Mongoose Proj

Matishalin Patel, Michael Cant, and Rufus Johnstone

3 1 Abstract

4 Lorem Ipsum

s keywords:

6 intragroup cooperation, intergroup conflict, game theory, social evolution

2 Introduction

- 8 Intergroup conflict is thought to be the key driver in the evolution of coop-
- 9 eration. However our understanding of the key evolutionary and ecological
- drivers of inter group conflict is far from complete. In social mammals both
- between and within group conflict is variable and seems positively or neg-
- atively correlated with between and within group cooperation. This variety
- of responses shows that a better understanding of the driver of coopera-
- tion and conflict are needed to fully explain how within and between group
- 15 conflict evolves in social mammals.
- Previous models have shown that intergroup conflict can favour within
- group cooperation. However these models often link the payoffs of cooper-
- ation and conflict so as to enable a direct synergism between the two. This
- approach may make sense for some complicated behaviours such as tribal
- 20 warfare in human societies, but simpler behaviours or those more prevalent

in social mammals more generally may not follow this pattern. Specifically,
we might expect the opposite to be true — performing well in intergroup
encounters makes one less willing or able to cooperate with others or vice
versa.

Previous work has also focused on non-conditional traits that do not take into account the fact that benefits and costs of intergroup conflict are highly dependent on the internal state of the group and the environment. The economic and political theory literature on war argues that resource inequality drives human conflict but few studies have explored that same logic to the evolution of intergroup conflict in social mammals.

In this paper we explicitly model a group structured population where
each group varies in number of individuals and in resource quality. Groups
engage in Tullock contests where the winner gains one of the losers resources. Individuals play conditional strategies of intergroup conflict and
cooperation and they are allowed perfect knowledge of their own state but
not their opponents. ¡findings¿

- 3 Model

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, $q \in \mathbb{Z}$: $q \in [1, Q]$, 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 **F** with elements $f_{q,n}$. Equally, the evolved strategies of cooperation, **X**, and conflict, **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 **F**' which describes how demographic processes and between patch interactions affect the frequency of each patch type.

6 3.1 Environmental transitions

The environment may gain and lose resources naturally through variation in various abiotic and biotic factors that are not controllable by the individuals we model. This represents the natural gain and loss from the environment.

$$E_{q,n} = \sum_{q_1=1}^{Q} \sum_{q_2=1}^{Q} t_{q_2,q_1} f_{q_2,n} - t_{q_1,q_2} f_{q_1,n}$$
 (1)

where, E is the matrix of changes due to environment, E is a E matrix with entries being this environmental rate of change. In our model we further specified that the matrix E is a sparse matrix with a subdiagonal where all entries equal to some gain value and a superdiagonal where all values equal to a loss value. This ensures gains and losses happen in stepwise manner and patches may not gain or lose more than one resource at once.

3.2 Natural mortality

Death may occur through natural causes at any time causing a patch to lose members. We modelled beth the cooperative and competitive traits as causing a cost to survival. The cooperative trait however offset that cost by reducing overall mortality on the patch based on the average cooperation level. This gives the matrix M as the changes in frequency due to mortality events:

$$M_{q,n} = \sum_{n=1}^{N} (n+1) f_{q,n+1} m_{q,n+1} - n f_{q,n} m_{q,n} , \qquad (2)$$

where,

$$m_{q,n} = B \exp\left(-n\left(\frac{n \ x_{q,n}}{n}\right)\right) + \mu_x x_{q,n}^2 + \mu_y y_{q,n}^2$$
 (3)

74 3.3 Local Births

In patches with at least one individual that are not at the maximum group

size N there can be birth events. Which are modelled by matrix B:

$$B_{q,n} = \sum_{q=1}^{Q} \sum_{n=1}^{N} -1_{n=1}$$
 (4)

77 References

78 A Resource Dependence Perspective on Intergroup Conflict: The

9 Synthesis of Two Theories - McCarthy - 2018 - Journal of

80 Theoretical Social Psychology - Wiley Online Library (n.d.),

https://onlinelibrary.wiley.com/doi/abs/10.1002/jts5.22.

Bowles, S. (2006), 'Group Competition, Reproductive Leveling, and the

83 Evolution of Human Altruism', *Science* **314**(5805), 1569–1572.

Bowles, S. (2009), 'Did Warfare Among Ancestral Hunter-Gatherers Af-

fect the Evolution of Human Social Behaviors?', Science 324(5932), 1293–

₈₆ 1298.

Bowles, S., Choi, J.-K. and Hopfensitz, A. (2003), 'The co-evolution of in-

- dividual behaviors and social institutions', Journal of Theoretical Biology
- 22**3**(2), 135–147.
- 90 Boyd, R., Gintis, H., Bowles, S. and Richerson, P. J. (2003), 'The evolution
- of altruistic punishment', Proceedings of the National Academy of Sciences
- 92 **100**(6), 3531–3535.
- ⁹³ Cant, M. A., Nichols, H. J., Thompson, F. J. and Vitikainen, E. (2016),
- Banded mongooses: Demography, life history, and social behavior, in
- W. D. Koenig and J. L. Dickinson, eds, 'Cooperative Breeding in Verte-
- brates', Cambridge University Press, Cambridge, pp. 318–337.
- 97 Choi, J.-K. and Bowles, S. (2007), 'The Coevolution of Parochial Altruism
- and War', Science **318**(5850), 636–640.
- 99 Claire Thesis Chapter (n.d.).
- Cornwallis, C. K., Botero, C. A., Rubenstein, D. R., Downing, P. A., West,
- S. A. and Griffin, A. S. (2017), 'Cooperation facilitates the colonization of
- harsh environments', *Nature Ecology & Evolution* **1**(3).
- De Dreu, C. K. W., Gross, J., Méder, Z., Giffin, M., Prochazkova, E., Krikeb,
- J. and Columbus, S. (2016), 'In-group defense, out-group aggression, and
- coordination failures in intergroup conflict', Proceedings of the National
- Academy of Sciences of the United States of America 113(38), 10524–10529.
- Downing, P. A., Griffin, A. S. and Cornwallis, C. K. (2020), 'Group forma-
- tion and the evolutionary pathway to complex sociality in birds', *Nature*
- 109 Ecology & Evolution 4(3), 479–486.
- Garfinkel, M. R. and Skaperdas, S. (2006), 'Economics of Conflict: An
- Overview', SSRN Electronic Journal.
- Inzani, E., Marshall, H. H., Thompson, F. J., Kalema-Zikusoka, G., Cant,
- M. A. and Vitikainen, E. I. K. (2019), 'Spontaneous abortion as a re-

- sponse to reproductive conflict in the banded mongoose', *Biology Letters*15(12), 20190529.
- Ito, H., Katsumata, Y., Hasegawa, E. and Yoshimura, J. (2017), 'The promotion of cooperation by the poor in dynamic chicken games', *Scientific Reports* **7**(1), 43377.
- Johnstone, R. A. and Cant, M. A. (2008), 'Sex Differences in Dispersal and the Evolution of Helping and Harming.', *The American Naturalist* 172(3), 318–330.
- Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L. and Stanback, M. T. (1992), 'The Evolution of Delayed Dispersal in Cooperative Breeders', *The Quarterly Review of Biology* **67**(2), 111–150.
- Lehmann, L. (2011), 'The Demographic Benefits of Belligerence and Bravery: Defeated Group Repopulation or Victorious Group Size Expansion?',

 PLOS ONE 6(7), e21437.
- Lehmann, L. and Feldman, M. W. (2008), 'War and the evolution of belligerence and bravery', *Proceedings of the Royal Society B: Biological Sciences* 275(1653), 2877–2885.
- Patel, M., Raymond, B., Bonsall, M. B. and West, S. A. (2019), 'Crystal toxins and the volunteer's dilemma in bacteria', *Journal of Evolutionary Biology* 32(4), 310–319.
- Patel, M., West, S. A. and Biernaskie, J. M. (2020), 'Kin discrimination, negative relatedness, and how to distinguish between selfishness and spite', *Evolution Letters* **4**(1), 65–72.
- Rusch, H. (2014*a*), 'The evolutionary interplay of intergroup conflict and altruism in humans: A review of parochial altruism theory and prospects for its extension', *Proceedings of the Royal Society B: Biological Sciences* 281(1794).

- Rusch, H. (2014*b*), 'The evolutionary interplay of intergroup conflict and altruism in humans: A review of parochial altruism theory and prospects for its extension', *Proceedings of the Royal Society B: Biological Sciences* 281(1794).
- Sheppard, C. E., Inger, R., Macdonald, R., Barker, S., Jackson, A., Thompson, F., Vitikainen, E., Cant, M. A. and Marshall, H. (2018), 'Intragroup competition predicts individual foraging specialisation in a group-living mammal'.
- The Impact of Resource Uncertainty and Intergroup Conflict on Harvesting in the Common-Pool Resource Experiment — SpringerLink (n.d.), https://link.springer.com/article/10.1007/s10640-017-0193-9.
- Thompson, F. J., Cant, M. A., Marshall, H. H., Vitikainen, E. I. K., Sanderson,
 J. L., Nichols, H. J., Gilchrist, J. S., Bell, M. B. V., Young, A. J., Hodge,
 S. J. and Johnstone, R. A. (2017), 'Explaining negative kin discrimination
 in a cooperative mammal society', *Proceedings of the National Academy of*Sciences 114(20), 5207–5212.
- Thompson, F. J., Marshall, H. H., Vitikainen, E. I. K. and Cant, M. A. (2017),

 'Causes and consequences of intergroup conflict in cooperative banded

 mongooses'.
- Thompson, F. J., Marshall, H. H., Vitikainen, E. I., Young, A. J. and Cant,
 M. A. (2017), 'Individual and demographic consequences of mass eviction
 in cooperative banded mongooses', *Animal Behaviour* **134**, 103–112.
- Vila, J. C. C., Jones, M. L., Patel, M., Bell, T. and Rosindell, J. (2019), 'Uncovering the rules of microbial community invasions', *Nature Ecology & Evolution* 3(8), 1162–1171.