**Leaders of war: modelling the evolution of conflict among heterogeneous groups**

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**ABSTRACT**

War, in human and animal societies, can be extremely costly but can also offer significant benefits to the victorious group. We might expect groups to go into battle when the potential benefits of victory (*V*) outweigh the costs of escalated conflict (*C*), however, *V* and *C* are unlikely to be distributed evenly in heterogenous groups. For example, some leaders that make the decision to go to war may monopolise the benefits at little cost to themselves (“exploitative” leaders). By contrast, other leaders may willingly pay increased costs, above and beyond their share of *V* (“heroic” leaders). We investigated conflict initiation and conflict participation in an ecological model where single-leader-multiple-follower groups came into conflict over natural resources. We found that small group size, low migration rate, and frequent interaction between groups increased intergroup competition and the evolution of “exploitative” leadership; while converse patterns favoured increased intragroup competition and the emergence of “heroic” leaders. We also found evidence of an alternative “shared effort” outcome. Parameters that favoured high contributing “heroic” leaders, and low-contributing followers, facilitated transitions to more peaceful outcomes. We outline and discuss the key testable predictions of our model for empiricists studying intergroup conflict in humans and animals.

**KEYWORDS:** Leadership; Intergroup conflict; Game theory; Collective action problem; multi-level selection; Cooperation.

**INTRODUCTION**

War, defined as violent intergroup conflict (1), is one of the most conspicuous and destructive behaviours exhibited by *Homo sapiens*. Human warfare is highly variable, encompassing both small-scale skirmishes between bands of hunter-gatherers (2, 3) and the more organised, industrial conflict characteristic of the last century (3). Although sometimes considered a uniquely human enterprise (4–6), war has analogues in intergroup conflict observed across the animal kingdom, from territorial border contests between chimpanzees (*Pan troglodytes*) (7–9), to the battle lines of banded mongooses (*Mungos mungo*) (10, 11) and mass colony raids in army ants (12). Such violent behaviours might only be expected to evolve when the fitness costs, e.g. serious injury or death (9, 11, 13), are outweighed by the potential benefits of victory, e.g. the expansion of territory (9, 14), access to limited resources (8, 11, 13, 15, 16) or increases to prestige, status and reputation (17). However, this simple understanding – that war should evolve when the benefits are greater than the costs – becomes more complicated when considering heterogenous groups (18).

Social groups are intrinsically heterogeneous (19), with members that may differ in leadership status (20), social rank (14, 19–22), sex (13, 19, 20, 23), size (19), personality (19, 24, 25) or age (19, 20, 23), among other factors. This heterogeneity is likely to lead to individual differences in the risks and rewards of fighting (13, 19, 26, 27). For example, in African lions (*Panthera leo*), there are consistent differences between individuals in their willingness to engage in territory disputes, as some “laggard” females consistently hang back and exploit the fighting effort of others (24, 28). Similarly, in many primates such as vervet monkeys (*Chlorocebus pygerythrus*) (22), blue monkeys (*Cercopithecus mitis*) (29), Japanese macaques (*Macaca fuscata*) (23) and Verreaux’s sifakas (*Propithecus verreauxi*) (30), individuals contribute more towards intergroup conflict the higher their social rank and position in the dominance hierarchy. This is different from modern human societies in which studies of the US military have shown that the risks of sustaining physical combat injuries (31, 32), or experiencing poor mental health (33, 34), both decrease with increasing military rank. How inter-individual differences in the risks and rewards of conflict affect evolved levels of conflict effort and the propensity to initiate conflict has been little studied to date.

Two recent evolutionary models (13, 27) have examined how within-group heterogeneity affects the evolution of intergroup conflict. Gavrilets and Fortunato (27) asked how heterogeneity influences individual levels of investment in conflict effort between heterogeneous groups. They modelled intergroup conflict as a collective action problem in which individuals pay personal fitness costs to increase the probability of winning an intergroup fight. Specifically, they examined the evolution of conflict effort when group members occupied different social ranks, which determined priority of access to a contested resource. “Leaders” – which were assumed to be high-ranking individuals – benefited from priority of access and so received a higher value from the contested resource relative to low-ranking individuals. Given this disparity between ranks, low-ranking individuals were found to evolve low levels of conflict effort, but this reduction was more than compensated by elevated investment from high ranking individuals (27). Surprisingly, this lead to outcomes at which low-ranking individuals obtain higher fitness than high-ranking individuals. This is because the non-participatory followers are able to free-ride and benefit from the “heroic” leadership and increased conflict effort of their leaders (27).

A second model by Johnstone *et al.* (13) examined how a different form of leadership (decision making, not dominance) affected the probability of escalated conflict between groups. Specifically, Johnstone *et al*. (13) adapted the classic Hawk-Dove model (35) to investigate the evolution of conflict-escalating behaviours when leaders control decisions about whether their group fights or not. This model predicts that where leaders receive a disproportionately large reward, or are at a disproportionately low risk, they are more likely to lead their group into escalated fights with other groups (13). Such “warmongering” behaviour evolves because fighting increases the individual fitness of war leaders (who made the decisions), even when it leads to negative consequences for their followers (13). It is for this reason that exploitative warmongering behaviour has been hypothesised to be responsible for amplified levels of violence in both non-human animal (13) and human societies (36, 37). This model is supported with empirical data from banded mongooses (13), where dominant females are thought to selfishly lead male followers into violent and dangerous intergroup encounters in search of extra-group mating opportunities for themselves (13, 38). In contrast to Gavrilets and Fortunato’s model (27), the exploitative leadership model predicts that leaders should obtain much higher fitness payoffs than the followers as a result of intergroup conflict.

These two modelling approaches thus focus on two related but distinct aspects of the question of how heterogeneity affects conflict behaviour: Gavrilets and Fortunato (27) focus on the evolutionary stable strategy for investment in conflict effort, whereas Johnstone *et al.* (13) focus on the decision of whether to initiate and escalate conflict. What emerges from these two frameworks is a continuum between two extreme types of war leaders: “heroic” leaders, who invest much more in conflict than low-ranking followers, versus “exploitative” leaders, who initiate conflicts but invest relatively little.

Our aim here is to provide a more general model of the evolution of intergroup conflict behaviour, and to generate ecologically relevant predictions regarding conflict investment and escalation in heterogeneous groups. In the process, we synthesise and generalise the two theoretical approaches introduced above. Our model allowed fighting investment to evolve such that individuals could exhibit greater or lesser contribution to the conflict. This is consistent with the approach taken by Gavrilets and Fortunato (27), and unlike the Johnstone *et al.* model (13), in which all followers had enforced participation in fighting. We adopted heterogeneity of decision-making from Johnstone *et al.* (13). Specifically, only leaders were responsible for conflict decision making, which is consistent with leadership as defined in the relevant literature (21, 39). In keeping with both Gavrilets and Fortunato (27) and Johnstone *et al.* (13), we assume that leaders benefit more from the rewards of fighting. However, we also test the model with a full range of benefit distributions, biased either for or against the leaders.

We use the model to explore key ecological and demographic conditions that can favour different forms of conflict leadership. We also focus on scenarios where populations evolve relatively peaceful versus hostile interactions. The outcome is a set of novel, testable predictions relevant for empiricists studying intergroup conflicts in both human and non-human animal systems.

**METHODS**

*Broad overview of model*

See Fig. 1 for a graphical representation of the model. We simulate intergroup encounters using a finite population of distinct groups consisting of a single leader and multiple followers (Initialised with *Ngr* = 200 groups of *N* = 20 individuals; Table 1; see row 1 in Fig. 1). Upon meeting, the leaders of each group decide to play a “hawk” (aggressive) or “dove” (peaceful) strategy (35). Costs *C* (modelled as mortalities)and benefits *V* (modelled as births) are distributed to winning and losing groups (see row 2) based upon their strategy played (Table 2), and, if conflict escalates, a summed fighting effort of the group (Fig. 2). Following the resolution of encounters, a sequence of events takes place to mimic natural population dynamics (26). Firstly, random births and deaths are applied to re-establish a stable carrying capacity (row 3). Secondly, possible group fission takes place, where larger groups are more likely to split (40–46) (row 4). Finally, possible migration between groups can occur (row 5). This process is then repeated with the surviving groups for *N* = 20,000 rounds.

The leader of each group is chosen at random in the first round, and randomly re-assigned if the present leader dies. The rest of the group are assigned as followers. All individuals are assigned three fixed genes on a continuous scale between 0-1: i) Hawk-Dove score (*HD,* probabilistic propensity to play “hawk” rather than “dove” if the individual is leader), ii) Leader Contribution (*LC,* fighting effort if the individual is leader) and iii) Follower Contribution (*FC,* fighting effort if an individual is a follower). Importantly, all individuals are assigned values for all three genes, but which genes are expressed depends on their status as a leader or follower, which may change over time. For example, a leader will express their *HD* and *LC* gene but will also carry a dormant *FC* gene to pass on to offspring. Likewise, followers’ *HD* and *LC* genes remain dormant unless they become a leader. Each individual in the starting population is initialised with *HD*, *LC* and *FC* scores of 0.5. From this starting point, a mutation value is appliedwith each offspring created (mean = parent value; with standard deviation *Mut* applied; see Table 1), but each gene is bounded to take a value between 0 and 1. Asexual reproduction is assumed for simplicity (47, 48).

**Table 1. Parameter Table.** Default values for each parameter are in **bold**. Default values define the value taken for each variable when exploring other parameters in non-bold.*V* and *Ni* remained fixed and are investigated as relative to *C* and *Ngr* respectively. Parameters, including defaults, were chosen to illustrate a wide range of resulting outcomes (based on preliminary findings). We encourage researchers to use our code to explore other values and/or data-driven parameterisation of the model: [www.github.com/sankeydan/leadersOfWarModel](http://www.github.com/sankeydan/leadersOfWarModel).

|  |  |  |
| --- | --- | --- |
| **Parameter** | **Short form** | **Parameter values or calculation** |
| Round | N/A | **20,000** |
| Number of groups in starting population | *Ngr* | 100, **200,** 300, 400, 500 |
| Size of each group in starting population | *Ni* | **20** |
| Max group size | *Max* | 40, 50, 60, **70**, 80, 90 |
| Mutation strength | *Mut* | 0.005, **0.01**, 0.015, 0.02, 0.025 |
| Migration probability | *Mig* | 0, 0.01, **0.02**, 0.03, 0.04 |
| Value of resource | *V* | **6** |
| Cost of escalated conflict | *C* | 2, 4, **6**, 8, 10 |
| Pyrrhic Constant | *Pyr* | 0, **0.15,** 0.3, 0.5, 1 |
| Encounter rate | *Er* | 1, **2**, 3, 4, 8 |
| Reproductive skew in favour of leader | *Skew* | 0.5, 1, **2,** 3, 4 |

*Intergroup encounters*

Groups randomly encounter one another in pairwise interactions according to the encounter rate (*Er*), which determines the mean number of encounters per group per round of the model (see row 2. Fig. 1). The random generation of encounters allows multiple interactions between the same groups while other groups possibly avoid interaction altogether (in a given round). Encounters are resolved sequentially in the order in which they were generated. If a participating group becomes extinct in a prior interaction within the same round (e.g., if all group members die in the previous conflict) then all this group’s following interactions are cancelled.

Encounters begin with the focal and opponent leaders each making the binary decision whether to play an aggressive “hawk” strategy with probability *HD*, or peaceful “dove” strategy with probability (1 – *HD*). For example, a leader with a *HD* score of 0.8 would play “hawk” 80% of the time. All encounters beside hawk-hawk (i.e., hawk-dove, dove-hawk, dove-dove) are resolved without escalated conflict according to the payoffs listed in the interaction table (Table 2). For example, if an aggressive “hawk” group encounters a peaceful “dove” group, then the hawk group will obtain all the benefits of the resource (*V*), which is left uncontested by the fleeing dove group.

If two “hawks” meet, then the encounter escalates to a conflict where only one group can obtain the resource *V*. The other group will pay a cost for losing an escalated conflict which we define as *C* for the losing group. Winners are determined by totalling the fight contribution scores of each participating group (i.e., leaders’ *LC* + all followers’ *FC* scores) with the greater score determining the winner (Fig. 2A, B). We thus treat all group members as “perfect substitutes”, meaning that they are all equal in their capacity to contribute towards their group’s fighting effort (49, 50). “Perfect substitutes” is the most widely utilised group impact function when modelling intergroup conflict (26, 50, 51).

*Costly victories*

So far in our model, the average payoff for hawks is equivalent to the classical formulation of the hawk-dove game where hawks meeting hawks receive a payoff = (35). However, we also consider a modification to the payoff structure by including a parameter whereby winning groups also pay a cost of conflictdetermined by a pyrrhic *Pyr* parameter(Table 2). Such scenarios are reminiscent of a costly pyrrhic victory, originally named after the devastating casualties suffered by the victor King Pyrrhus against the Romans in the Battle of Asculum in 279 BC (52). This parameter reflects the reality that even victorious groups will often suffer casualties during a fight (this is also true of individual contests; (53)). As a real-world example, we provide data from banded mongooses (data collected from 13 mongoose groups between February 2000 and January 2020), where 4 of 34 deaths attributed to intergroup conflict occurred within winning groups (data provided in Table S1; 78 battles either ended in no deaths, or none were recorded). *Pyr* is bounded in our model between 0 and 1 and is used to calculate the winning group’s mortality cost (*C* \* *Pyr*,Table 2). Banded mongooses would be modelled with a *Pyr* of 0.13 (calculated from the ratio of 4:30; above), and we used a rounded 0.15 as the default parameter in our model (see Table 1). The conflict mortality rate observed in banded mongooses is similar to that of both chimpanzees and humans (13), although values of *Pyr* are unattainable from these data. When *Pyr =* 1, both winners and losers suffer the same costs of fighting. In extreme instances, this could lead to pyrrhic victories where the costs of fighting, even if successful, negate most or even all of the benefits obtained from the resource (*V*). Importantly, we can still recapture payoff structures comparable to the classic hawk-dove model by simply allowing *Pyr* = 0 (winning groups pay no costs).

**Table 2. Payoffs for different focal vs opponent strategies.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Focal strategy** | **Opponent strategy** | **Focal win / lose escalated conflict** | **Costs (number of mortalities to focal group)** | **Benefits (number of reproductions to focal group)** |
| Hawk | Hawk | Win; escalated | (*C \* Pyr*) | *V* |
| Hawk | Hawk | Lose; escalated | *C* | 0 |
| Hawk | Dove | Win; non-escalated | 0 | *V* |
| Dove | Hawk | Lose; non-escalated | 0 | 0 |
| Dove | Dove | Draw; non-escalated | 0 | *V*/2 |

*Payoff resolution*

Payoffs are resolved after each intergroup encounter according to the outcome table (Table 2). Values of *V* and *C* are directly translated into reproductions and mortalities, respectively. Payoffs are resolved such that mortalities take place first, and then any reproductions occurring afterwards do so from among the surviving group members. For example, if a victorious group suffers costs of *C* \* *Pyr* = 4 and wins a payoff of *V* = 6, the group will lose four group members through mortality, and then gain six new members through reproduction (how these reproductions are distributed between individuals in the group is explained below). Mortalities represent either direct mortality during combat, or those that occur indirectly, such as through infected wounds or from loss of access to resources (9). Reproduction represents how the spoils of war, such as increased territory size or access to food and mating opportunities can directly be translated into increased reproductive output (15).

Distribution of costs (mortalities)

The value of *C* (or *C* \* *Pyr*) equates to the number of mortalities that the group will suffer. If *C \* Pyr* is not an integer, the fraction is converted into a probability that another individual will perish. (For example, if *C \* Pyr* = 3.5, the winning group will suffer three or four mortalities with equal probability.) Mortalities are applied sequentially and distributed proportional to the effort that group members contributed towards the fight. Therefore, individuals that are most influential in contribution towards a group victory (Fig. 2B)are also the most likely to die when the group suffers mortalities (Fig. 2C). More specifically, the probability of death within a group is determined as the effort of the individual divided by the summed effort of the group (also see Fig. 2A, C):

Where *n* is the number of followers in the group, *LC* is the *LC* score of the leader and *FCx* is the *FC* score of the focal follower *x*.

If the number of mortalities a group receives exceeds the number of contributing group members (*LC* or *FC* > 0) then, once mortalities have been applied to contributing group members, mortalities are applied at random among non-contributing group members (*LC* or *FC* = 0). At any point, if groups consist of fewer than two individuals (one leader, and one follower) then they are considered extinct and removed from the population.

Distribution of benefits (reproductions)

In our model, the probability of reproduction does not depend upon individual fight contribution scores (*LC* or *FC*). Some studies have suggested that highly contributing fighters are more attractive and expected to benefit from increased reproductive success, e.g. “sexy soldiers” (15, 54, 55), whereas others have argued that the costs of fighting decrease the reproductive success of fighters relative to non-combatants, e.g. “worn-out warriors” (56–58) . Rather than arbitrarily choosing a position on this argument, the probability of each individual reproducing in our model is distributed through the group evenly, except leaders which exhibit a *skew* that reflects their share of reproduction relative to the followers. We test a range of conditions from *skew*<1 (leaders reproduce less and have lower fitness than followers, e.g., lions (24) and theoretical models (59, 60)) through *skew*=1 (everyone reproduces roughly equally e.g., plain zebras and bottlenose dolphins (20)) to *skew*>1 (leaders have higher likelihood of reproducing, e.g., meerkats, hyenas and white-faced capuchins (20)). Consistent with both Gavrilets and Fortunato (27), and Johnstone *et al.* (13) we chose a positive *skew* as default (*skew* =2*;* Table 1).

*Population dynamics*

Finite population modelling

At the end of each round, after all paired encounters have been resolved, we simulate biologically relevant changes to the population structure. Our model assumes that population size is limited by resources in the environment and tends toward a stable carrying capacity (61, 62) (see row 3. Fig. 1). Therefore, after resolving all payoffs from intergroup encounters in a given round, we apply additional reproductions or mortalities to ensure the population size remains stable and prevent it either depleting to zero or increasing to unsustainable levels. Both outcomes are possible in this model, because of encounters with asymmetric payoffs whereby one group gains a different amount (in reproduction) than the other group loses (in mortality). At this step, both reproduction and mortality are applied equally and randomly, despite any differences in leader status or genotype scores. Any new individuals born inherit a follower status in the same group as their parent.

Fission

Next, we incorporate group splits, which become more likely with increasing group size, and for which there is empirical (40, 42, 44, 45) and theoretical (41, 43, 46) evidence (see row 4. Fig. 1). In our model, splitting is inevitable if groups are at or above the maximum group size parameter *Max* (Table 1) and impossible for group sizes fewer than four, because two is the minimum viable group size for each daughter group (i.e., one leader and one follower). Group splitting for groups between four and *Max* individuals is governed by a standard exponential increase, meaning splitting has a low probability that increases exponentially as group size approaches *Max*. In nature, the size of each subgroup after splitting can be highly variable, from evictions of small subgroups (63) to larger (relatively even) group splits (64, 65). Our model does not bias between large or small group splits, and so determines the size of the daughter group from a uniform distribution with a minimum group size of two and a maximum of one half the total group size (rounded down in the case of decimals). When a group splits, the leader remains in position to lead the larger, parent group (if daughter and parent groups are the same size, then the leader is assigned to a daughter/parent group at random. A new randomly selected leader – chosen amongst followers – is assigned to lead the daughter group. Leadership has been demonstrated to arise spontaneously from previously identical individuals through a runaway process starting with minimal stochasticity (59), which validates this choice within our model.

Migration

Intergroup migration is the final step in each round of the model (see row 5. Fig. 1). Migration dynamics have a large effect on population structure and relatedness, which in turn can predict pro-social behaviours towards own group members (26, 66, 67) and hostility towards other groups (26, 67), such as the willingness to fight (26, 68, 69), which we investigate here. Therefore, a migration parameter is an appropriate inclusion. All followers can migrate (i.e., change groups) at the end of each round. The probability that any follower will migrate each round is determined by *Mig* (see Table 1). When migrating, an individual emigrates to another group at random and with equal probability.

**RESULTS**

*Model iterations*

We ran 15 iterations of each set of parameters tested in our model (Table 1) to understand the influence of each parameter on the emergent population (sample size = 15 per set of model parameters). During the simulation, for each group, in each round, we output the leader’s *HD* and *LC* score, and one mean *FC* value from all their followers (but see Fig. S1 in Supplementary Materials for output using the *FC* of each individual follower). For analysis, a mean of the population phenotype for each trait was calculated from the last 5000 rounds (representing 25% of the model) and taken for further analysis. Waiting 15000 generations allowed the model to stabilise beyond the point at which no more changes to the phenotype were observed (which was typically prior to 5000 generations).

*Follower and leader contributions*

We found that both “heroic” leader outcomes (high leader contribution, low follower contribution) and “exploitative” leader outcomes (low leader contribution, high follower contribution) emerged readily within our model, in addition to another condition we term a “shared effort” outcome (high leader contribution, high follower contribution).

Varying the maximum group size (*Max*) was found to greatly influence leader contributions (*LC*) and follower contributions (*FC*), with increasing group size causing a shift in outcome from all individuals contributing highly (“shared effort”), to a “exploitative” leader outcome, and then to a “heroic” leader outcome (Fig. 3A). Similar trends were also found with increasing values of the cost of escalated conflict *C* (Fig. 3B)*,* and migration rate *Mig* (Fig. 3C), whereas increasing the encounter rate, *Er,* resulted in a transition in outcomes in the opposing direction (Fig. 3D). At low values of reproductive skew (*skew*) leaders contributed more than followers and vice versa at higher values (Fig. 3E).

*Evolution of hostile interactions*

We found *HD* score was highly correlated with follower contribution (*FC*) (Fig. 4A, B), such that aggressive “hawk” strategies were more common when groups had higher *FC* scores (Pearson Correlation Coefficient = 0.999; correlation between models displayed in Fig. 4A with those in Fig. 4B, *N* = 150). This is a strikingly high correlation when considering that the two genes evolved independently and suggests a possible causal relationship. However, *HD* score (as well as *FC*) also decreased when there were higher costs (*C* – Fig. 4A; and *Pyr* – Fig. S2). Therefore, a valid alternative hypothesis to a causal relationship between leader *HD* and follower *FC* is that costs of conflict are driving both leader *HD* and follower *FC*. To further investigate the effect of follower contribution on hawkishness independent of fighting costs, we fixed the values of *C* and *Pyr* at default values (Table 1), and changed other variables known – from our results (Fig. 3; Fig. S3) – to favour high or low levels of *FC* (Table 3, Fig. 4 C), and then measured the outcomes.

**Table 3: Comparison of low *FC*, default and high *FC* starting conditions.** Parameters not shown take the same values as the defaults in Table 1.

|  |  |  |  |
| --- | --- | --- | --- |
| **Parameter** | **Low *FC* Conditions** | **Default Conditions** | **High *FC* Conditions** |
| Max group size | 90 | 70 | 50 |
| Migration probability | 0.04 | 0.02 | 0.01 |
| Encounter rate | 1 | 2 | 3 |
| Reproductive skew in favour of leader | 1 | 2 | 4 |

We found that *HD* score could still covary with follower contributions (*FC*), despite fixing costs (*C* and *Pyr*) (Fig. 4C). When the model was parametrised with conditions known to favour high follower contributions, *HD* score increased (Table 3; Fig. 4C). When conditions favoured low follower contributions, *HD* score decreased (Table 3; Fig. 4C), although not to zero because hawks can always invade pure dove populations through frequency-dependent selection (35).

**DISCUSSION**

We have used a single-leader-multiple-follower evolutionary model to explore the effect of ecology and demography on conflict initiation and conflict participation in warfare between heterogenous groups. Our results suggest that demographic and ecological parameters can shift the population between three classes of outcomes: from “heroic leadership” with low contributing followers, through “exploitative leadership” with high contributing followers and “shared effort” outcomes, with both leaders and followers participating in conflict. For example, when 1) the maximum group size is high, 2) intergroup encounters are infrequent, 3) leaders reproduce less than followers, 4) the costs of escalated conflict are high or 5) follower migration rates are high, then leaders contribute more during conflict relative to followers (“heroic” leaders). These outcomes – where followers are less willing to participate – are associated with relatively more peaceful intergroup encounters at the population level, and the evolution of conflict avoidance strategies. In contrast, outcomes with high participation levels among followers are strongly correlated with increased intergroup aggression and hostility.

*Evolution of conflict investment*

In order to explain the different range of outcomes from our model it is useful to invoke the framework of multi-level selection (47, 70–72). Here, changes to parameters either emphasise intergroup conflict (and selection at the level of the group) or intragroup conflict (and selection at the level of the individual). Within-group altruism (e.g. high fight contribution) is more likely to evolve with high intergroup and low intragroup conflict (73–75). As a first example, consider changes to the intergroup encounter rate, which directly encodes higher rates of intergroup conflict into the model. With increased encounter rates, high participating “cooperative” groups outcompete lower participating “selfish” groups (which tend toward extinction). As a result, both follower and leader participation increase at higher intergroup encounter rates (Fig. 3D). Conversely, increased migration rates are known to enhance intragroup competition and undermine cooperation (76–78). This is because high-participating groups are vulnerable to invasion by selfish individuals who participate very little but can free-ride on the efforts of a cooperative group. Another factor promoting intragroup conflict is maximum group size. It is well known that larger group sizes can result in increased susceptibility to collective action problems (18, 79, 80), with each individual shying away from sharing the costs necessary to produce a public good (in our case, victory in intergroup conflict).

Although this multi-level selection argument explains the contribution patterns of followers, it does not explain why leaders contribute differently than followers across much of the range of parameters we explored. Here, it becomes important how often high participation from a leader will be decisive in determining victory for their group. Consider the case where intergroup conflict levels are high, but not extreme, for example *Er* = 5 from Fig. 3D. Here, follower participation is large across the population (i.e., FC is close to 1), and therefore all leaders are likely to have highly willing followers. In such cases (with summed fighting strength approximately equal to group size) it would take a meeting of two almost-identically sized groups for a highly participating leader to swing the outcome in their favour. In most cases, the increased risk of mortality (associated with high participation) is enough to outweigh this small probability of benefit, and leaders shirk away from battle as a result. This echoes the result of Johnstone et al. (13) where leaders exploit their high-participating followers. At the other end of the scale, as follower participation declines, the group’s success will be highly dependent upon the participation from their leaders, and thus high participation from leaders becomes favourable. Gavrilets and Fortunato (27) found a similar result, whereby high-ranking individuals applied extra effort to offset a collective action problem and overcome the reduced contributions of the lower-ranking individuals.

Our choice to treat all group member contributions as “perfect substitutes” (26, 49–51), meaning that all individuals having equal capacity to contribute to a fight, could limit the generalisability of our results across different contexts of intergroup conflict. For example, in some taxa such as wolves and banded mongooses, some individuals (notably older males) have a disproportionate influence on conflict outcomes (81; Green et al. *in review)*. Extreme examples are provided in the economics literature where a “weakest link” (e.g., high interdependence between group members) and “best shots” (e.g., champion warfare) group impact function explore only the least and highest contributor respectively (50, 51). Another approach, not explored in our model here, is to differentiate participation on the basis of attack or defence. Models that consider this approach find differential investment depending on whether resources are being defended or attacked (82). Nevertheless, a summed “perfect substitutes” approach, as used in our own model, is the most widely utilised group impact function (50, 51), and its use successfully captures many of the common elements of intergroup conflict (e.g., larger groups are more likely to win).

*Real world relevance of parameters*

Maximum Group Siz*e (Max)*

Our results suggest that in larger groups, high-ranking leaders will contribute more towards battles than followers. Supporting this finding are observations from spotted hyena (*Crocuta crocuta*) clans, which may contain 90 or more individuals (83). Within these clans, high-ranking adult females are most often observed at the front line during conflict (20, 84). As these individuals are also disproportionately responsible for initiating conflict (84), we would also predict (after accounting for any other differences in other important ecological variables) i) that larger groups within the population would be more aggressive (Fig. S4), and ii) lower levels of conflict in hyena populations with larger clan sizes (e.g. 90+ in Kenya (83, 84)) than smaller clan sizes (e.g., 15+ in Namibia (85, 86)) (Fig. S4). Conversely, humans do not fit the outcomes of the model, with leaders of larger groups having been shown to contribute less (20). We suggest that differences in humans could be due to coercion, including but not limited to punishment (87, 88), or the spread of cultural ideas from the leaders to followers to induce within-group altruism (89, 90). To test the relevance of our conclusions in humans, the intergroup game we propose could be broadly replicated in experiments involving human participants following methods from a large body of experimental work into contest theory (for reviews see: (50, 91)).

Intergroup Migration Rate *(Mig)*

Increased migration rates led to decreased contributions among followers and increased contributions in leaders (Fig 2C). As migration rates increase, cooperation can be more easily undermined by faster reproducing non-cooperators (69). Followers evolve non-cooperation, and leaders “pick up the slack” to remain competitive with other groups, and avoid individual and group extinction, consistent with Gavrilets and Fortunato’s conclusion (27). In animal systems where the potential for intergroup migration is limited, e.g., there are high dispersal costs (92), we would expect to see groups consisting of highly contributing followers and aggressive and “exploitative” leaders. Yellow baboons (*Papio cynocephalus*) appear to support this prediction, because males are highly vulnerable to predation during solo dispersals (93), and also participate in frequent, and often lethal, intergroup conflict (94, 95).

Reproductive skew in favour of the leader *(Skew)*

Our model predicts that increased reproductive skew (biased towards the leader) will select for more cooperative followers and “exploitative” leaders, who are best able to minimise their mortality risk and therefore maximise the length of their reproductive tenures (Fig 3E). When leaders have low contribution, competition between groups will favour high contribution from followers. As reproductive skew increases, the follower contributions rise, as they are determined increasingly by the leaders (who will be motivated to sire highly contributing offspring) and less by follower reproduction (who will be motivated to decrease contributions). Different animal systems, with varying degrees of skew, represent ways to test this prediction. For example, in African lions, the relative fitness benefits of intergroup conflict are skewed against the leading females (e.g., *skew* <1)(20), which our model predicts will lead to low contribution scores among followers (Fig. 3E). This is seen in nature, with observations of “laggard” females who are reluctant to participant in territorial conflicts (24, 28). By contrast, meerkats have a high degree of reproductive skew, with leaders able to monopolise the benefits from intergroup conflict (20). Given that these leaders are the same individuals which initiate conflicts (14, 20), our model provides a direct prediction, that we would expect contribution scores among these leaders to be lower than the mean contributions of followers once battles ensue (Fig 2E). Furthermore, we might predict that leaders would exhibit “warmongering” behaviour, initiating more conflict than is beneficial for their group (13, 14).

*Evolution of conflict initiation and hostility between groups*

Classic work has shown that the frequency of escalated conflict observed in a population is highly dependent on the costs of fighting (35). We show that whether groups interact peacefully or are hostile to one another is dependent not only upon these costs, quantified in our model through *C* (Fig. 4A) and *Pyr* (Fig. S2 in Supplementary Materials), but also the contribution of followers (Fig. 4C). This finding is intuitive, as leaders will be incentivized to escalate more conflicts when they are supported by large numbers of ready and willing followers, compared to when their followers are reluctant to participate in conflict.

In some non-human animal or human societies followers might not have the freedom to individually lower their contributions. This might be the case in banded mongooses, where there are high levels of group synchrony (96) and acting alone is not an option due to predation risk (96, 97). In humans, the presence of coercion and punishment, such as court martials for cowardice as was common during World War I (98), may provide a similar constraint on the evolution of follower contributions, and serve to sustain higher-than-expected levels of aggression. Conversely, if the costs of conflict increase or the contribution levels of followers are chosen freely, then more mixed hawk-dove strategies are favoured, and the mean population level of intergroup aggression decreased. This result provides a testable prediction for researchers studying intergroup conflict, namely that for populations with larger maximum group sizes, higher migration rates or lower frequency of intergroup encounters, we would find a lower level of escalated intergroup conflict.

Mixed Hawk-Dove strategies are more peaceful when compared with non-negotiable fighting over every resource, as is the case when populations play purely hawk strategies. However, hawks will continue to succeed when invading majority dove populations (35), eliminating the possibility of entirely peaceful populations (Fig. 4C). Exploring these mixed strategy populations, we found that, within the same population, larger groups were more likely to exploit their favourable position and behave more aggressively than small groups (Fig. S4). This difference between the aggression levels of small and large groups increases as maximum group size increases, even as population mean conflict levels decrease. This may be reflected in modern international interactions, whereby larger powerful nations are rarely challenged by smaller ones, and have been found to start more wars (99).

The work presented here provides a base model which may now be extended further to explore whether any conditions can reduce the evolution of intergroup hostility further than we observed here. For example, a classic argument in political theory (100–102) is that more democratic societies, with more distributed and shared forms of decision making, are expected to evolve to be more peaceful, relative to non-democratic societies (such as the dictatorial one-leader, multiple-follower groups we have presented here). Democratising the conflict initiation process, e.g., by allowing multiple individuals to “vote” and contribute towards a collective hawk-dove strategy, would constitute a simple extension to our model to test this theory directly. We could also start to model the cultural evolution of strategies, allowing for dynamics such as coercion and copying, rather than using fixed genotypes as presented in the model here. Finally, we could allow for alliance formations between groups, which rational actors may seek when conditions are favourable (50, 103). Extending our model in such a way would provide a way to adapt it to different, related questions of interest, in both the animal and human sciences.

**CONCLUSION**

Our model shows how ecological and demographic conditions influence the evolution of intergroup warfare, both in terms of differential follower and leader participation, and variable rates of aggression. In the process, we have been able to generalise two previous evolutionary models (13, 27) of intergroup conflict and generate new ecologically relevant predictions. The parameter values we have chosen, such as maximum group size, intergroup migration rate, and intergroup encounter rate are designed to be tractable and measurable for empiricists, and we encourage other researchers to test the hypotheses implicit in our model directly in their own study systems.

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**AUTHOR CONTRIBUTIONS**

D.W.E.S and K.L.H. conceived the idea for the paper under the supervision of M.A.C.; D.W.E.S and K.L.H wrote the code for the model, with input from M.A.C, R.A.J and all other co-authors; K.L.H and D.W.E.S wrote the manuscript with extensive feedback from all co-authors.

**CODE AVAILABILITY**

All code is freely available at [www.github.com/sankeydan/leadersOfWarModel](http://www.github.com/sankeydan/leadersOfWarModel).

**FIGURE CAPTIONS**

**Figure 1. Schematic of model process in simplified population of three groups.** All rows are discussed in greater detail in Methods. **Row 1.** population as it stood following the previous round (for the first round see section *Broad overview of model*). Groups each have one leader (purple), multiple followers (green) and a group ID (numbered). **Row 2.** Encounters are generated and payoffs are then resolved (Table 2). **Row 3.** Random deaths or births are applied with equal probability for each member of the population to re-establish the same population size. **Row 4.** Fission. **Row 5.** Migration. **Row 6.** New population will feed back into row 2, for the next round. There were *N* = 20,000 rounds in each of our iterations of the model. Each iteration was repeated 15 times for a distinct set of parameters.

**Figure 2: Contributions: a trade-off between group fighting success and individual mortality.** Illustration of how escalated conflicts are resolved between two groups (each group *N* = 5) (escalated conflict occurs when both groups play a “hawk” strategy). Leaders are coloured (red or blue) while followers are black. Group membership and identity is consistent throughout the three panels. **A)** Each individual positioned according to their *LC* score (leaders) or *FC* score (followers), such that higher values represent individuals who contribute more to the fight and are positioned closer to a figurative ‘battle line’. The group on the left side of the battle line is described as having a “heroic” leader (*LC* higher than group mean *FC*) whereas the group on the right side of the battle line have a more “exploitative”, low contributing leader (*LC* lower than group mean *FC*). **B)** A sum of each group’s contribution score (leaders *LC* and all followers *FC*) determines their group’s combined fighting strength (ordered from lowest to highest contribution scores). Here, the group with the “heroic” leader have a greater summed score and would win the fight. **C)** Each individuals’ contribution score also determines their individual risk of death when mortalities are suffered as a result of escalated conflict (ordered from lowest to highest contribution scores). This mortality probability is an individual’s contribution score, divided by the summed score of their group.

**Figure 3. Influence of ecological or demographic parameters on fighting contribution scores.** Follower contribution (*FC*; green) and leader contributions (*LC*; purple) (mean (dots) ± SE (bars); see raw data in Fig. S3). All other variables not on x-axis are set at default values (highlighted in bold in Table 1). Each unique combination of parameters ran 15 times, with each model run representing one datum (population mean of followers’ *FC* or leaders’ *LC* for final 5000 rounds of an iteration).

**Figure 4. Hawk-dove decision (*HD*) driven by low costs and high follower contribution scores.** **A)** *HD* score (mean ± SE for 15 iterations) as evolved under parameters fixed at the default values except for cost (*C*), which varies on the x axis. **B)** (as in **A**) except showing evolved follower contribution *FC* score (mean ± SE for 15 iterations). **C)** *HD* score when parameter values favoured different levels of follower contribution (*FC*). This shows that even when costs *C* and *Pyr* were frozen at default values (6 and 0.15 respectively), mean hawkishness (*HD score*) of populations increased from low *FC*,through default, to high *FC* conditions (Table 3; *N* = 15 replicated iterations for each condition), suggesting *FC* has an independent causal influence on *HD*.

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