

Todo list

link and make

do each section biol and add example case (f11)

Mongoose Proj

Matishalin Patel, Michael Cant, and Rufus Johnstone

1 Abstract

Lorem Ipsum

keywords:

intragroup cooperation, intergroup conflict, game theory, social evolution

2 Introduction

Intergroup conflict is thought to be the key driver in the evolution of cooperation ???. However our understanding of the key evolutionary and ecological drivers of inter group conflict is far from complete. In social organisms both between and within group conflict is variable and seems both positively or negatively correlated with between and within group cooperation (?). This variety of responses shows that a better understanding of the driver of cooperation and conflict are needed to fully explain how within and between group conflict evolves. These traits of cooperation and conflict can have large fitness consequences and are often key to the animals behaviour and lifecycle (??). Understanding these drivers has real impact on the implementation of conservation strategies and predicting responses to habitat disturbances.

21 Previous models have shown that intergroup conflict can favour within
22 group cooperation. However, these models often link the payoffs of coop-
23 eration and conflict so as to enable a direct synergism between the two (??).
24 This assumption is suited to answer certain questions in the evolution of
25 human societies however hides the tension between cooperation and con-
26 flict that exists in other cooperative groups. Specifically, we might expect
27 performing well in intergroup encounters makes one less willing or able to
28 cooperate with others or vice versa. This could be due to fatigue caused
29 by intergroup effort reducing the ability for individuals to cooperate within
30 groups or some epistatic behavioural effect where aggression behaviours be-
31 tween groups are generalised to within group interactions.

32 In nature organisms evolve complex behaviours that respond adap-
33 tively to the current situation it finds itself in. Individuals in smaller groups
34 might fight harder whereas in larger groups they might cooperate more as
35 benefits are synergistic. These state dependent behaviours are crucial as
36 they allow conditional behaviour that is adapted to the individuals specific
37 circumstance rather than only doing what is optimal on average.

38 ? proposed that cooperation increased in harsh environments. Evi-
39 dence since then has been varied, it is true that harsh environments are
40 colonised at a greater rate by cooperative species (?). However, it is not
41 clear if harshness itself selects for cooperation. Previous theoretical work
42 has shown that resource limitation does select for cooperative strategies by
43 essentially modifying the payoffs of the underlying game (??). Establishing
44 how cooperation and conflict interact with resources however has been hard
45 as previous models have not explicitly separated the sociality of between-
46 group conflict and within-group cooperation from each other and with an
47 underlying ecological measure of resource availability (harshness).

48 In this paper we model two separate traits one controlling between-
49 group conflict and one controlling within-group cooperation. They are both

50 social traits that are fully conditional on the individuals group's size and re-
51 sources. This removes the correlations between within group and between
52 group behaviour, of ? and ?, and explicitly allows the payoffs of these be-
53 haviours to be mediated by explicit modelling of an underlying resource
54 that determines individual fitness. This allows us to better understand the
55 trade-offs between within-group and between-group behaviours interacting
56 with changing ecological conditions.

57 We investigate how cooperation and conflict evolve when resources
58 are scarce or abundant. We also analyse how the wealth and size of a
59 group affects their investment into cooperation and conflict. We find that
60 harsher environments increase cooperation but only increase conflict up to
61 a point beyond which it decreases again. We also find that in harsh environ-
62 ments conflict increases with richness but in benign environments conflict
63 decreases with quality. Group size increasing decreases both cooperation
64 and conflict in all environments. We also analyse the effect of holding a
65 population at a fixed evolutionary endpoint but varying the environment.
66 This simulates a rapid ecological perturbation. We find that making rich-
67 adapted populations poorer and making poor-adapted populations richer
68 both increase the rate of conflicts in the population and so increase mortal-
69 ity due to fighting.

70 **3 Model**

71 We modelled an infinite asexual population split into groups that each
72 defend a exclusive territory. Each group is contains 0 to N individuals,
73 and contains 0 to Q units of a generic resource. Each individual in the
74 population can invest some variable amount of effort into two traits: X ,
75 within-group cooperation; and, Y , between-group conflict.

76 The state of the population at any given time is characterised by the
77 frequencies of each possible group state $\{q, n\}$, where q is the number of

78 resources the group has and n is the number of individuals in the group.
79 This forms a matrix $F_{q \times n}$ where each entry $f_{q,n}$ is the frequency of that state
80 amongst groups in the population. The traits of cooperation (X) and conflict
81 (Y) are also defined as $q \times n$ matrices where each entry is the strategy an actor
82 plays in that state.

83 We model the demographic and ecological dynamics of the population
84 in continuous time. The frequencies of the different group states is altered
85 by various events which are summarised below (see appendix A):

86 **Resource loss and gain** — Resources appear and disappear from groups. The
87 rate at which resources are lost or gained is derived from the environ-
88 mental harshness and the persistence of resources and is independent
89 of group state. Resources are not consumed by the individuals in a
90 group but give the same benefit to all members of the group equally
91 regardless of group state.

92 **Deaths** — Individuals die at a base mortality rate unaffected by state. In-
93 vestment into either cooperation or conflict increases that risk of death.
94 However, mortality for all group members is reduced by the group
95 level investment into cooperation.

96 **Births** — There is a base per capita reproductive rate which increases by
97 each resource an individual has access to with a density dependent
98 effect. If a group has reached its maximum size only dispersing off-
99 spring survive. Offspring disperse to any other group in the popula-
100 tion at random.

101 **Fights** — Groups encounter other groups based on their frequencies and
102 a constant encounter rate. When two groups encounter one another
103 there is a fight decided by a Tullock contest. The winner then takes
104 one resource from the loser, if the winner doesn't already control the
105 maximum number of resources and the loser has a resource to lose.

106 3.1 Key variables

107 In the results section several key variables are varied: migration (d), en-
108 counter rate (ϵ), environmental harshness (θ), and resource persistence (γ).
109 The details of the simulation we have included in appendix A. However, we
110 include below a brief summary of the biological significance of the varied
111 parameters and their affect on group states.

112 **migration rate (d)** The proportion of young that disperse from their natal
113 patch, $d \in [0, 1]$. This strongly determines within group relatedness as
114 $d \rightarrow 0$ relatedness increases within the group.

115 **encounter rate (ϵ)** The rate at which two groups encounter each other, we
116 assume the law of mass action and weight each mass action term by ϵ .
117 In the simulations this was varied on a logarithmic scale $\epsilon \in \{0.0625,$
118 $0.125, 0.25, 0.5, 1, 2, 4, 8, 16\}$.

119 **environmental harshness (θ)** Resources in the simulation can be gained or
120 lost outside of fights through chance. This abstracts away many abi-
121 otic and biotic factors. Harshness is the proportion of all loss or gain
122 events that are loss events, $\theta \in [0, 1]$. A harshness close of 0.5 is a en-
123 vironment where gain or loss are equally likely. Whereas a harshness
124 close to 0 (resource gain is more common than loss) is a very bountiful
125 environment and harshness close to 1 (resource loss is more common
126 than gain) is extremely desolate.

127 **resource persistence (γ)** The average time to event until a patch experi-
128 ences a change in resources, either gain or loss, $\gamma \in \mathbb{N}^*$. High values
129 lead to a unchanging environment where groups inherit very stable
130 resource levels. Whereas low values lead to rapidly changing resource
131 levels with respect to the harshness level.

132 3.2 Evolving traits

133 In the model we focus on two key traits that determine an individuals
 134 behaviour. Cooperation X represents a public good trait with some private
 135 benefit that directly reduces mortality for all member of a group. This could
 136 be though of as a provisioning behaviour or alarm call. Conflict Y is another
 137 social trait which represents investment or participation in intergroup con-
 138 flicts. The group total of Y is used as a measure of group effort to resolve
 139 conflicts:

$$P(\text{victory}) = \frac{\sum Y_1 + \delta}{\sum Y_1 + \sum Y_2 + 2\delta}. \quad (1)$$

140 Where, Y_i is the set of individual investments for group i and δ is a very
 141 small error term to prevent division by zero and when both parties invest
 142 zero the probability of victory is $0.5 \left(\frac{\delta}{2\delta} \right)$.

143 3.2.1 Effect of cooperation (X)

144 The trait X determines the within group cooperation in the model. Co-
 145 operation decreases the mortality of all individuals in a patch by the sum of
 146 the total cooperation in the patch. Given a certain state $\{q, n\}$ the mortality
 147 of individuals in that state will be:

$$M_{q,n} = \mu_B * \exp\left(-(n-1)x_{q,n}^l - x_{q,n}^f\right) + \mu_X \left(x_{q,n}^f\right)^2 + \mu_Y \left(y_{q,n}^f\right)^2. \quad (2)$$

148 Where, μ_B represents a baseline mortality which is offset by investment into
 149 x^f by the focal individual and x^l by the other group members. There is a
 150 personal direct benefit to cooperation as well as a public benefit so produc-
 151 tion of the good by solo individuals is still favoured. Investment in state
 152 $\{q, n\}$ results in mortality increasing by the last two terms which cause an
 153 accelerating cost as investment increases.

154 3.2.2 Effect of conflict (Y)

155 The trait **Y** is the effort an individual puts in to winning a fight between
156 groups. Groups fight over resources and the losing group is forced to relin-
157 quish one unit of resource to the winning group. Unless it is the groups last
158 remaining resource or the winner already holds the maximum number of
159 resources possible in which cases a fight has no effect. The chance a group
160 in state $\{q, n\}$ wins against a group in state $\{q', n'\}$ is given by:

$$V(q, n, q', n') = \frac{y_{q,n}^f + (n-1)y_{q,n}^l + \delta}{y_{q,n}^f + (n-1)y_{q,n}^l + n'y_{q',n'} + 2\delta}. \quad (3)$$

161 Where, ϵ is a very small quantity that ensures division by zero does not
162 occur and if neither side invests in the conflict the outcome is random (in
163 simulations $\delta = 10^{-8}$).

164 4 Results

165 4.1 Effect of harshness on Cooperation and Conflict.

166 Starting from a completely benign environment both cooperation and
167 conflict are at their minimum evolved levels (fig1). As harshness increases
168 both cooperation and conflict increase in an accelerating way. Cooperation
169 continues to increase so in very harsh environments populations evolve to
170 cooperate the most. However, conflict investment peaks at just after 0.5
171 harshness when the more resources are lost than gained overall.

172 This intermediate maximisation of conflict is due to the effects on harsh-
173 ness on the distribution of group sizes. Harsh environments skew popula-
174 tions towards many poor groups. This means encounters are predominantly
175 between groups that do not have resources and so conflict is not favoured.
176 Equally in benign environments the distribution of groups is heavily skewed
177 to rich groups meaning encounters are predominantly between groups that

link and
make

178 cannot gain more resources and so conflict is also low.

179 Despite this shift from poor to rich populations being largely symmet-
180 rical around harshness 0.5 reduction in conflict occurs alter around 0.6.
181 This occurs because resource value does continue to increase with harsh-
182 ness so though the number of fights is maximised at exactly harshness 0.5
183 the resource value drives fighting up until around harshness 0.6 when in-
184 vestment starts to decline as the populations shift to extreme poverty.

185 **4.2 Effect of encounter rate on Cooperation and Conflict**

186 The encounter rate between groups had a strong effect on the evolution
187 of conflict but a smaller effect on cooperation. As encounter rate increases
188 there is a marked increase into investment in conflict. This increase does
189 saturate though as high encounter rates mean resources become worthless
190 as they cannot be retained. This leads to a maximum encounter rate be-
191 yond which conflict no longer is selected to increase further. Cooperation
192 increases slightly with encounter rate but on a much smaller relative scale.

193 **4.3 Group wealth and size**

194 In the simulations groups are defined by two factors th number of
195 individuals in the group (size) and the number of resources they control
196 (wealth). Through conflict groups can increase their wealth and indirectly
197 their size through reproduction. Also through cooperation groups can pre-
198 vent mortality and grow in size and their perform better in fights.

199 ?? shows how conflict is expressed across wealth levels for different
200 environmental harshnesses. In benign (low harshness) environments con-
201 flict decreases with quality level as most groups are rich and rich groups
202 can't lose resources to other rich groups. As harshness decreases conflict
203 increases as the frequency of the different quality levels evens out. Then
204 at high harshnesses the population flips completely to being mostly poor

205 groups that again cannot lose resources to other poor groups and don't have
206 any rich groups to prey upon. This leads to low conflict in small groups and
207 high conflict in rich groups. So in harsh environments rich groups are high
208 in conflict to protect themselves against the poor groups that predominate
209 and in benign environments poor groups are the most aggressive to prey
210 upon the rich groups that predominate.

211 Group size has a negative correlation with individual investment in
212 both conflict and cooperation (??). The group level investment in coopera-
213 tion increases with group size, whereas the group total investment in con-
214 flict decreases(??). Cooperation in the model has a private benefit which
215 leads to a high per capita investment independent of the group. However,
216 conflict is a public good so in large groups with lower relatednesses indi-
217 viduals decrease their contributions dramatically.

218 5 Discussion

219 We found that as the environment became more harsh, in that resources
220 disappeared at a greater rate than they were generated, then conflict in-
221 creased up to a maximum value after which conflict decreased again. The
222 higher the rate of conflicts the more investment into conflict was made by
223 individuals however this did saturate at high encounter rates and no further
224 increase in conflict was observed. For cooperation we found that increasing
225 encounter rate and environmental harshness both had a small positive ef-
226 fect on cooperation. We found that investment into conflict increased with
227 wealth in harsh environments and decreased with wealth in benign envi-
228 ronments. And we found that individual investment into both cooperation
229 and conflict decreased with group size but group investment in cooperation
230 still increased overall with group size.

231 ? proposed that cooperation increased in harsh environments. Evi-
232 dence since then has been varied, it is true that harsh environments are

233 colonised at a greater rate by cooperative species (?). However, it is not
234 clear if harshness itself selects for cooperation. Previous theoretical work
235 has shown that resource limitation does select for cooperative strategies by
236 essentially modifying the payoffs of the underlying game (??). Our results
237 also show an increase in cooperation from benign to poor environments.
238 However, the increase in within group cooperation leads to higher levels
239 of between group conflict. So cooperation does increase but only towards
240 group members. Which leads to more harmonious groups united in conflict
241 rather than any type of utopian population wide cooperation.

242 The shift in state distributions drives the pattern we see in how con-
243 flict varies with group wealth and with harshness. In harsh environments
244 all groups are poor which leads to low conflict as encountered groups have
245 no resources to steal and equally in benign environments the need to fight
246 is low amongst naturally rich groups. This maximisation of conflict in in-
247 termediate environments is relevant when thinking about environmental
248 change. Supplementary feeding is performed in a number of conservation
249 strategies primarily in scavenging species and predators (?). Negative im-
250 pacts such as stress and disease spread have been analysed before (?). Our
251 results point to the possibility of a more indirect result in that increasing
252 feeding for a species in harsh conditions might drive selection for higher
253 levels of aggression especially if the feeders are claimable or in some way
254 controllable by a group. In addition, already well provisioned species if
255 their supplementation is removed or disrupted could also increase their lev-
256 els of conflict. These predictions are however evolutionary ones. On shorter
257 timescales it would be useful to extend our results by displacing evolved
258 strategies into new environmental regimes and measuring changes in ex-
259 pressed cooperation and conflict.

260 The effect of low and high harshness in our model is partially driven
261 by the fact we do not allow groups at the maximum resource level to take

resources from other groups. We could instead allow rich groups to essentially swap a claimed resource for an old resource generating an empty patch with the discarded resource and removing a resource from the losing group. This would remove some of the selection against conflict at high resource levels as fights between two groups at the maximum resource levels would still harm the loser. This would probably have the effect of raising the overall investment in conflict amongst rich groups but would not affect the overall pattern of intermediate harshness maximising conflict as the same non-interaction still makes sense for poor groups and intermediate harshness will still maximise the number of possible fights occurring in a population as the distribution of states is more even.

It is known that the major cost from intergroup conflict in some species is in mortality from the fight. However, our model does not include direct encounter based mortality as a cost of fighting. To include this we would need to include a more sophisticated fight logic that allowed avoidance and initiation of a fight. Otherwise mortality would just become a constant scaling cost from encounter rate and not a cost of investment into conflict. Also if mortality is dependent or independent of personal investment could play an important role. To maintain comprehension we did not explore these angles in the basic model but armed with the understanding from the paper future work is well placed to answer these questions.

The effect of disruption was measured by displacing populations evolved to a certain harshness regime and evaluating the change in the population wide conflict level.

1. Harsher environs favoured increased conflict up until too much of the population was poor.
2. Harsher environs always selected for higher cooperation though change was small relatively

- 290 3. encounter rate increasing drove higher conflict in harsh environemnts
291 but again with an intermediate optimum.
- 292 4. cooperation increased with higher encounter rates but the shift was
293 again quite small.
- 294 5. in harsh environs rich groups invested most in conflict in benign en-
295 virones poor groups invested most.
- 296 6. increasing group size decreased both conflict and cooperation how-
297 ever group level cooperation went up and conflict went down.

298 **5.1 comparisons**

- 299 1. yes groups more social in harsh environs but they are investing in be-
300 tween group conflict rather than within group cooperation (though
301 obviously structural)
- 302 2. "altruism" is higher in harsh environs.
- 303 3. larger groups are more cooperative but each individual is less (economies
304 of scale + private benefit).
- 305 4. larger groups invest less in fighting (resources worth less? relatedness
306 decreases and no private benefit to fighting)

307 **5.2 next steps**

- 308 1. add mortality from fights to give personal cost more directly. cur-
309 rently asymmetric benefits but not costs.
- 310 2. allow resources to be destroyed and groups to still deny resources even
311 when they can't gain them.
- 312 3. stop fights with empty patches jsut have promotion for dipspersal.
- 313 4. look at perturbations and assess out of context response.

A Model Description

do each section
biol
and add ex-
ample case
(f11)

In our model we sought to understand the link between resource richness for an cooperative group and their resulting investments into two social traits. The first trait is a cooperative trait modelled as a simple public good which helped all member of the patch to survive for longer (\mathbf{X}). The second is a competitive trait modelled as a simple blind bid game the winning group then gaining control of one of the loser's resources (\mathbf{Y}).

We modeled an infinite population consisting of individual patches. A patch is identified by its quality level, $q \in \mathbb{Z} : q \in [0, Q]$, and the number of individuals on the patch, $n \in \mathbb{Z} : n \in [0, N]$. Where the maximum quality, Q , and maximum group size, N , are predetermined parameters.

The distribution of patches in the population can therefore be described by a $q \times n$ matrix \mathbf{F} with elements $f_{q,n}$. Equally, the evolved strategies of cooperation, \mathbf{X} , and conflict, \mathbf{Y} are matrices which indicate the strategy of individual in state $\{q, n\}$.

To find the stable distribution of patch frequencies we first derived the equations for how frequencies change in the model. We constructed a matrix \mathbf{F}' which describes how demographic processes and between patch interactions affect the frequency of each patch type. Furthermore we define matrices \mathbf{W}' and \mathbf{R}' which denote the change in fitness and the change in relatedness within patches respectively (see appendix A).

We then solved for the steady state, $\mathbf{F}' = [0]_{q \times n}$ yielding the frequencies of each state in the population at equilibrium. These equilibrium frequencies, \mathbf{F}^* , are then used to solve for the equilibrium fitness values, \mathbf{W}^* , and the equilibrium relatedness values, \mathbf{R}^* .

The updating of the traits is done by taking selection gradients with respect to the two trait matrices, $\mathbf{X}_{q \times n}$ and $\mathbf{Y}_{q \times n}$. These selection gradients are then used to update the evolved values of \mathbf{X} and \mathbf{Y} . Then the new equilibrium values of \mathbf{F} , \mathbf{W} , and \mathbf{R} are used as to generate the new selection

344 gradient and iterate until the selection gradient converges to $[0]_{q \times n}$.

345 **A.1 Environmental Variables**

346 The environment is defined by two variables enviornmental harshness,
347 θ , and resource stagnation, γ . These are defined using two values gain and
348 loss. Which denote the chance that a patch spontaneously loses or gains a
349 resource.

$$\theta = \frac{\text{loss}}{\text{gain} + \text{loss}} \quad (\text{A.1})$$

$$\gamma = \frac{1}{\text{gain} + \text{loss}} \quad (\text{A.2})$$

350 **A.2 Lifecycle outline**

351 The following section contains verbal descriptions of the various mod-
352 elling steps that were taken to construct the recursion equations for the fre-
353 quencies, fitness and relatedness matrices. We have included the generated
354 equations for the patches of state $\{q = 2, n = 2\}$ with a maximum $Q = 3$ and
355 $N = 3$. So all population and individual matrices are 3×3 . We include the
356 added terms for the frequency equations only to aid understanding for ex-
357 act representations for fitness and relatedness recursions we would direct
358 the reader to the simulation files.

359 **A.2.1 Environmental transitions**

360 A patch can stochastically gain or lose a resource. These events are
361 independent and random and happen on a per patch basis.

$$\Delta_{\text{Environ}} = gF_{1,2} + lF_{3,2} - gF_{2,2} - lF_{2,2}. \quad (\text{A.3})$$

Where, the first term is the addition from poorer patches gaining a resource, the second is the addition from richer patches losing a resource and the penultimate and ultimate are subtractions from gain and loss of resource away from the focal state.

A.2.2 Mortality

Each individual has a chance of death which occurs independently.

$$\Delta_{\text{Mortality}} = -F_{2,2}M_{2,2} + 2F_{2,3}M_{2,3}. \quad (\text{A.4})$$

Where, the first term is the mortality in the current state and the second is the mortality from the state with one more individual. Note N is 1-indexed making state $F_{2,3}$ one with 2 resources and 2 individuals.

A.3 Local births

Each individual on a patch produces offspring according to productivity, P , and these offspring are non-dispersing with probability $1 - d$.

$$\Delta_{\text{births}} = -F_{2,2}P_{2,2}(1 - d). \quad (\text{A.5})$$

Where, the only term is the subtraction of those patches that transition away to state $F_{2,3}$.

A.4 Immigration

Each patch produces dispersing offspring that join a global pool and immigrate into patches at random.

$$\Delta_{\text{Imm}} = d\bar{P}F_{2,1} - d\bar{P}F_{2,2}. \quad (\text{A.6})$$

Where, \bar{P} is the average dispersing offspring each group encounters. The first term is then transitions due to immigration from patches one size smaller and the second term is the transitions away from the focal state to one size larger groups. Adults do not disperse only offspring.

A.5 Fights

For this section the possible states have been reduced to two different resource levels and two group sizes, to aid in comprehension. Fights occur between groups based on a mass action dynamic and an encounter rate term ϵ which is the same for all groups.

$$\Delta_{\text{fights}} = -\epsilon F_{1,1} F_{2,2} \left(1 - \frac{\delta + C_{2,2}}{2\delta + C_{2,2}} \right) + \frac{\epsilon F_{1,2} F_{2,1} (\delta + C_{1,2})}{2\delta + C_{1,2}} - \epsilon F_{1,2} F_{2,2} \left(1 - \frac{\delta + C_{2,2}}{2\delta + C_{1,2} + C_{2,2}} \right) + \frac{\epsilon F_{1,2} F_{2,2} (\delta + C_{1,2})}{2\delta + C_{1,2} + C_{2,2}}. \quad (\text{A.7})$$

Each term in the above equation relates to one possible fighting scenario that can occur to group with state $q = 2$ and $n = 2$. The first term is the loss of resource to a group of type $\{q = 1, n = 1\}$. Second, is the influx from groups of state $\{1, 2\}$ winning fights against state $\{2, 1\}$. Third, is the efflux from state $\{2, 2\}$ losing fights to state $\{1, 2\}$. Fourth is the influx of state $\{1, 2\}$ winning fights against the focal state $\{2, 2\}$.