

Todo list

link and make

concluding para

do each section biol and add example case (f11)

Mongoose Proj

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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 (Radford et al., 2016; Kappeler and Silk, 2010; Barker et al., 2012). 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 (Radford et al., 2016). 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 (Thompson et al., 2017; Vitikainen et al., 2019). Understanding these drivers has real impact on the implementation of conservation strategies and predicting responses to habitat disturbances.

22 Previous models have shown that intergroup conflict can favour within
23 group cooperation. However, these models often link the payoffs of cooper-
24 ation and conflict so as to enable a direct synergism between the two (Choi
25 and Bowles, 2007; ?). This assumption is suited to answer certain questions
26 in the evolution of human societies however hides the tension between co-
27 operation and conflict that exists in other cooperative groups. Specifically,
28 we might expect performing well in intergroup encounters makes one less
29 willing or able to cooperate with others or vice versa. This is not to say that
30 nuanced behaviours cannot evolve, but the early stages of the evolution of
31 a behaviour might have this independence of action.

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 are
36 crucial as they allow conditional behaviour that is adapted to the individu-
37 als specific circumstance rather than only doing what is optimal on average.

38 Kropotkin (1902) proposed that cooperation increased in harsh envi-
39 ronments. Evidence since then has been varied, it is true that harsh envi-
40 ronments are colonised at a greater rate by cooperative species (Cornwallis
41 et al., 2017). However, it is not clear if harshness itself selects for cooper-
42 ation. Previous theoretical work has shown that resource limitation does
43 select for cooperative strategies by essentially modifying the payoffs of the
44 underlying game (Requejo and Camacho, 2011; Smaldino et al., 2013). Es-
45 tablishing how cooperation and conflict interact with resources however has
46 been hard as previous models have not explicitly separated the sociality of
47 between-group conflict and within-group cooperation from each other and
48 with an underlying ecological measure of harshness.

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

51 social traits that are fully conditional on the individuals group's size and
52 resources. This removes the correlations between within group and between
53 group behaviour, of Choi and Bowles (2007) and Lehmann and Feldman
54 (2008), and explicitly allows the payoffs of these behaviours to be mediated
55 by explicit modelling of an underlying resource that determines individual
56 fitness. This allows us to better understand the trade-offs between within-
57 group and between-group behaviours interacting with changing ecological
58 conditions.

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

72 **3 Model**

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

78 The state of the population at any given time is characterised by the

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

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

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

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

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

103 **Fights** — Groups encounter other groups based on their frequencies and
104 a constant encounter rate. When two groups encounter one another
105 there is a fight decided by a Tullock contest. The winner then takes

one resource from the loser, if the winner doesn't already control the maximum number of resources and the loser has a resource to lose.

3.1 Key variables

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

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

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

environmental harshness (θ) Resources in the simulation can be gained or lost outside of fights through chance. This abstracts away many abiotic and biotic factors. Harshness is the proportion of all loss or gain events that are loss events, $\theta \in [0, 1]$. A harshness close of 0.5 is an environment where gain or loss are equally likely. Whereas a harshness close to 0 (resource gain is more common than loss) is a very bountiful environment and harshness close to 1 (resource loss is more common than gain) is extremely desolate.

resource persistence (γ) The average time to event until a patch experiences a change in resources, either gain or loss, $\gamma \in \mathbb{N}^*$. High values lead to a unchanging environment where groups inherit very stable

resource levels. Whereas low values lead to rapidly changing resource levels with respect to the harshness level.

3.2 Evolving traits

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

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

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

3.2.1 Effect of cooperation (X)

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

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

Where, μ_B represents a baseline mortality which is offset by investment into x^f by the focal individual and x^l by the other group members. There is a personal direct benefit to cooperation as well as a public benefit so production of the good by solo individuals is still favoured. Investment in state

154 $\{q, n\}$ results in mortality increasing by the last two terms which cause an
155 accelerating cost as investment increases.

156 3.2.2 Effect of conflict (Y)

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

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

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

166 4 Results

167 4.1 Effect of harshness on Cooperation and Conflict.

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

174 This intermediate maximisation of conflict is due to the effects on harsh-
175 ness on the distribution of group sizes. Harsh environments skew popula-
176 tions towards many poor groups. This means encounters are predominantly

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177 between groups that do not have resources and so conflict is not favoured.
178 Equally in benign environments the distribution of groups is heavily skewed
179 to rich groups meaning encounters are predominantly between groups that
180 cannot gain more resources and so conflict is also low.

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

187 **4.2 Effect of encounter rate on Cooperation and Conflict**

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

195 **4.3 Group wealth and size**

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

201 ?? shows how conflict is expressed across wealth levels for different
202 environmental harshnesses. In benign (low harshness) environments con-
203 flict decreases with quality level as most groups are rich and rich groups

204 can't lose resources to other rich groups. As harshness decreases conflict
205 increases as the frequency of the different quality levels evens out. Then
206 at high harshnesses the population flips completely to being mostly poor
207 groups that again cannot lose resources to other poor groups and don't have
208 any rich groups to prey upon. This leads to low conflict in small groups and
209 high conflict in rich groups. So in harsh environments rich groups are high
210 in conflict to protect themselves against the poor groups that predominate
211 and in benign environments poor groups are the most aggressive to prey
212 upon the rich groups that predominate.

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

220 **5 Discussion**

221 We found that as the environment became more harsh, in that resources
222 disappeared at a greater rate than they were generated, then conflict in-
223 creased up to a maximum value after which conflict decreased again. The
224 higher the rate of conflicts the more investment into conflict was made by
225 individuals however this did saturate at high encounter rates and no further
226 increase in conflict was observed. For cooperation we found that increasing
227 encounter rate and environmental harshness both had a small positive effect
228 on cooperation.

229 We found that investment into conflict increased with wealth in harsh
230 environments and decreased with wealth in benign environments. And we
231 found that individual investment into both cooperation and conflict de-

232 creased with group size but group investment in cooperation still increased
233 overall with group size.

234 Kropotkin (1902) proposed that cooperation increased in harsh envi-
235 ronments. Evidence since then has been varied, it is true that harsh envi-
236 ronments are colonised at a greater rate by cooperative species (Cornwallis
237 et al., 2017). However, it is not clear if harshness itself selects for cooper-
238 ation. Previous theoretical work has shown that resource limitation does
239 select for cooperative strategies by essentially modifying the payoffs of the
240 underlying game (Requejo and Camacho, 2011; ?). Our results also show
241 an increase in cooperation from benign to poor environments. However,
242 the increase in within group cooperation leads to higher levels of between
243 group conflict. So cooperation does increase but only towards group mem-
244 bers. Which leads to more harmonious groups united in conflict rather than
245 any type of utopian population wide cooperation.

246 The shift in state distributions drives the pattern we see in how con-
247 flict varies with group wealth and with harshness. In harsh environments
248 all groups are poor which leads to low conflict as encountered groups have
249 no resources to steal and equally in benign environments the need to fight
250 is low amongst naturally rich groups. This maximisation of conflict in in-
251 termediate environments is relevant when thinking about environmental
252 change. Supplementary feeding is performed in a number of conservation
253 strategies primarily in scavenging species and predators (Oro et al., 2008).
254 Negative impacts such as stress and disease spread have been analysed be-
255 fore (Murray et al., 2016). Our results point to the possibility of a more indi-
256 rect result in that increasing feeding for a species in harsh conditions might
257 drive selection for higher levels of aggression especially if the feeders are
258 claimable or in some way controllable by a group. In addition, already well
259 provisioned species if their supplementation is removed or disrupted could
260 also increase their levels of conflict. These predictions are however evolu-

261 tionary ones. On shorter timescales it would be useful to extend our results
262 by displacing evolved strategies into new environmental regimes and mea-
263 suring changes in expressed cooperation and conflict.

264 The effect of low and high harshness in our model is partially driven
265 by the fact we do not allow groups at the maximum resource level to take
266 resources from other groups. We could instead allow rich groups to es-
267 sentially swap a claimed resource for an old resource generating an empty
268 patch with the discarded resource and removing a resource from the losing
269 group. This would remove some of the selection against conflict at high re-
270 source levels as fights between two groups at the maximum resource levels
271 would still harm the loser. This would probably have the effect of raising
272 the overall investment in conflict amongst rich groups but would not af-
273 fect the overall pattern of intermediate harshness maximising conflict as
274 the same non-interaction still makes sense for poor groups and intermedi-
275 ate harshness will still maximise the number of possible fights occurring in
276 a population as the distribution of states is more even.

277 It is know that the major cost from intergroup conflict in some species
278 is in mortality from the fight Cant et al. (2016). However, our model does
279 not include direct encounter based mortality as a cost of fighting. To include
280 this we would need to include a more sophisticated fight logic that allowed
281 avoidance and initiation of a fight. Otherwise mortality would just become
282 a constant scaling cost from encounter rate and not a cost of investment into
283 conflict. Also if mortality is dependent or independent of personal invest-
284 ment could play an important role. To maintain comprehension we did not
285 explore these angles in the basic model but armed with the understanding
286 from the paper future work is well placed to answer these questions.

287

concluding
para

288 1. Harsher environs favoured increased conflicy up until too much of te
289 popualtion was poor.

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

300 5.1 comparisons

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

309 5.2 next steps

- 310 1. add mortality from fights to give personal cost more directly. cur-
311 rently asymmetric benefits but not costs.
- 312 2. allow resources to be destroyed and groups to still deny resources even
313 when they can't gain them.

314 3. stop fights with empty patches jsut have promotion for dipspersal.

315 4. look at perturbations and assess out of context response.

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360 A Model Description

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

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

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

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

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

386 The updating of the traits is done by taking selection gradients with
387 respect to the two trait matrices, $\mathbf{X}_{q \times n}$ and $\mathbf{Y}_{q \times n}$. These selection gradients
388 are then used to update the evolved values of \mathbf{X} and \mathbf{Y} . Then the new equi-
389 librium values of \mathbf{F} , \mathbf{W} , and \mathbf{R} are used as to generate the new selection
390 gradient and iterate until the selection gradient converges to $[0]_{q \times n}$.

391 **A.1 Environmental Variables**

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

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

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

396 **A.2 Lifecycle outline**

397 The following section contains verbal descriptions of the various mod-
398 elling steps that were taken to construct the recursion equations for the fre-
399 quencies, fitness and relatedness matrices. We have included the generated
400 equations for the patches of state $\{q = 2, n = 2\}$ with a maximum $Q = 3$ and
401 $N = 3$. So all population and individual matrices are 3×3 . We include the
402 added terms for the frequency equations only to aid understanding for ex-
403 act representations for fitness and relatedness recursions we would direct
404 the reader to the simulation files.

405 **A.2.1 Environmental transitions**

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

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

408 Where, the first term is the addition from poorer patches gaining a resource,
409 the second is the addition from richer patches losing a resource and the
410 penultimate and ultimate are subtractions from gain and loss of resource

411 away from the focal state.

412 **A.2.2 Mortality**

413 Each individual has a chance of death which occurs independently.

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

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

417 **A.3 Local births**

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

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

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

422 **A.4 Immigration**

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

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

425 Where, \bar{P} is the average dispersing offspring each group encounters. The
426 first term is then transitions due to immigration from patches one size smaller
427 and the second term is the transitions away from the focal state to one size
428 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 a 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 $\{2, 2\}$.