Todo list

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 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 (Thompson et al., 2017; Vitikainen et al., 2019).

Previous models have shown that intergroup conflict can favour within group cooperation. However, these models often link the payoffs of cooperation and conflict so as to enable a direct synergism between the two (Choi and Bowles, 2007; **?**). This assumption is suited to answer certain questions in the evolution of human societies however hides the tension between cooperation and conflict that exists in other cooperative groups. Specifically, we might expect performing well in intergroup encounters makes one less willing or able to cooperate with others or vice versa.

example of where it does and doesnt work

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

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

In this paper we model two separate traits one controlling between-group conflict and one controlling within-group cooperation. They are both social traits that are fully conditional on the individuals group's size and resources. This removes the correlations between within group and between group behaviour, of Choi and Bowles (2007) and Lehmann and Feldman (2008), of previous models and explicitly allows the payoffs of these behaviours to be mediated by explicit modelling of an underlying resource that determines individual fitness. This allows us to better understand the trade-offs between within-group and between-group behaviours interacting with changing ecological conditions.

We investigate how cooperation and conflict evolve when resources are scarce or abundant. We also analyse how the wealth and size of a group affects their investment into cooperation and conflict. We find that harsher environments increase cooperation but only increase conflict up to a point beyond which it decreases again. We also find that in harsh environments conflict increases with richness but in benign environments conflict decreases with quality. Group size increasing decreases both cooperation and conflict in all environments.

3 Model

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

The state of the population at any given time is characterised by the frequencies of each possible group state $\{q, n\}$, where q is the number of resources the group has and n is the number of individuals in the group. This forms a matrix $\mathbf{F}_{q \times n}$ where each entry $f_{q,n}$ is the frequency of that state amongst groups in the population. The traits of cooperation (X) and conflict (Y) are also defined as $q \times n$ matrices where each entry is the strategy an actor plays in that state.

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

Resource loss and gain — Resources appear an disappear from groups. The rate at which resources are lost or gained is derived from the environmental harshness and the persistence of resources and is independent of group state. Resources are not consumed by the individuals in a group but give the same benefit to all members of the group equally regardless of group state.

Deaths — Individuals die at a base mortality rate unaffected by state. Investment into either cooperation or conflict increases that risk of death. However, mortality for all group members is reduced by the group level investment into cooperation.

Births — There is a base per capita reproductive rate which increases by each resource an individual has access to with a density dependent effect. If a group has reached it's maximum size only dispersing offspring survive. Offspring disperse to any other group in the population at random.

Fights — Groups encounter other groups based on their frequencies and a constant encounter rate. When two group encounter one another 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 $d \to 0$ 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 opf 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 a 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:

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

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:

$$M_{q,n} = \mu_B * \exp\left(-(n-1)\,x^l_{q,n} - x^f_{q,n}\right) + \mu_X\left(x^f_{q,n}\right)^2 + \mu_Y\left(y^f_{q,n}\right)^2. \tag{2}$$

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

3.2.2 Effect of conflict (Y)

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

$$V(q, n, q', n') = \frac{y^f_{q,n} + (n-1)y^l_{q,n} + \delta}{y^f_{q,n} + (n-1)y^l_{q,n} + n'y_{q',n'} + 2\delta}. \tag{3}$$

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

4 Results

4.1 Effect of harshness on Cooperation and Conflict.

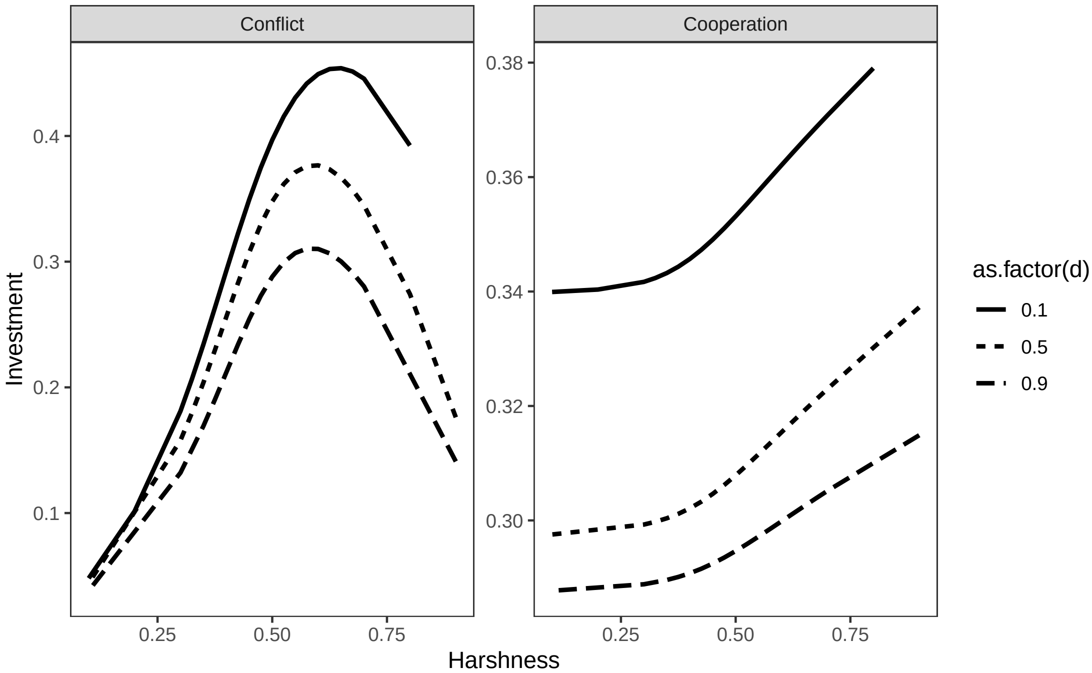

Figure 1

Starting from a completely benign environment both cooperation and conflict are at their minimum evolved levels (fig1). As harshness increases both cooperation and conflict increase in an accelerating way. Cooperation continues to increase so in very harsh environments populations evolve to cooperate the most. However, conflict investment peaks at just after 0.5

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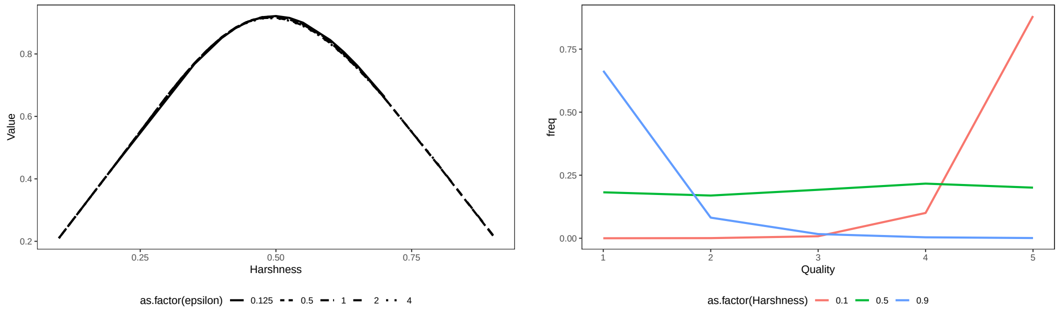

(a) (b)

Figure 2

harshness when the more resources are lost than gained overall.

This intermediate maximisation of conflict is due to the effects on harshness on the distribution of group sizes. Harsh environments skew populations towards many poor groups. This means encounters are predominantly between groups that do not have resources and so conflict is not favoured. Equally in benign environments te distribution of groups is heavily skewed to rich groups meaning encounters are predominantly between groups that cannot gain more resources and so conflict is also low.

Despite this shift from poor to rich populations being largely symmetrical around harshness 0.5 reduction in conflict occurs alter around 0.6. This occurs because resource value does continue to increase with harshness so though the number of fights is maximised at exactly harshness 0.5 the resource value drives fighting up until around harshness 0.6 when investment starts to decline as the populations shift to extreme poverty.

4.2 Effect of encounter rate on Cooperation and Conflict

The encounter rate between groups had a strong effect on the evolution of conflict but a smaller effect on cooperation. As encounter rate increases there is a marked increase into investment in conflict. This increase does saturate though as high encounter rates mean resources become worthless as they cannot be retained. This leads to a maximum encounter rate be-

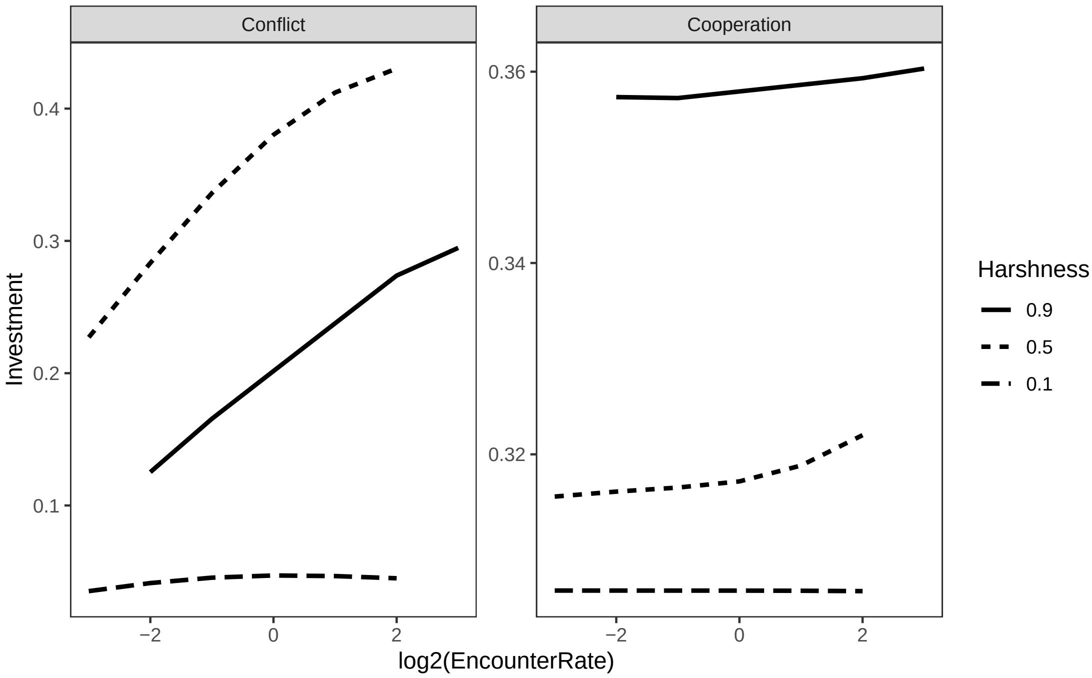

Figure 3

yond which conflict no longer is selected to increase further. Cooperation increases slightly with encounter rate but on a much smaller relative scale.

4.3 Group wealth and size

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

Figure 4 shows how conflict is expressed across wealth levels for different environmental harshnesses. In benign (low harshness) environments conflict decreases with quality level as most groups are rich and rich groups can't lose resources to other rich groups. As harshness decreases conflict increases as the frequency of the different quality levels evens out. Then at high harshnesses the population flips completely to being mostly poor groups that again cannot lose resources to other poor groups and don't have

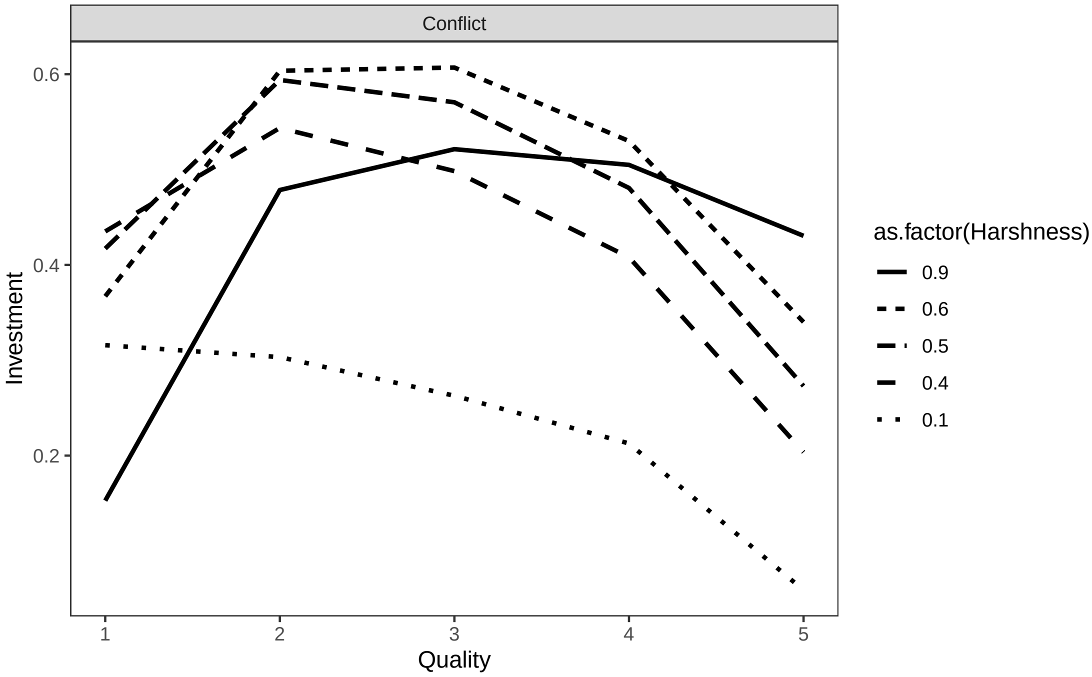

Figure 4

any rich groups to prey upon. This leads to low conflict in small groups and high conflict in rich groups. So in harsh environments rich groups are high in conflict to protect themselves against the poor groups that predominate and in benign environments poor groups are the most aggressive to prey upon the rich groups that predominate.

Group size has a negative correlation with individual investment in both conflict and cooperation (fig. 5). The group level investment in cooperation increases with group size, whereas the group total investment in conflict decreases(fig. 6). Cooperation in the model has a private benefit which leads to a high per capita investment independent of the group. However, conflict is a public good so in large groups with lower relatednesses individuals decrease their contributions dramatically.

5 Discussion

We found that as the environment became more harsh, in that resources disappeared at a greater rate then they were generated, then conflict in-

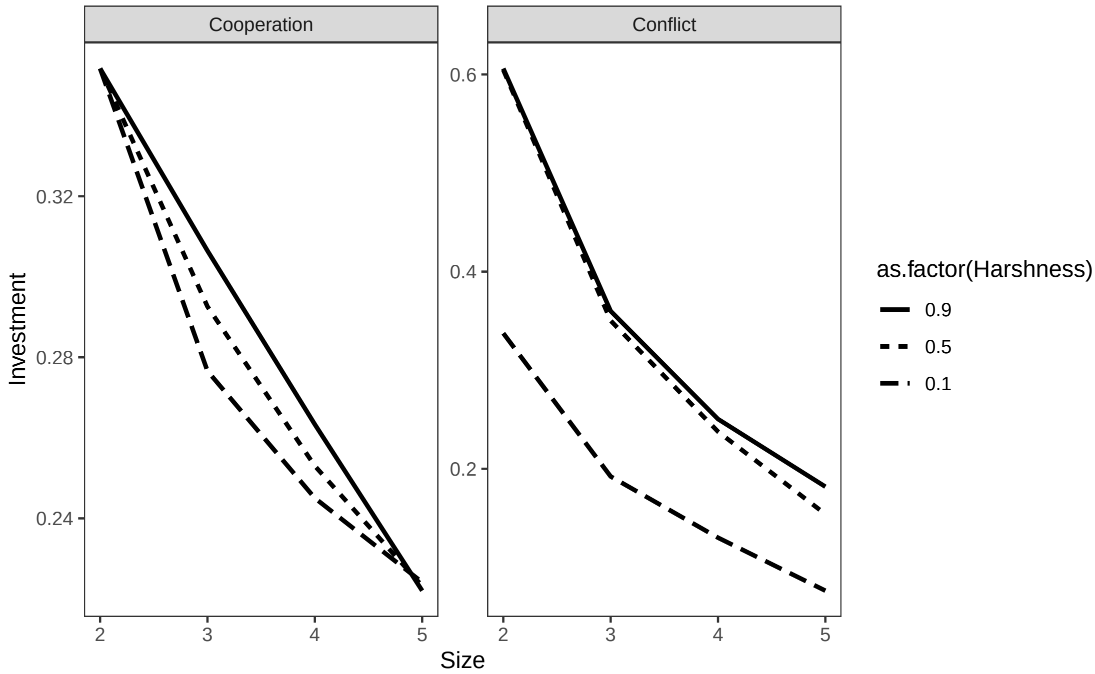

Figure 5

creased up to a maximum value after which conflict decreased again. The higher the rate of conflicts the more investment into conflict was made by individuals however this did saturate at high encounter rates and no further increase in conflict was observed. For cooperation we found that increasing encounter rate and environmental harshness both had a small positive effect on cooperation.

We found that investment into conflict increased with wealth in harsh environments and decreased with wealth in benign environments. And we found that individual investment into both cooperation and conflict decreased with group size but group investment in cooperation still increased overall with group size.

Kropotkin (1902) proposed that cooperation increased in harsh environments. Evidence since then has been varied, it is true that harsh environments are colonised at a greater rate by cooperative species (Cornwallis et al., 2017). However, it is not clear if harshness itself selects for cooperation. Previous theoretical work has shown that resource limitation does select for cooperative strategies by essentially modifying the payoffs of the

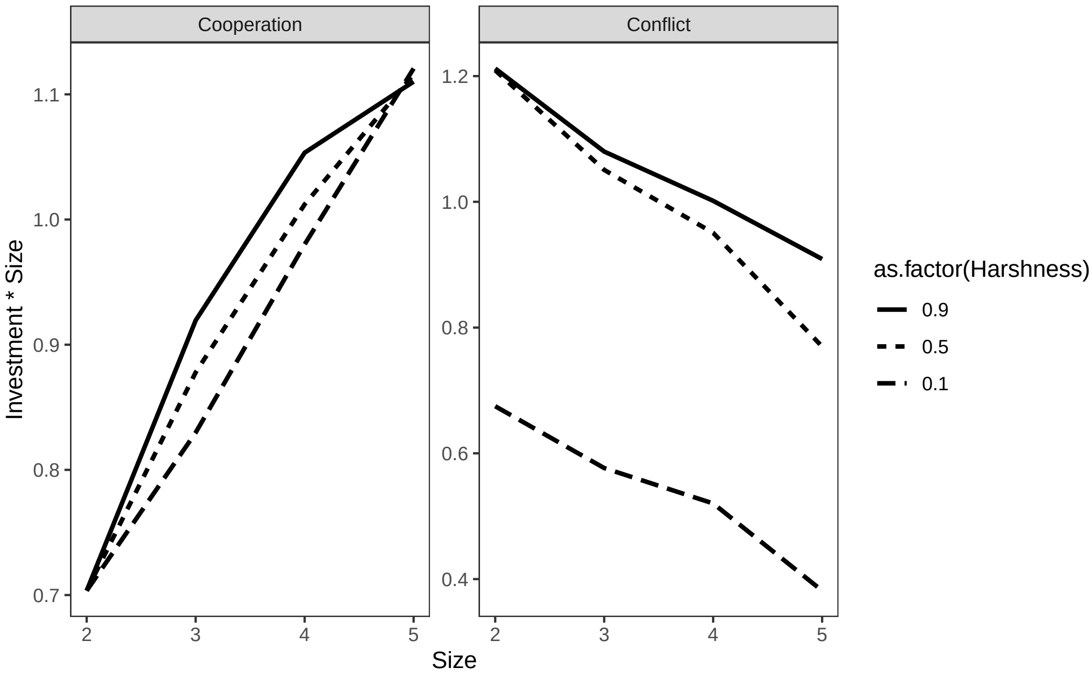

Figure 6

underlying game (Requejo and Camacho, 2011; **?**). Our results also show an increase in cooperation from benign to poor environments. However, the increase in within group cooperation leads to higher levels of between group conflict. So cooperation does increase but only towards group members. Which leads to more harmonious groups united in conflict rather than any type of utopian population wide cooperation.

The shift in state distributions drives the pattern we see in how conflict varies with group wealth and with harshness. In harsh environments all groups are poor which leads to low conflict as encountered groups have no resources to steal and equally in benign environments the need to fight is low amongst naturally rich groups. This maximisation of conflict in intermediate environments is relevant when thinking about environmental change. Supplementary feeding is performed in a number of conservation strategies primarily in scavenging species and predators (Oro et al., 2008). Negative impacts such as stress and disease spread have been analysed before (Murray et al., 2016). Our results point to the possibility of a more indirect result in that increasing feeding for a species in harsh conditions might drive selection for higher levels of aggression especially if the feeders are claimable or in some way controllable by a group. In addition, already well provisioned species if their supplementation is removed or disrupted could also increase their levels of conflict. These predictions are however evolutionary ones. On shorter timescales it would be useful to extend our results by displacing evolved strategies into new environmental regimes and measuring changes in expressed cooperation and conflict.

The effect of low and high harshness in our model is partially driven 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 know that the major cost from intergroup conflict in some species is in mortality from the fight Cant et al. (2016). 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.

concluding para

1. Harsher environs favoured increased conflicy up until too much of te popualtion was poor.
2. Harsher environs always selected for higher cooperation though change was small relatively
3. encounter rate increasing drove higher conflict in harsh environemnts but again with an intermediate optimum.
4. cooperation increased with higher encounter rates but the shift was again quite small.
5. in harsh environs rich groups invested most in conflict in benign environs poor groups invested most.
6. increasing group size decreased both conflict and cooperation however group level cooperation went up and conflict went down.

5.1 comparisons

1. yes groups more social in harsh environs but they are investing in between group conflict rather than within group cooperation (though obviously structural)
2. ”altruism” is higher in harsh environs.
3. larger groups are more cooperative but each individual is less (economies of scale + private benefit).
4. larger groups invest less in fighting (resources worth less? relatedness decreases and no private benefit to fighting)

5.2 next steps

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

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A Model Description

do each section biol and add example 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 (**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 (**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 **F**, **W**, and **R** are used as to generate the new selection gradient and iterate until the selection gradient converges to $[0]_{q\times n}$.

A.1 Environmental Variables

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

$$\theta = \frac{\text{loss}}{\text{gain}+\text{loss}} \tag{A.1}$$

$$\gamma = \frac{1}{\text{gain}+\text{loss}} \tag{A.2}$$

A.2 Lifecycle outline

THe following section contains verbal descripitions of the various modelling steps that were taken to construct the recursion equations for the frequencies, fitness and relatedness matrices. We have included the generated equations for the patches of state $\{q = 2, n = 2\}$ with a maximum $Q = 3$ and $N = 3$. So all population and individual matrices are 3×3. We include the added terms for the frequency equations only to aid understanding for exact representations for fitness and relatedness recursions we would direct the reader to the simulation files.

A.2.1 Environmental transitions

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

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

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.

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

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 $1-d$.

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

Where, the only term is the subtraction of those patche 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.

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

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 he 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 ona 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 $\{2, 2\}$.