggression are weaker than those to in-group defense, and (ii) aggressor groups frequently fail to win the conflict, and waste individual resources on ineffective out-group aggression. This failure is (iii) unlikely to be caused by a lack of motivation to contribute to out-group aggression: Experiment 1 showed that peer punishment motivated individuals to contribute more to out-group aggression (but not to in-group defense) yet such higher contributions did not translate into increased success-rate for out-group aggression, leading to more wasted resources and lower overall welfare. Experiment 2 suggested that the relatively low success-rate for aggressor groups can be (iv) attributed to a failure to align and coordinate individual contributions to out-group aggression into effective collective action. This possibility was tested directly by computing, as an index of coordination, the within-episode intra-class correlation for contributions [*47; Materials and Methods*]. Relative to baseline, sequential decision-making increased coordination in aggressor groups more than in defender groups (Fig 3A). As shown also, sequential decision-making improved coordination more than peer punishment, and coordination predicted success for out-group aggression (r=0.30, t[90] = 2.94, p=0.004, Fig 3B). It follows that the aggressor group's failure to subordinate its defender is due to the aggressor's tougher task at coordinating within-group contributions into effective out-group aggression.

Willingness to contribute, coordinated collective action, and aggressor success-rates, were revealed in an intergroup conflict that modeled a clashing of out-group aggression by one antagonist, and in-group defense by its opponent. Real world analogies are group-hunting carnivores facing prey aggressively defending themselves, boards of directors attempting and warding-off hostile-takeover, tribal raiding and warfare, and most interstate disputes. For example, of the 2,209 documented interstate conflicts since the Congress of Vienna in 1816 [*27,48,49*], 67% were between aggressors seeking territorial or policy change in states that tried to defend the status quo [*Materials and Methods*]. Similar to our model, these aggressor-defender conflicts typically see aggressor success-rate around 35%—aggressor states win less than 30% of the interstate conflicts they are involved in, and industry boards pushing for hostile take-over are successful only 40% of the time (Fig 4A)[*50—52; Materials and Methods*]. Even hunting groups of wolves, lions, jackal, or killer whales are successful once in every three attempts (33%; Fig 4B) [*24,44,53—59;Materials and Methods*].

The finding that, across species and types of intergroup conflict, aggressors succeed 1/3 of the time on average may be due to the need to coordinate collective action into a costly attack sometimes, but not all the time. Indeed, aggressing all the time is energetically impossible. Also, it would set a permanent high level of in-group defense, and prohibit defender groups from being lured into an illusionary state of safety, with lowered defense and concomitant higher probability of successful capture [*31*]. To trump in-group defense, aggressors need to launch surprise attacks. Next to a willingness to sacrifice private resources, this requires careful within-group coordination.

Our conclusions derive, in part, from two laboratory experiments and may be limited to the specific parameters used to design the Intergroup Aggressor-Defender Conflict. In many intergroup conflicts, including those analyzed here, a single failure to defend adequately will result in the death for the prey yet following a failure to capture, a predator can find an alternative prey. As noted, however, attacking is very costly and when a predator repeatedly fails on consecutive attacks, it dies just like the prey that fails to adequately defend. Similarly, a company attempting but failing a hostile take-over may be weakened to the extent that bankruptcy cannot be avoided. Thus, whereas in the current experiments both aggressor and defender groups received a full reset of their endowments on each new round, oftentimes such reset can be less abundant, substantially delayed, and the cost of unsuccessful attack may be (much) higher than in our experiments. Whether these deter individuals from contributing to out-group aggression, or stimulate contributions and facilitate coordination of collective action, remains an issue for further research.

It has been argued that histories of intergroup conflict and competition may have acted as selection pressures favoring self-sacrificial contributions to one's group's fighting capacity, and contributed to the development and spread of institutions and technologies that enable groups to coordinate their members' activities and contributions [3,14]. Current findings align with these possibilities. However, the relatively high success rate of in-group defense suggests that evolutionary and cultural pressures may have favored capacities for cooperation and coordination when the group goal is to defend, rather than to expand, dominate, and exploit.

Materials and Methods

Experiments were approved by the University of Amsterdam Psychology Research Ethics Board (files 2014-WOP-3451 and 2015-WOP-4531); subjects provided written informed consent prior to the experiment, and were debriefed. Subjects were recruited on the University campus through an online recruiting web-site, for a study announced as "human decision making in groups." The experimental instructions used neutral language throughout (e.g., groups were referred to as Group A and B, contributions were labelled investments, and terms like in-group defense and out-group aggression were avoided). All subjects passed a comprehension check that consisted of two complete scenarios for one episode of the IADC from the perspective of their role, with their group winning and losing the episode, respectively. Experiments involved no deception and subjects received €10 show-up fee and M=€3.62 (range 0—€10) for their performance. Personal earnings in both experiments were based on the average of two randomly selected baseline episodes and two punishment (Exp. 1) or sequential decision-making (Exp. 2) episodes, provided that earnings would not drop below the €10 show-up fee and that both groups were rewarded equally (per local policies within our research laboratories). To preserve confidentiality, earnings were calculated afterwards and transferred to the subject's bank account.

Game-theoretic Analysis. Game-theoretic equilibria for the IADC game–with two three-person groups, each member assumed to have risk-neutral preferences and having a discretionary resource to invest from–were numerically estimated using a modified version of an algorithm developed by [35] in Matlab. The resulting unique mixed-strategy Nash equilibrium assigns the same strategy for players within the same group. For each pure strategy (range 0–20), the probabilities for investing in out-group aggression (in-group defense) are $p(0)$ = 0.5322 (0.0105); $p(1)$ = 0.0876 (0.5615); $p(2)$ = 0.045 (0.1050); $p(3)$ = 0.0321 (0.0249); $p(4)$ = 0.0068 (0.0241); $p(5)$ = 0.0067 (0.0198); $p(6)$ = 0.0095 (0.0894); $p(7)$ = 0.0283 (0.0844); $p(8)$ = 0.1125 (0.0087); $p(9)$ = 0.0152 (0.0076); $p(10)$ = 0.0066 (0.0067); $p(11)$ = 0.0054 (0.0051); $p(12)$ = 0.0046 (0.0044); $p(13)$ = 0.0054 (0.0050); $p(14)$ = 0.0134 (0.0064); $p(15)$ = 0.0594 (0.0080); $p(16)$ = 0.0147 (0.0089); $p(17)$ = 0.0043 (0.0073); $p(18)$ = 0.0024 (0.0053); $p(19)$ = 0.0019 (0.0040); and $p(20)$ = 0.0015 (0.0031). Thus, assuming common belief in rationality in individual group members, out-group aggression (in-group defense) is expected to average 10.15 (9.77), and aggressors (defenders) should win (survive) 32.45% (67.55%) of the episodes.

An alternative approach is to treat groups as single agents, with each group having risk-neutral preferences and being endowed with 20 x 3 = 60 resources. The strategies played in equilibrium imply that both groups only assign positive probabilities to strategies between 0 and 38 [*viz. 30*]. This yields expected out-group aggression (in-group defense) of 5.41 (7.25), and aggressors (defenders) should win (survive) 37.51% (62.49%) of the episodes. These estimates differ more from observed contributions and success-rates than those predicted by the admittedly more realistic individual-level equilibria.

Indexing Within-group Coordination. The ICC(2) describes how strongly individuals in the same group resemble each other. Unlike most other correlation measures it operates on data structured as groups, rather than data structured as paired observations. The index can be used to assess the amount of statistical interdependence within a particular social system (e.g., work-team) underlying individual-level data (e.g., individual ratings of group cohesion). Higher ICC(2) values reflect the level of consensus + consistency one would expect if an individual contributor was randomly selected from his or her group and within a particular decision round, and his or her scores were compared to the mean score (i.e., estimated true score) obtained from this group [47]. Thus, higher ICC(2) values in essence mean that group members are more similar to each other in the contributions made to their group's fighting capacity.

Additional Results. In both Experiments we explored the influence of conflict episode in 2(role) x 2(treatment) x 5(episode) ANOVAs. In Exp. 1, we found no effects involving episode, all Fs<1.28, all ps>0.25. In Exp. 2 we found that the role x sequence effect on dispersion (Fig 2B) was qualified by a role x sequence x episode effect, $F(4,18)$=4.736, p=0.009. The lower dispersion in aggressor groups under sequential decision-making disappeared in the final episode, which may reflect an end-game effect. We suggest that our main conclusions hold across conflict episodes.

In Exp. 1 we looked at ***targets of punishment***. We identified weak contributors (g≤5) receiving punishment ("weak contributors punished") or not ("weak contributors not punished"), and strong contributors (g≥15) receiving punishment ("strong contributors punished") or not ("strong contributors not punished"). A 2(role) x 2(contributor type: weak/strong) x 2(contributor type punished: yes/no) within-session ANOVA showed that in aggressor groups, more weak than strong contributors were punished (M=3.0 vs. M=1.2; $F[1,23]$=10.33, p=0.005), whereas in defender groups, both types were equally unlikely to receive punishment (M=1.10 vs. M=1.24; $F[1,23]$=0.02, p=0.890). Thus, especially aggressor groups biased punishment towards their weak contributors.

In both Experiments we examined ***individual wealth*** as a function of treatment and role. Intergroup conflict is wasteful and the experimental game mirrored this. Investments were always wasted, and individuals in defender (aggressor) groups could earn between 0 and 20 (0 and 40). Despite these differences in stakes, however, individuals in aggressor (defender) groups lost about 30% (35%) of their individual wealth (final wealth/20EE). In Experiment 1 we observed effects for role ($F[1,22]$=289.53, p≤0.0001, and punishment ($F[1,22]$=3.32, p=0.081 (marginal). Individuals in aggressor groups experienced a greater loss in wealth under punishment (M=14.206 versus M=15.317), as did individuals in defender groups (M=7.111 versus M=7.633). These numbers are conservative estimates because they ignore wealth reductions due to punishing others and being punished. In Exp. 2 we found that wealth was affected by both role ($F[1,21]$=254.13, p≤0.001), and role x decision-making procedure ($F[1,21]$=7.91, p=0.010): Under sequential decision-making, individuals in aggressor groups saw less wealth reduction than in baseline conditions (M=14.803. SE=0.609 vs. 13.469, SE=0.806); individuals in defender groups lost more under sequential decision-making (M = 6.712, SE = 0.654 vs. M = 5.724, SE = 0.649) which is a direct consequence of their aggressors becoming more effective under sequential decision-making (see Fig 2D). Thus, in aggressor groups the introduction of peer punishment reduced, and sequential decision-making increased wealth.

Because individuals were randomly assigned to groups we had all-male, all-female and mixed gender groups. A meta-analysis [16] found no significant differences between male and female participants in costly contributions to in-group efficiency, or out-group competitiveness. This we replicate here: Across current experiments, correlations between group-level contributions, within-group dispersion, and success-rate for in-group defense and out-group aggression on the one hand, and the number of males in aggressor and defender groups on the other ranged between -0.251 and +0.112, with all ps≥0.10. Current findings and conclusions generalize across gender and group composition, and we suggest that contributing to the group's fighting capacity may not be sex-specific.

Archival Analyses: Interstate conflict, hostile take-overs, and group-hunting predators. The Correlates of War project provides descriptive information on 2,586 interstate (militarized) conflicts since the Congress of Vienna in 1816 [48,49]. We integrated distinct datasets (MIDA and MIDB; Versions 4.01; both downloaded July 15, 2014 from www.correlatesofwar.org) to determine the structure of the interstate conflict as being symmetrical (0=between two aggressor states, or between two defender states) or asymmetrical (1=between an aggressor and a defender state). States are "revisionist" (aggressor) when they desire change in territory, policy, or government in their antagonist; "non-revisionists" (defenders) in contrast, seek to preserve and maintain the status quo with regard to territory, policy, or government [48,49]. Exactly two-third (67%) was between an aggressor and a defender state, and 33% was symmetrical ($\chi^2[1,2209]$=494.45, p≤0.0001). The datasets also contained coding for the outcome of these aggressor-defender disputes: aggressors were unsuccessful in 1,057 disputes (985 ended in a stalemate, and 72 ending in victory to the defender). Aggressors were relatively victorious in 239 disputes, reaching either a compromise (76), or a clear victory (163). Two-hundred sixty cases were coded "unclear." Excluding these gives a conservative estimate of aggressor success of 18%; coding "unclear" as aggressor success gives a liberal 38% – the point estimate thus being 28% (see also Fig 4B).

Following a survey of the literature on hostile takeover [26] we retained three sources that provided sufficient statistical detail on the number of hostile take-overs that were, or were not successful. Takeover attempts were defined as hostile when the target firm (defender) officially rejects an offer but the acquirer (aggressor) persists with the takeover [26], and thus represent a clashing of out-group aggression and in-group defense (e.g., the use of "poison pills"). Success was coded as take-over completed (1) or abandoned (0). Mitchell and Mulherin [51] analyzed takeover activity by major industrial corporations between 1982–1989. Takeover attempts considered friendly were successful in 268 out of 286 documented cases (93.7%); Takeover attempts considered hostile were successful in 85 out of the 243 documented cases (35%). Schneper and Guillen [50] collected data on 37 countries between 1988—1998 and detected 952 hostile takeover attempts, of which 336 were coded as successful (35%). Secondary analyses on data from Muehlfeld, Sahib, and van Witteloostuijn [52], who examined takeover activity in the newspaper industry between 1981 and 2000, revealed that 3,173 of the 3,615 cases were coded friendly and 442 as hostile. Completion rate was 76% for friendly, and 53% for hostile takeovers (235/442). This figure is higher than those reported in [50,51], possibly because these other sources considered mostly publicly listed companies with often sophisticated measures against hostile take-overs (e.g., "poison pills"). This may be less so in smaller companies present in the data from [52] and the lack of defense mechanisms may explain the higher success-rate seen for hostile take-overs. Notwithstanding the variability in years of study, type of industry, and geo-political regions, the sample-size weighted success-rate for hostile takeovers averages (656/1,637)=40% (Figure 4B)

Success-rates for group-hunting predators were obtained by (i) tracking citations to [*24,25*], (ii) surveying Web of Science (Nov. 2015) using the search terms "group" (or "collective") AND "hunting" (or "predation;" "predators;" "carnivores") AND "success" (or "kills;" "attacks;" "killings", "prey capture") and (iii) tracking citations to articles obtained under (i) and (ii). Included in the analysis here are reports focusing on mammalian predators with prey fighting back as the dominant response (rather than fleeing), and providing sufficient statistical detail to obtain a reliable estimate of predator success. Retained are [*44,53—59*].

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