In-group defense, out-group aggression, and coordination failures in intergroup conflict

Carsten K. W. De Dreu[a,b,1], Jörg Gross[a,b], Zsombor Méder[c], Michael Giffin[a], Eliska Prochazkova[a], Jonathan Krikeb[b], and Simon Columbus[d]

[a]Institute of Psychology, Leiden University, 2333 AK Leiden, The Netherlands; [b]Center for Experimental Economics and Political Decision Making, University of Amsterdam, 1018 WB Amsterdam, The Netherlands; [c]Humanities, Arts and Social Sciences, Singapore University of Technology and Design, Singapore 487372; and [d]Department of Experimental and Applied Psychology, Vrije Universiteit Amsterdam, 1081 BT Amsterdam, The Netherlands

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Intergroup conflict persists 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 multiround 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 the 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 (vs. 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 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 for 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 their resources (3, 4), something from which individual group members benefit too. Indeed, groups that most effectively elicit contributions from their members are most likely to be victorious, and perhaps intergroup competition and conflict pressure 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 (*i*) defend their in-group against out-group aggression; (*ii*) to aggressively exploit and subordinate the out-group; or (*iii*) 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 nontrivial 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 chimpanzees raiding their neighbors (11), to hostile takeovers in the marketplace (26), and to 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 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.

Significance

Across a range of domains, from group-hunting predators to 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 rivaling 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, such as leadership, communication, and infrastructure.

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[1]To whom correspondence should be addressed. Email: c.k.w.de.dreu@fsw.leidenuniv.nl.

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If in-group defense is indeed more intrinsically motivating and spontaneous, groups preparing for in-group defense should face fewer noncontributors 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 a 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 an intergroup aggressor–defender conflict (IADC) game. Six individuals randomly divided into three-person aggressor and defender groups each received 20 Experimental Euros from which they could contribute g ($0 \leq g_i \leq 20$) to their group's pool C ($0 \leq C \leq 60$). 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 $C_{aggressor} \leq C_{defender}$, defenders survived, and individuals on both sides kept their remaining endowments ($20 - g_i$). Thus, individual contributions in aggressor (defender) groups reflect out-group aggression (in-group defense). We used the game to test whether individual contributions to out-group aggression are weaker than those to in-group defense, examine how this possible difference translates into aggressor's success in subordinating its defender, and determine whether possible failures to subordinate defender groups are the result of 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 females; median age, 21 y). In Exp. 2, n = 132 subjects participated (78 females; median age, 22 y). In each experiment, one session involved six subjects divided at random into a three-person aggressor and a three-person defender group; Exp. 1 thus has 24 (144/6) IADC sessions, and Exp. 2 had 22 (132/6) IADC sessions. In both experiments, the six individuals invited for a single 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 Methods*). Thereafter, subjects indicated their contribution g ($0 \leq g_i \leq 20$) to their group's pool C and 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 feedback 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 follows). The order in which blocks were presented was counter balanced and found not to qualify the conclusions drawn here.

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 social welfare perspective contrasts with both individual and group welfare considerations. Specifically, the IADC has mixed-strategy Nash equilibria in which individuals contribute to out-group aggression (versus in-group defense) on average mean = 10.15 (versus mean = 9.77). This analysis also implies that aggressor (versus defender) groups win (versus survive) 32.45% (versus 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 (mean = −2.401; SE = 0.567), and in-group defense exceeded (mean = 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 [mean = −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 relatively low willingness to contribute to the aggressor's fighting capacity. If true, sanctioning arrangements that are known to increase contributions to public goods should 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 may also 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 or members (13, 19, 36–39). Experiments have shown that individuals punish to motivate others to contribute more and 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, the presence of peer punishment increased contributions to the group's fighting capacity, especially in aggressor groups, and whether such relative increase in out-group aggression translates into 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 point from the punisher i's Experimental Euros (EE), and 3 points 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) × 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. 1*A*). 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 [$F(1, 23) = 14.52$; $P = 0.001$], and dispersion was not influenced by punishment [Fig. 1*B*; role × punishment: $F(1, 23) = 1.26$; $P = 0.276$]. Zooming in on noncontributors (individuals who invested zero, within groups and across episodes), ANOVA revealed effects for role [$F(1, 23) = 21.22$; $P = 0.001$], punishment [$F(1, 23) = 9.25$; $P = 0.006$], and role × punishment [$F(1, 23) = 8.60$; $P = 0.008$] (Fig. 1*C*). 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

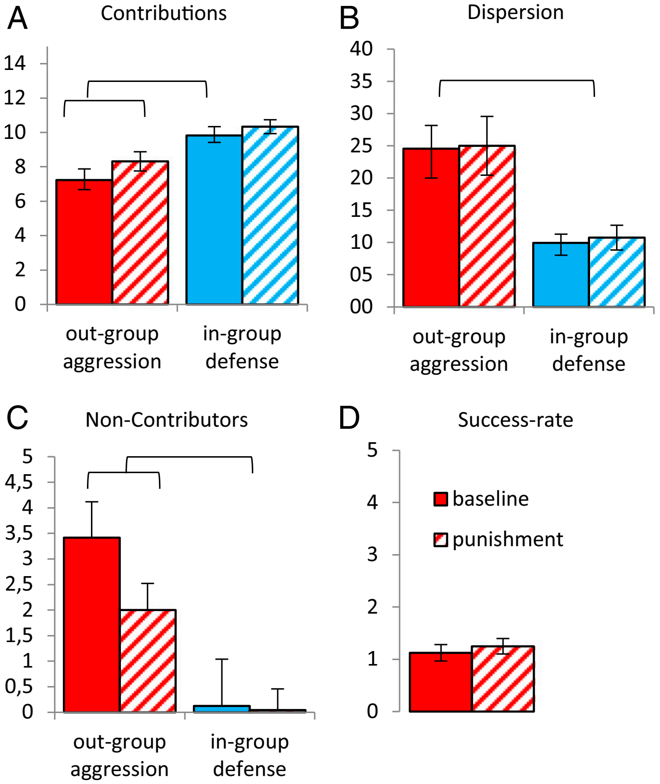

Fig. 1. Peer punishment in intergroup aggressor–defender conflict (displayed mean ± 1 SE). Connectors indicate difference at $P \leq 0.05$. (*A*) Contributions (range, 0–20). (*B*) Within-group variance (dispersion). (*C*) Number of noncontributors per group across conflict episodes (range, 0–5). (*D*) Aggressor success (range, 0–5).

increased out-group aggression more than in-group defense. This increased motivation notwithstanding, punishment failed to increase success: Aggressor groups only won 23.75% of all episodes, a success rate not conditioned by punishment [$F(1, 23) \leq 0.35$; all $P \geq 0.588$] (Fig. 1*D*).

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: out-group aggression fails because of poor coordination. If true, arrangements that enable groups to align their contributions into coordinated fighting should be particularly effective in aggressor groups, thus increasing their success rate. One such arrangement is sequential decision-making (40, 41, 51), 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 such as 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 their decision, and then the remaining third player made their 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) × 2 (decision-making procedure: simultaneous/sequential) mixed-model ANOVA. Contributions to in-group defense were higher than to out-group aggression [$F(1, 21) = 29.30$; $P \leq 0.001$) and were not affected by decision-making procedure [$F(1, 21) = 0.07$; $P = 0.799$] or the role × procedure interaction [$F(1, 21) = 2.71$; $P = 0.115$] (Fig. 2*A*). As in Exp. 1, dispersion was larger for out-group aggression than for in-group defense [$F(1, 21) = 5.42$; $P = 0.030$]. However, a role × 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. 2*B*). Zooming in on noncontributors, ANOVA revealed effects for role [$F(1, 21) = 17.52$; $P \leq 0.001$] and role × procedure [$F(1, 21) = 6.36$; $P = 0.020$] (Fig. 2*C*). 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 the aggressor's success, from 20% under simultaneous decision-making to 35% under sequential decision-making [$F(1, 21) = 6.05$; $P = 0.023$) (Fig. 2*D*).

Conclusions and Discussion

The experiments together showed that individual contributions to out-group aggression are weaker than those to in-group defense, and aggressor groups frequently fail to win the conflict and waste individual resources on ineffective out-group aggression. This failure is unlikely to be caused by a lack of motivation to contribute to out-group aggression. Exp. 1 showed that peer punishment motivated individuals to contribute more to out-group aggression

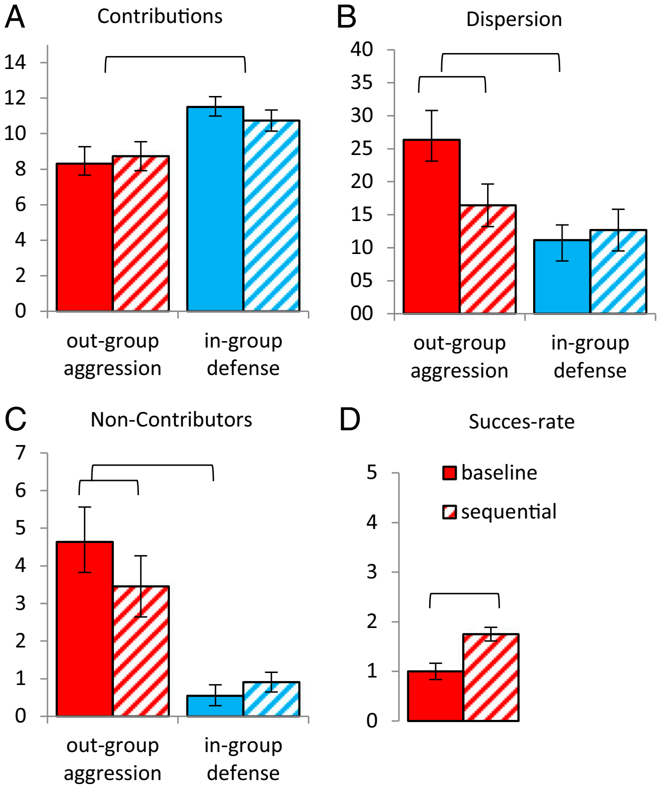

Fig. 2. Sequential decision-making in intergroup aggressor–defender conflict (displayed mean ± 1 SE). Connectors indicate difference at $P \leq 0.05$. (*A*) Contributions (range, 0–20). (*B*) Within-group variance (dispersion). (*C*) Number of noncontributors per group across conflict episodes (range, 0–5). (*D*) Aggressor success (range, 0–5).

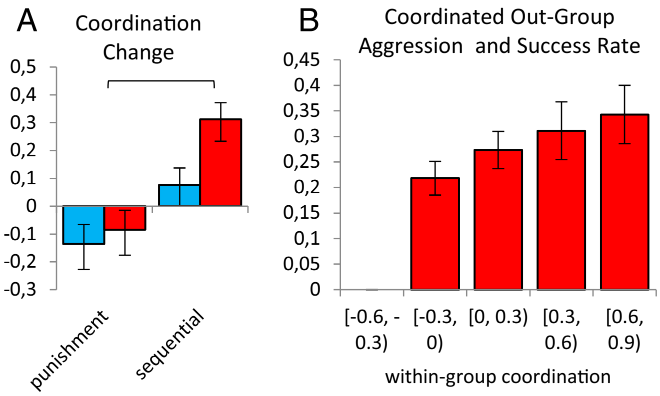

Fig. 3. Coordination in intergroup aggressor–defender conflict (displayed mean intraclass correlation ± 1 SE). Connectors indicate difference at $P \leq 0.05$. (*A*) Change from baseline when punishment or sequential decision-making is introduced. Blue (red) bars are defender (aggressor) groups. (*B*) Aggressor success as a function of aggressor's within-group coordination.

(but not to in-group defense), yet such higher contributions did not translate into increased success rates for out-group aggression, leading to more wasted resources and lower overall welfare.

Exp. 2 suggested that the relatively low success rate for aggressor groups can be 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 intraclass correlation for contributions (47) (*Materials and Methods*). Relative to baseline, sequential decision-making increased coordination in aggressor groups more than in defender groups (Fig. 3*A*). Also, as shown, 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. 3*B*]. It follows that the aggressor group's failure to subordinate its defender is a result of the aggressor's tougher task of 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 a 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), 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 an aggressor success rate of around 35%: aggressor states win less than 30% of the interstate conflicts in which they are involved, and industry boards pushing for hostile takeover are successful only 40% of the time (Fig. 4*A*) (49–51) (*Materials and Methods*). Even hunting groups of wolves, lions, jackals, or killer whales are successful once in every three attempts (33%; Fig. 4*B*) (24, 44, 52–58) (*Materials and Methods*).

The finding that, across species and types of intergroup conflict, aggressors succeed a third of the time on average may be a result of the need to coordinate collective action into a costly attack sometimes, but not all of the time. Indeed, aggressing all of 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, launching surprise attacks 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 IADC. In many intergroup conflicts, including those analyzed here, a single failure to defend adequately will result in the death for the prey, yet after 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 takeover 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 a reset can be less abundant or 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

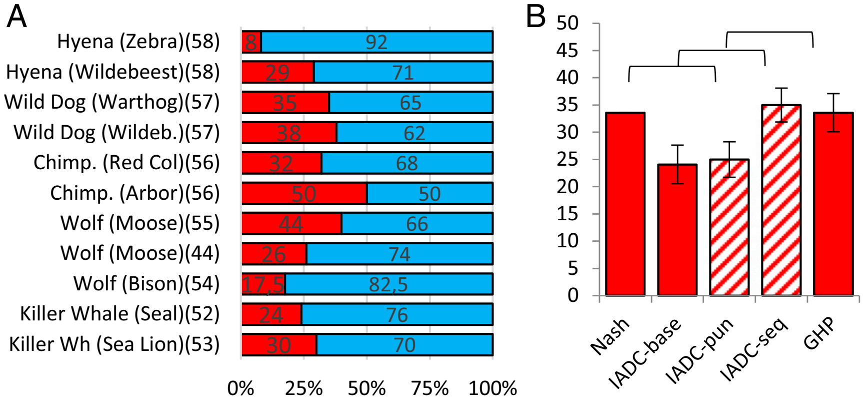

Fig. 4. Aggressor-defender success-rates. (*A*) Percentage of successful attacks by group-hunting animals (and their prey). Red (blue) bars are predator (prey). Numbers in bars are observed cases; bracketed numbers in *y* axis are source references. (*B*) Nash estimate for aggressor's success in the IADC (Nash), observed aggressor success in baseline treatments of Exp. 1 and Exp. 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 ± 1 SE); connectors indicate difference at $P \leq 0.05$.

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 before the experiment and were debriefed. Subjects were recruited on the university campus through an online recruiting website 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 group B, contributions were labeled investments, and terms such as 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 a €10 show-up fee and mean = €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 afterward 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 a discretionary resource to invest from, were numerically estimated using a modified version of an algorithm developed by Chatterjee (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 $20 \times 3 = 60$ resources. The strategies played in equilibrium imply that both groups only assign positive probabilities to strategies between 0 and 38 (i.e,, ref. 30). This approach 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 intraclass correlation [(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 with the mean score (i.e., estimated true score) obtained from this group (47). Thus, higher ICC(2) values in essence mean 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) × 2 (treatment) × 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 × sequence effect on dispersion (Fig. 2*B*) was qualified by a role × sequence × 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 ($g \leq 5$) receiving punishment ("weak contributors punished") or not ("weak contributors not punished"), and strong contributors ($g \geq 15$) receiving punishment ("strong contributors punished") or not ("strong contributors not punished"). A 2 (role) × 2 (contributor type: weak/strong) × 2 (contributor type punished: yes/no) within-session ANOVA showed that in aggressor groups, more weak than strong contributors were punished [mean = 3.0 vs. mean = 1.2; $F(1, 23) = 10.33$; $P = 0.005$), whereas in defender groups, both types were equally unlikely to receive punishment [mean = 1.10 vs. mean = 1.24; $F(1, 23) = 0.02$; $P = 0.890$]. Thus, in particular, aggressor groups biased punishment toward their weak contributors.

In both experiments, we examined individual wealth as a function of treatment and role. Intergroup conflict is wasteful, which the experimental game mirrored. Investments were always wasted, and individuals in defender (aggressor) groups could earn between 0 and 20 EE (0 and 40 EE). Despite these differences in stakes, however, individuals in aggressor (defender) groups lost about 30% (35%) of their individual wealth (final wealth/20 EE). In Exp. 1, we observed effects for role [$F(1, 22) = 289.53$; $P \leq 0.0001$] and punishment [$F(1, 22) = 3.32$; $P = 0.081$] (marginal). Individuals in aggressor groups experienced a greater loss in wealth under punishment (mean = 14.206 vs. mean = 15.317), as did individuals in defender groups (mean = 7.111 vs. mean = 7.633). These numbers are conservative estimates because they ignore wealth reductions resulting from punishing others and being punished. In Exp. 2, we found that wealth was affected by both role [$F(1, 21) = 254.13$; $P \leq 0.001$] and role × 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 [mean = 14.803 (SE = 0.609) vs mean = 13.469 (SE = 0.806)]; individuals in defender groups lost more under sequential decision-making [mean = 6.712 (SE = 0.654) vs. mean = 5.724 (SE = 0.649)], which is a direct consequence of their aggressors becoming more effective under sequential decision-making (Fig. 2*D*). 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-sex 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. The absence of significant sex differences was replicated here: Across current experiments, correlations among 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 sex and group composition, and we suggest that contributing to the group's fighting capacity may not be sex-specific.

Archival Analyses: Interstate Conflict, Hostile Takeovers, 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 (27, 48). 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; nonrevisionists (defenders), in contrast, seek to preserve and maintain the status quo with regard to territory, policy, or government (27, 48). Exactly two-thirds (67%) were between an aggressor and a defender state, and 33% were symmetrical ($\chi^2[1,2209] = 494.45$; $P \leq 0.0001$). 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 ended 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%, with the point estimate thus being 28% (see also Fig. 4*B*).

After a survey of the literature on hostile takeover (26), we retained three sources that provided sufficient statistical detail on the number of hostile takeovers that were or were not successful. Takeover attempts were defined as hostile when the target firm (defender) officially rejected an offer but the acquirer (aggressor) persisted 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 takeover completed (1) or abandoned (0). Mitchell and Mulherin (50) analyzed takeover activity by major industrial corporations between 1982 and 1989. Takeover attempts considered friendly were successful in 268 of 286 documented cases (93.7%); Takeover attempts considered hostile were successful in 85 out of the 243 documented cases (35.0%). Scheper and Guillen (49) collected data on 37 countries between 1988 and 1998 and detected 952 hostile takeover attempts, of which 336 were coded as successful (35.3%). Secondary analyses on data from Muehfeld, Sabib, and Van Witteloostuijn (51), 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 53.2% for hostile takeovers (235/442). This figure is higher than those reported in refs. 49 and 50, possibly because these other sources considered mostly publicly listed companies with often sophisticated measures against hostile takeovers (e.g., "poison pills"). Such measures may be less developed or even absent altogether in the smaller companies present in the data from (51), and the lack of defense mechanisms may explain the higher success rate seen for hostile takeovers. Notwithstanding the variability in years of study, type of industry, and geopolitical regions, the sample size weighted success rate for hostile takeovers averages 40.1% (656/1,637).

Success rates for group-hunting predators were obtained by tracking citations to refs. 24 and 25; 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 tracking citations to articles obtained under the first two methods. 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 refs. 44 and 52–58.

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