Todo list

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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) ?). This assumption is suited to answer certain questions

23 in the evolution of human societies however hides the tension between co-

24 operation and conflict that exists in other cooperative groups. Specifically,

25 we might expect performing well in intergroup encounters makes one less

26 willing or able to cooperate with others or vice versa. example of where it

27 In nature organisms evolve complex behaviours that respond adap-

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

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

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

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

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

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

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

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

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

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

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

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

40 tablishing how cooperation and conflict interact with resources however has

41 been hard as previous models have not explicitly separated the sociality of

42 between-group conflict and within-group cooperation from each other and

43 with an underlying ecological measure of harshness.

44 In this paper we model two separate traits one controlling between-

45 group conflict and one controlling within-group cooperation. They are both

46 social traits that are fully conditional on the individuals group’s size and re-

47 sources. This removes the correlations between within group and between

48 group behaviour, of [Choi and Bowles](#_bookmark9) [(2007)](#_bookmark9) and [Lehmann and Feldman](#_bookmark12)

49 [(2008),](#_bookmark12) of previous models and explicitly allows the payoffs of these be-

50 haviours to be mediated by explicit modelling of an underlying resource

does and doesnt work

51 that determines individual fitness. This allows us to better understand the

52 trade-offs between within-group and between-group behaviours interacting

53 with changing ecological conditions.

54 We investigate how cooperation and conflict evolve when resources are

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

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

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

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

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

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

61 conflict in all environments.

62 3 Model

63 We modelled an infinite asexual population split into groups that each

64 defend a exclusive territory. Each group is contains 0 to *N* individuals,

65 and contains 0 to *Q* units of a generic resource. Each individual in the

66 population can invest some variable amount of effort into two traits: *X*,

67 within-group cooperation; and, *Y* , between-group conflict.

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

69 frequencies of each possible group state {*q, n*}, where *q* is the number of

70 resources the group has and *n* is the number of individuals in the group.

71 This forms a matrix fl*q*×*n* where each entry *fq,n* is the frequency of that state

72 amongst groups in the population. The traits of cooperation (*X*) and conflict

73 (*Y* ) are also defined as *q*×*n* matrices where each entry is the strategy an actor

74 plays in that state.

75 We model the demographic and ecological dynamics of the population

76 in continuous time. The frequencies of the different group states is altered

77 by various events which are summarised below (see appendix [A):](#_bookmark19)

78 Resource loss and gain — Resources appear an disappear from groups. The

79 rate at which resources are lost or gained is derived from the environ-

80 mental harshness and the persistence of resources and is independent

81 of group state. Resources are not consumed by the individuals in a

82 group but give the same benefit to all members of the group equally

83 regardless of group state.

84 Deaths — Individuals die at a base mortality rate unaffected by state. In-

85 vestment into either cooperation or conflict increases that risk of death.

86 However, mortality for all group members is reduced by the group

87 level investment into cooperation.

88 Births — There is a base per capita reproductive rate which increases by

89 each resource an individual has access to with a density dependent

90 effect. If a group has reached it’s maximum size only dispersing off-

91 spring survive. Offspring disperse to any other group in the popula-

92 tion at random.

93 flights — Groups encounter other groups based on their frequencies and

94 a constant encounter rate. When two group encounter one another

95 there is a fight decided by a Tullock contest. The winner then takes

96 one resource from the loser, if the winner doesn’t already control the

97 maximum number of resources and the loser has a resource to lose.

98 3.1 Key variables

99 In the results section several key variables are varied: migration (*d*), en-

100 counter rate (*c*), environmental harshness (*θ*), and resource persistence (*γ*).

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

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

103 parameters and their affect on group states.

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

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

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

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

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

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

110 0*.*125*,* 0*.*25*,* 0*.*5*,* 1*,* 2*,* 4*,* 8*,* 16}.

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

112 lost outside opf fights through chance. This abstracts away many abi-

113 otic and biotic factors. Harshness is the proportion of all loss or gain

114 events that are loss events, *θ* ∈ [0*,* 1]. A harshness close of 0*.*5 is a en-

115 vironment where gain or loss are equally likely. Whereas a harshness

116 close to 0 (resource gain is more common than loss) is a very bountiful

117 environment and harshness close to 1 (resource loss is more common

118 than gain) is extremely desolate.

119 resource persistence (*γ*) The average time to event until a patch experi-

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

121 lead to a unchanging environment where groups inherit very stable

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

123 levels with respect to the harshness level.

124 3.2 Evolving traits

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

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

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

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

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

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

131 conflicts:

, *Y* + *δ*

1

,

*P*(victory) =

*Y*1 + , *Y*2 + 2*δ .* (1)

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

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

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

.

2*δ*

135 3.2.1 Effect of cooperation (X)

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

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

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

139 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)

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

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

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

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

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

145 accelerating cost as investment increases.

146 3.2.2 Effect of conflict (Y)

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

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

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

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

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

152 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*

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

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

155 simulations *δ* = 10−8).

156 4 Results

# 157 4.1 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

158 Starting from a completely benign environment both cooperation and

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

link and make

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

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

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

0.8

0.75

0.6

Value

0.50

0.4

0.25

freq

0.2

0.25 0.50 0.75

Harshness

0.00

1 2 3 4 5

Quality

as.factor(epsilon) 0.125 0.5 1 2 4

(a)

Figure 2

as.factor(Harshness) 0.1 0.5 0.9

(b)

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

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

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

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

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

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

169 to rich groups meaning encounters are predominantly between groups that

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

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

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

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

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

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

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

# 177 4.2 Effect of encounter rate on Cooperation and Conflict

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

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

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

181 saturate though as high encounter rates mean resources become worthless

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

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 3

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

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

# 185 4.3 Group wealth and size

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

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

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

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

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

191 Figure [4](#_bookmark4) shows how conflict is expressed across wealth levels for dif-

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

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

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

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

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

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

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 4

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

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

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

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

202 upon the rich groups that predominate.

203 Group size has a negative correlation with individual investment in

204 both conflict and cooperation (fig. [5).](#_bookmark5) The group level investment in co-

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

206 in conflict decreases(fig. [6).](#_bookmark6) Cooperation in the model has a private bene-

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

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

209 nesses individuals decrease their contributions dramatically.

210 5 Discussion

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

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

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 5

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

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

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

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

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

218 on cooperation.

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

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

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

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

223 overall with group size.

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

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

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

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

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

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

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 6

230 underlying game [(Requejo and Camacho,](#_bookmark15) [2011;](#_bookmark15) ?). Our results also show

231 an increase in cooperation from benign to poor environments. However,

232 the increase in within group cooperation leads to higher levels of between

233 group conflict. So cooperation does increase but only towards group mem-

234 bers. Which leads to more harmonious groups united in conflict rather than

235 any type of utopian population wide cooperation.

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

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

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

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

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

241 termediate environments is relevant when thinking about environmental

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

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

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

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

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

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

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

249 provisioned species if their supplementation is removed or disrupted could

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

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

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

253 suring changes in expressed cooperation and conflict.

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

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

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

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

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

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

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

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

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

263 fect the overall pattern of intermediate harshness maximising conflict as

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

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

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

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

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

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

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

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

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

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

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

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

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

277 concluding

para

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

279 popualtion was poor.

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

281 was small relatively

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

283 but again with an intermediate optimum.

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

285 again quite small.

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

287 virons poor groups invested most.

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

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

290 5.1 comparisons

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

292 tween group conflict rather than within group cooperation (though

293 obviously structural)

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

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

296 of scale + private benefit).

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

298 decreases and no private benefit to fighting)

299 5.2 next steps

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

301 rently asymmetric benefits but not costs.

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

303 when they can’t gain them.

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

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

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340  A Model Description

341

342

343

344

345

346

347

348

349

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

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

350 individuals on the patch, *n* ∈ Z : *n* ∈ [0*, N* ]. Where the maximum quality, *Q*,

351 and maximum group size, *N* , are predetermined parameters.

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

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

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

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

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

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

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

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

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

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

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

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

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

365 the equilibrium relatedness values, R∗.

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

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

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

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

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

# 371 A.1 Environmental Variables

372 The environment is defined by two varaibles enviornmental harshness,

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

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

375 resource.

loss

*θ* = gain + loss (A.1)

1

*γ* = gain + loss (A.2)

376 A.2 Lifecycle outline

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

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

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

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

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

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

383 act representations for fitness and relatedness recursions we would direct

384 the reader to the simulation files.

385 A.2.1 Environmental transitions

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

387 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)

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

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

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

391 away from the focal state.

392 A.2.2 Mortality

393 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)

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

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

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

397 A.3 Local births

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

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

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

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

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

402 A.4 Immigration

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

404 immigrate into patches at random.

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

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

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

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

408 larger groups. Adults do not disperse only offspring.

409 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

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

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

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

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

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

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