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[do each section biol and add example case (f11)](#_bookmark20) . . . . . . . . . . . . .

1 Mongoose Proj

# 2 Matishalin Patel, Michael Cant, and Rufus Johnstone

3 1 Abstract

4 Lorem Ipsum

5 keywords:

6

7 tion

intragroup cooperation, intergroup conflict, game theory, social evolu-

8 2 Introduction

9 Intergroup conflict is thought to be the key driver in the evolution of

10 cooperation . However our understanding of the key evolutionary and eco-

cite

11 logical drivers of inter group conflict is far from complete. In social organ-

12 isms both between and within group conflict is variable and seems posi-

13 tively or negatively correlated with between and within group cooperation

14 . This variety of responses shows that a better understanding of the driver

cite

15 of cooperation and conflict are needed to fully explain how within and be-

16 tween group conflict evolves. These traits of cooperation and conflict can

17 have large fitness consequences [(Thompson et al.,](#_bookmark17) [2017;](#_bookmark17) [Vitikainen et al.,](#_bookmark18)

18 [2019).](#_bookmark18)

19 Previous models have shown that intergroup conflict can favour within

20 group cooperation. However, these models often link the payoffs of cooper-

21 ation and conflict so as to enable a direct synergism between the two [(Choi](#_bookmark9)

22 [and Bowles, 2007;](#_bookmark9) [Lehmann and Feldman, 2008).](#_bookmark12) This assumption is suited

23 to answer certain questions in the evolution of human societies however

24 hides the tension between cooperation and conflict that exists in other coop-

25 erative groups. Specifically, we might expect performing well in intergroup

26 encounters makes one less willing or able to cooperate with others or vice

27 vers

a.

In nature organisms evolve complex behaviours that respond adap-

example of where it does and

doesnt work

28

29 tively to the current situation it finds itself in. Individuals in smaller groups

30 might fight harder whereas in larger groups they might cooperate more as

31 benefits are synergistic. These state dependent behaviours are crucial are

32 crucial as they allow conditional behaviour that is adapted to the individu-

33 als specific circumstance rather than only doing what is optimal on average.

34 Our model has two novel features. Firstly, individuals have conditional

35 behaviour that depends on group size and group wealth. Secondly, we treat

36 cooperation and conflict as two separately evolving traits and allow invest-

37 ment in neither if that is optimal. This enables a complex interaction be-

38 tween the emergence of stable group state distributions and the evolution

39 of two independently evolving conditional behaviours.

40 We investigate how cooperation and conflict evolve when resources are

41 scarce or abundant. We also analyse how the wealth and size of a group

42 affects their investment into cooperation and conflict. We find that harsher

43 environments increase cooperation but only increase conflict up to a point

44 beyond which it decreases again. We also find that in harsh environments

45 conflict increases with richness but in benign environments conflict de-

46 creases with quality. Group size increasing decreases both cooperation and

47 conflict in all environments.

48 3 Model

49 We modelled an infinite population split into groups that each defend

50 territories. Each group is formed of up to *N* haploid individuals, and each

51 group controls up to *Q* units of a generic resource. Each individual can

52 invest into a within group cooperation trait, *X*, and a between group com-

53 petition trait, *Y* .

54 As the population is infinite we keep track of the frequencies of each

55 group state {*q, n*}, where *q* is the number of resources the group has and *n*

56 is the number of individuals in the group. This forms a matrix fl*q*×*n* where

57 each entry *fq,n* is the frequency of that state amongst groups in the popula-

58 tion. The traits of cooperation (*X*) and conflict (*Y* ) are also defined as *q* × *n*

59 matrices where each entry is the strategy an actor plays in that state.

60 Cooperation in the model reduces mortality for the actor and all other

61 members of the group in exchange for a private cost of increased mortality

62 for the actor. The effort into conflict is summed for all group members and

63 that total effort is compared between two fighting groups to determine the

64 winner. Winners claim a resource from the losing group unless the loser has

65 no resource to give or the winner has reached the maximum resource level.

66 The environment is modelled using two parameters. Harshness (*θ*) and

67 resource stagnation (*γ*). Harshness is the chance that a change in resources

68 results in the loss of a resource and resource stagnation is the average time

69 between an event that changes resource levels. These are environmental pa-

70 rameters and are assumed to be unchanging during a simulation and out-

71 side of an individuals control.

72 Resources are immutable and give the same benefit to every member

73 of a group they are not divided or shared. Resources benefit individuals by

74 increasing the number of offspring an individual produces.

75 3.1 Key variables

76 In the simulations several key variables are varied: migration (*d*), en-

77 counter rate (*c*), environmental harshness (*θ*), and resource stagnation (*γ*).

78 The details of the simulation we have included in appendix [A.](#_bookmark19) However, we

79 include below a brief summary of the biological significance of the varied

80 parameters and their affect on group states.

81 migration rate (*d*) The proportion of young that disperse from their natal

82 patch, *d* ∈ [0*,* 1]. This strongly determines within group relatedness as

83 *d* → 0 relatedness increases within the group.

84 encounter rate (*c*) The rate at which two groups encounter each other, we

85 assume the law of mass action and weight each mass action term by *c*.

86 In the simulations this was varied on a logarithmic scale *c* ∈ {0*.*0625*,*

87 0*.*125*,* 0*.*25*,* 0*.*5*,* 1*,* 2*,* 4*,* 8*,* 16}.

88 environmental harshness (*θ*) Resources in the simulation can be gained

89 or lost outside opf fights through chance. This abstracts away many

90 abiotic and biotic factors. Harshness is the proportion of all loss or

91 gain events that are loss events, *θ* ∈ [0*,* 1]. A harshness close of 0*.*5 is

92 a environment where gain or loss are equally likely. Whereas a harsh-

93 ness close to 0 is a very bountiful environment and harshness close to

94 1 is extremely desolate.

95 resource stagnation (*γ*) The average time to event until a patch experi-

96 ences a change in resources, either gain or loss, *γ* ∈ N∗. High values

97 lead to a unchanging environment where groups inherit very stable

98 resource levels. Whereas low values lead to rapidly changing resource

99 levels with respect to the harshness level.

100 3.2 Evolving traits

101 In the model we focus on two key traits that determine an individuals

102 behaviour. Cooperation *X* represents a public good trait with some private

103 benefit that directly reduces mortality for all member of a group. This could

104 be though of as a provisioning behaviour or alarm call. Conflict *Y* is another

105 social trait which represents investment or participation in intergroup con-

106 flicts. The group total of *Y* is used as a measure of group effort to resolve

107 conflicts:

, *Y* + *δ*

1

,

*P*(victory) =

*Y*1 + , *Y*2 + 2*δ .* (1)

108 Where, *Yi* is the set of individual investments for group *i* and *δ* is a very

109 small error term to prevent division by zero and when both parties invest

110 zero the probability of victory is 0*.*5 *δ*

.

2*δ*

111 3.2.1 Effect of cooperation (X)

112 The trait X determines the within group cooperation in the model. Co-

113 operation decreases the mortality of all individuals in a patch by the sum of

114 the total cooperation in the patch. Given a certain state {*q, n*} the mortality

115 of individuals in that state will be:

2

*l f f*

*f* 2

*Mq,n* = *µB* ∗ exp

−(*n* − 1) *xq,n* − *xq,n*

+ *µX*

*xq,n*

+ *µY*

*yq,n*

*.* (2)

116 Where, *µB* represents a baseline mortality which is offset by investment into

117 *xf* by the focal individual and *xl* by the other group members. There is a

118 personal direct benefit to cooperation as well as a public benefit so produc-

119 tion of the good by solo individuals is still favoured. Investment in state

120 {*q, n*} results in mortality increasing by the last two terms which cause an

121 accelerating cost as investment increases.

122 3.2.2 Effect of conflict (Y)

123 The trait Y is the effort an individual puts in to winning a fight between

124 groups. Groups fight over resources and the losing group is forced to relin-

125 quish one unit of resource to the winning group. Unless it is the groups last

126 remaining resource or the winner already holds the maximum number of

127 resources possible in which cases a fight has no effect. The chance a group

128 in state {*q, n*} wins against a group in state {*q*j*, n*j} is given by:

*V* (*q, n, q*j*, n*j) =

*y*

*q,n*

*q,n*

*f q,n*

+ (*n* − 1)*yl* + *δ*

*.* (3)

*f q,n*

*y*

+ (*n* − 1)*yl*

+ *n*j*yq*j *,n*

j + 2*δ*

129 Where, *c* is a very small quantity that ensures division by zero does not

130 occur and if neither side invests in the conflict the outcome is random (in

131 simulations *δ* = 10−8).

# 132 3.3 Effect of harshness on Cooperation and Conflict.

0.38

Conflict

Cooperation

0.4

0.36

0.3

Investment

0.2

0.34

0.32

as.factor(d)

0.1

0.5

0.9

0.1

0.30

0.25 0.50 0.75 0.25 0.50 0.75

Harshness

Figure 1

133 Starting from a completely benign environment both cooperation and

134 conflict are at their minimum evolved levels (fig1). As harshness increases

link and make

135 both cooperation and conflict increase in an accelerating way. Cooperation

136 continues to increase so in very harsh environments populations evolve to

137 cooperate the most. However, conflict investment peaks at just after 0*.*5

138 harshness when the more resources are lost than gained overall.

139 This intermediate maximisation of conflict is due to the effects on harsh-

140 ness on the distribution of group sizes. Harsh environments skew popula-

141 tions towards many poor groups. This means encounters are predominantly

142 between groups that do not have resources and so conflict is not favoured.

143 Equally in benign environments te distribution of groups is heavily skewed

144 to rich groups meaning encounters are predominantly between groups that

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

146 Despite this shift from poor to rich populations being largely symmet-

147 rical around harshness 0*.*5 reduction in conflict occurs alter around 0*.*6.

148 This occurs because resource value does continue to increase with harsh-

149 ness so though the number of fights is maximised at exactly harshness 0*.*5

150 the resource value drives fighting up until around harshness 0*.*6 when in-

151 vestment starts to decline as the populations shift to extreme poverty.

# 152 3.4 Effect of encounter rate on Cooperation and Conflict

153 The encounter rate between groups had a strong effect on the evolution

154 of conflict but a smaller effect on cooperation. As encounter rate increases

155 there is a marked increase into investment in conflict. This increase does

156 saturate though as high encounter rates mean resources become worthless

157 as they cannot be retained. This leads to a maximum encounter rate be-

158 yond which conflict no longer is selected to increase further. Cooperation

159 increases slightly with encounter rate but on a much smaller relative scale.

0.36

Conflict

Cooperation

0.4

0.3

Investment

0.2

0.34

Harshness

0.9

0.5

0.1

0.32

0.1

−2 0 2 −2 0 2

log2(EncounterRate)

Figure 2

# 160 3.5 Group wealth and size

161 In the simulations groups are defined by two factors th number of

162 individuals in the group (size) and the number of resources they control

163 (wealth). Through conflict groups can increase their wealth and indirectly

164 their size through reproduction. Also through cooperation groups can pre-

165 vent mortality and grow in size and their perform better in fights.

166 Figure [3](#_bookmark4) shows how conflict is expressed across wealth levels for dif-

167 ferent environmental harshnesses. In benign (low harshness) environments

168 conflict decreases with quality level as most groups are rich and rich groups

169 can’t lose resources to other rich groups. As harshness decreases conflict

170 increases as the frequency of the different quality levels evens out. Then

171 at high harshnesses the population flips completely to being mostly poor

172 groups that again cannot lose resources to other poor groups and don’t have

173 any rich groups to prey upon. This leads to low conflict in small groups and

174 high conflict in rich groups. So in harsh environments rich groups are high

175 in conflict to protect themselves against the poor groups that predominate

0.6

Conflict

0.4

Investment

0.2

as.factor(Harshness)

0.9

0.6

0.5

0.4

0.1

1 2 3 4 5

Quality

Figure 3

176 and in benign environments poor groups are the most aggressive to prey

177 upon the rich groups that predominate.

178 Group size has a negative correlation with individual investment in

179 both conflict and cooperation (fig. [4).](#_bookmark5) The group level investment in co-

180 operation increases with group size, whereas the group total investment

181 in conflict decreases(fig. [5).](#_bookmark6) Cooperation in the model has a private bene-

182 fit which leads to a high per capita investment independent of the group.

183 However, conflict is a public good so in large groups with lower related-

184 nesses individuals decrease their contributions dramatically.

185 4 Discussion

186 We found that as the environment became more harsh, in that resources

187 disappeared at a greater rate then they were generated, then conflict in-

188 creased up to a maximum value after which conflict decreased again. The

189 higher the rate of conflicts the more investment into conflict was made by

190 individuals however this did saturate at high encounter rates and no further

0.6

Cooperation

Conflict

0.32

0.28

Investment

0.4

as.factor(Harshness)

0.9

0.5

0.1

0.2

0.24

2 3 4 5 2 3 4 5

Size

Figure 4

191 increase in conflict was observed. For cooperation we found that increasing

192 encounter rate and environmental harshness both had a small positive effect

193 on cooperation.

194 We found that investment into conflict increased with wealth in harsh

195 environments and decreased with wealth in benign environments. And we

196 found that individual investment into both cooperation and conflict de-

197 creased with group size but group investment in cooperation still increased

198 overall with group size.

199 [Kropotkin](#_bookmark11) [(1902)](#_bookmark11) proposed that cooperation increased in harsh envi-

200 ronments. Evidence since then has been varied, it is true that harsh envi-

201 ronments are colonised at a greater rate by cooperative species [(Cornwallis](#_bookmark10)

202 [et al., 2017).](#_bookmark10) However, it is not clear if harshness itself selects for cooper-

203 ation. Previous theoretical work has shown that resource limitation does

204 select for cooperative strategies by essentially modifying the payoffs of the

205 underlying game [(Requejo and Camacho, 2011;](#_bookmark15) [Smaldino et al., 2013).](#_bookmark16) Our

206 results also show an increase in cooperation from benign to poor environ-

207 ments. However, the increase in within group cooperation leads to higher

1.1

1.2

1.0

Investment \* Size

0.9

1.0

0.8

as.factor(Harshness)

0.9

0.5

0.1

0.8

0.6

0.7

2 3 4 5

Cooperation

0.4

Size

2 3 4 5

Conflict

Figure 5

208 levels of between group conflict. So cooperation does increase but only to-

209 wards group members. Which leads to more harmonious groups united in

210 conflict rather than any type of utopian population wide cooperation.

211 The shift in state distributions drives the pattern we see in how con-

212 flict varies with group wealth and with harshness. In harsh environments

213 all groups are poor which leads to low conflict as encountered groups have

214 no resources to steal and equally in benign environments the need to fight

215 is low amongst naturally rich groups. This maximisation of conflict in in-

216 termediate environments is relevant when thinking about environmental

217 change. Supplementary feeding is performed in a number of conservation

218 strategies primarily in scavenging species and predators [(Oro et al., 2008).](#_bookmark14)

219 Negative impacts such as stress and disease spread have been analysed be-

220 fore [(Murray et al., 2016).](#_bookmark13) Our results point to the possibility of a more indi-

221 rect result in that increasing feeding for a species in harsh conditions might

222 drive selection for higher levels of aggression especially if the feeders are

223 claimable or in some way controllable by a group. In addition, already well

224 provisioned species if their supplementation is removed or disrupted could

225 also increase their levels of conflict. These predictions are however evolu-

226 tionary ones. On shorter timescales it would be useful to extend our results

227 by displacing evolved strategies into new environmental regimes and mea-

228 suring changes in expressed cooperation and conflict.

229 The effect of low and high harshness in our model is partially driven

230 by the fact we do not allow groups at the maximum resource level to take

231 resources from other groups. We could instead allow rich groups to es-

232 sentially swap a claimed resource for an old resource generating an empty

233 patch with the discarded resource and removing a resource from the losing

234 group. This would remove some of the selection against conflict at high re-

235 source levels as fights between two groups at the maximum resource levels

236 would still harm the loser. This would probably have the effect of raising

237 the overall investment in conflict amongst rich groups but would not af-

238 fect the overall pattern of intermediate harshness maximising conflict as

239 the same non-interaction still makes sense for poor groups and intermedi-

240 ate harshness will still maximise the number of possible fights occurring in

241 a population as the distribution of states is more even.

242 It is know that the major cost from intergroup conflict in some species

243 is in mortality from the fight [Cant et al. (2016).](#_bookmark8) However, our model does

244 not include direct encounter based mortality as a cost of fighting. To include

245 this we would need to include a more sophisticated fight logic that allowed

246 avoidance and initiation of a fight. Otherwise mortality would just become

247 a constant scaling cost from encounter rate and not a cost of investment into

248 conflict. Also if mortality is dependent or independent of personal invest-

249 ment could play an important role. To maintain comprehension we did not

250 explore these angles in the basic model but armed with the understanding

251 from the paper future work is well placed to answer these questions.

252 concluding

para

253 1. Harsher environs favoured increased conflicy up until too much of te

254 popualtion was poor.

255 2. Harsher environs always selected for higher cooperation though change

256 was small relatively

257 3. encounter rate increasing drove higher conflict in harsh environemnts

258 but again with an intermediate optimum.

259 4. cooperation increased with higher encounter rates but the shift was

260 again quite small.

261 5. in harsh environs rich groups invested most in conflict in benign en-

262 virons poor groups invested most.

263 6. increasing group size decreased both conflict and cooperation how-

264 ever group level cooperation went up and conflict went down.

265 4.1 comparisons

266 1. yes groups more social in harsh environs but they are investing in be-

267 tween group conflict rather than within group cooperation (though

268 obviously structural)

269 2. ”altruism” is higher in harsh environs.

270 3. larger groups are more cooperative but each individual is less (economies

271 of scale + private benefit).

272 4. larger groups invest less in fighting (resources worth less? relatedness

273 decreases and no private benefit to fighting)

274 4.2 next steps

275 1. add mortality from fights to give personal cost more directly. cur-

276 rently asymmetric benefits but not costs.

277 2. allow resources to be destroyed and groups to still deny resources even

278 when they can’t gain them.

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

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

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315  A Model Description

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325

326

In our model we sought to understand the link between resource rich- ness 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 (X). The sec- ond is a competitive trait modelled as a simple blind bid game the winning group then gaining control of one of the loser’s resources (Y).

We modeled an infinite population consisting of individual patches. A

patch is identified by its quality level, *q* ∈ Z : *q* ∈ [0*, Q*], and the number of individuals on the patch, *n* ∈ Z : *n* ∈ [0*, N* ]. Where the maximum quality, *Q*, and maximum group size, *N* , are predetermined parameters.

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

327 The distribution of patches in the population can therefore be described

328 by a *q* × *n* matrix fl with elements *fq,n*. Equally, the evolved strategies of

329 cooperation, X, and conflict, Y are matrices which indicate the strategy of

330 individual in state {*q, n*}.

331 To find the stable distribution of patch frequencies we first derived the

332 equations for how frequencies change in the model. We constructed a ma-

333 trix flj which describes how demographic processes and between patch in-

334 teractions affect the frequency of each patch type. Furthermore we define

335 matrices Wj and Rj which denote the change in fitness and the change in

336 relatedness within patches respectively (see appendix [A).](#_bookmark19)

337 We then solved for the steady state, flj = [0]*q*×*n* yielding the frequencies

338 of each state in the population at equilibrium. These equilibrium frequen-

339 cies, fl∗, are then used to solve for the equilibrium fitness values, W∗, and

340 the equilibrium relatedness values, R∗.

341 The updating of the traits is done by taking selection gradients with

342 respect to the two trait matrices, Xq×n and Yq×n. These selection gradients

343 are then used to update the evolved values of X and Y. Then the new equi-

344 librium values of fl, W, and R are used as to generate the new selection

345 gradient and iterate until the selection gradient converges to [0]*q*×*n*.

# 346 A.1 Environmental Variables

347 The environment is defined by two varaibles enviornmental harshness,

348 *θ*, and resource stagnation, *γ*. These are defined using two values gain and

349 loss. Which denote the chance that a patch spontaneously loses or gains a

350 resource.

loss

*θ* = gain + loss (A.1)

1

*γ* = gain + loss (A.2)

351 A.2 Lifecycle outline

352 THe following section contains verbal descripitions of the various mod-

353 elling steps that were taken to construct the recursion equations for the fre-

354 quencies, fitness and relatedness matrices. We have included the generated

355 equations for the patches of state {*q* = 2*, n* = 2} with a maximum *Q* = 3 and

356 *N* = 3. So all population and individual matrices are 3 × 3. We include the

357 added terms for the frequency equations only to aid understanding for ex-

358 act representations for fitness and relatedness recursions we would direct

359 the reader to the simulation files.

360 A.2.1 Environmental transitions

361 A patch can stochastically gain or lose a resource. These events are

362 independent and random and happen on a per patch basis.

∆Environ = *gF*1*,*2 + *lF*3*,*2 − *gF*2*,*2 − *lF*2*,*2 *.* (A.3)

363 Where, the first term is the addition from poorer patches gaining a resource,

364 the second is the addition from richer patches losing a resource and the

365 penultimate and ultimate are subtractions from gain and loss of resource

366 away from the focal state.

367 A.2.2 Mortality

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

∆Mortality = −*F*2*,*2*M*2*,*2 + 2*F*2*,*3*M*2*,*3 *.* (A.4)

369 Where, the first term is the mortality in the current state and the second is

370 the mortality from the state with one more individual. Note *N* is 1-indexed

371 making state *F*2*,*3 one with 2 resources and 2 individuals.

372 A.3 Local births

373 Each individual on a patch produces offspring according to productiv-

374 ity, *P*, and these offspring are non-dispersing with probability 1 − *d*.

∆births = −*F*2*,*2*P*2*,*2 (1 − *d*) *.* (A.5)

375 Where, the only term is the subtraction of those patche that transition away

376 to state *F*2*,*3.

377 A.4 Immigration

378 Each patch produces dispersing offspring that join a global pool and

379 immigrate into patches at random.

∆Imm = *dP*¯*F*2*,*1 − *dP*¯*F*2*,*2 *.* (A.6)

380 Where, *P*¯ is the average dispersing offspring each group encounters. The

381 first term is then transitions due to immigration from patches one size smaller

382 and the second term is the transitions away from he focal state to one size

383 larger groups. Adults do not disperse only offspring.

384 A.5 flights

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 ona mass action dynamic and a encounter rate term *c* which is the same for all groups.

∆fights = −*cF*1*,* 1*F*2*,* 2

!

1 *δ* + *C*2*,* 2

−

2*δ* + *C*2*,* 2

+ *cF*1*,* 2*F*2*,* 1 (*δ* + *C*1*,* 2)

2*δ* + *C*1*,* 2

−

!

*cF*1*,* 2*F*2*,* 2

1 *δ* + *C*2*,* 2

2*δ* + *C*1*,* 2 + *C*2*,* 2

−

+ *cF*1*,* 2*F*2*,* 2 (*δ* + *C*1*,* 2) *.* (A.7)

2*δ* + *C*1*,* 2 + *C*2*,* 2

385 Each term in the above equation relates to one possible fighting scenario

386 that can occur to group with state *q* = 2 and *n* = 2. The first term is the

387 loss of resource to a group of type {*q* = 1*, n* = 1}. Second, is the influx from

388 groups of state {1*,* 2} winning fights against state {2*,* 1}. Third, is the efflux

389 from state {2*,* 2} losing fights to state {1*,* 2}. Fourth is the influx of state {1*,* 2}

390 winning fights against the focal state {2*,* 2}.