https://doi.org/10.1093/pnasnexus/pgae224 Advance access publication 2 July 2024 Research Report

Influential individuals can promote prosocial practices in heterogeneous societies: a mathematical and agent-based model

Stefani A. Crabtree (Da,b,c,*, Colin D. Wren (Dd, Avinash Dixit (De and Simon A. Levin (Db,f

Edited By: Valerio Capraro

Abstract

In this paper, we examine how different governance types impact prosocial behaviors in a heterogenous society. We construct a general theoretical framework to examine a game-theoretic model to assess the ease of achieving a cooperative outcome. We then build a dynamic agent-based model to examine three distinct governance types in a heterogenous population: monitoring one's neighbors, despotic leadership, and influencing one's neighbors to adapt strategies that lead to better fitness. In our research, we find that while despotic leadership may lead towards high prosociality and high returns it does not exceed the effects of a local individual who can exert positive influence in the community. This may suggest that greater individual gains can be had by cooperating and that global hierarchical leadership may not be essential as long as influential individuals exert their influence for public good and not for public ill.

Keywords: common-pool resources, prosociality, game-theory, public-goods game, individual behavior

Significance Statement

Leadership styles play a critical role in helping to promote prosociality in society. This work demonstrates that while top-down despotic leadership may lead towards high prosociality and high returns it does not exceed the effects of a local individual who can exert positive influence within their community. This may suggest that greater individual gains can be had by cooperating and that global hierarchical leadership may not be essential as long as influential individuals exert their influence for public good.

Introduction

Disasters tend to engender short-term prosocial behaviors in citizens; neighbors offering aid for businesses impacted by floods (1), citizens with electricity offering use of it to those who need it (2), or citizens with masks donating them to caregivers early in the COVID-19 pandemic (3). Yet, often these prosocial behaviors seem to devolve over time to selfish behaviors favoring individuals and their families (4) as the crisis wanes or even as the crisis becomes less pressing and continues indefinitely. While the behavior of favoring oneself and one's immediate kin over the group may ascribe to an evolutionary optimum, over time this can lead to a decrease in fitness for the group itself. The interactions among individuals always lead to community success or community failure and depend on the balance of prosocial and defecting

behaviors. If the goal is to engender cooperative behavior over the long term, how can we foster prosocial behavior in a population of unrelated individuals in a lasting and sustaining way?

Researchers have puzzled over how to sustain prosocial behaviors over long periods and how to promote them in large societies (5–9). It is generally acknowledged that prosocial behaviors can be promoted and sustained more easily in small-scale societies due to their governance structure (4, 10–12), with questions on how bottom-up versus top-down leadership could change prosociality. In a paper that examines these different governance structures, Hooper et al. (10) modeled how small-scale societies could decide to elect a leader to help with defection in what they term a public goods game. They found that as groups scale up in size it is increasingly costly for individuals to monitor others for defection,



Competing Interest: The authors declare no competing interest.

Received: July 30, 2023. **Accepted:** May 30, 2024

© The Author(s) 2024. Published by Oxford University Press on behalf of National Academy of Sciences. This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (https://creativecommons.org/licenses/by-nc/4.0/), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact reprints@oup.com for reprints and translation rights for reprints. All other permissions can be obtained through our RightsLink service via the Permissions link on the article page on our site—for further information please contact journals.permissions@oup.com.

^aDepartment of Environment and Society, Utah State University, Logan, UT 84322, USA

^bThe Santa Fe Institute, Santa Fe, NM 87501, USA

^cCrow Canyon Research Institute, Crow Canyon Archaeological Center, Cortez, CO 81321, USA

^dDepartment of Anthropology, University of Colorado Colorado Springs, Colorado Springs, CO 80918, USA

^eDepartment of Economics, Princeton University, Princeton, NJ 08544, USA

^fDepartment of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08540, USA

^{*}To whom correspondence should be addressed: Email: stefani.crabtree@usu.edu

while a leader who spends all of their time leading and curtailing defection can help to increase prosociality. This mathematical model was then used as the basis of an agent-based model by Kohler et al. (12) where they allowed groups to form across the simulation and play a common-pool resource game, electing a leader if and when defection became too high.

While these studies may explain how leadership could arise in small-scale societies, the question of how to promote prosociality within communities that may already have leadership, and in realms outside of regular governance, is a question worth further examination. Moreover, understanding how different types of leadership can lead to different outcomes can have implications for the past; when we detect a prosocial outcome in the archaeological record such as a large public works project, we may or may not be able to ascertain the type of leadership that led to that project. Our work directly examines how prosociality can come out of different governance structures which can aid in interpretations of the past. In a more contemporary example, the COVID-19 pandemic is one recent test of prosociality globally among heterogeneous governance structures and we can examine how different governance types led to different outcomes.

In this paper, we ask: to what extent do different governance types impact prosocial behaviors? We construct a general theoretical framework to examine a game-theoretic model to assess the ease of achieving a cooperative outcome among a heterogenous population. We then build a dynamic agent-based model to examine three distinct governance types in a heterogenous population: monitoring one's neighbors, despotic leadership, and influencing one's neighbors to adapt strategies that lead to better fitness.

This work builds on theories of human cooperation and prosociality in the broad social science literature, such as Sigmund et al. (13) who examined sanctions on free riders to a common pool resource game. Our initial model for monitoring one's neighbors builds specifically on work by Hooper et al. (10) and Kohler et al. (12). These models examine how a heterogenous society of cooperators and defectors can come to equilibrium via means of punishing defectors. In a further examination of how punishment can lead toward larger group cooperation, Yilmaz and Bahçekapili (14) examine how the threat of supernatural punishment can promote human cooperation; when people are primed with the idea of eventual supernatural punishment they are less likely to defect. Within our model, we examine this phenomenon via the global leadership scenario; while punishment is not from a supernatural source, in this governance strategy a leader sets the tone for the full group and thus prevents future defection. Finally, we examine the phenomenon of individuals having influence within their social sphere for promoting prosociality. In Madeo and Mocenni (15), they examine the difference between what they term "selfregulation" (the decision of whether to defect or cooperate) versus social influence regulating prosocial behavior, while in Sigmund et al. (13) they demonstrate that social learning can help build institutions for governing common pool resources. Our influencer scenario examines this explicitly. Thus, our model specifically builds on the published literature to examine the ways that different governance strategies can promote or hinder prosociality. Each of these scenarios is examined in an agent-based model which allows for greater heterogeneity of agent-types and for evolutionary dynamics to unfold over time to examine which scenarios lead to prosocial gains or antisocial losses.

In this paper, in contrast to the work by Hooper et al. (10) and Kohler et al. (12) who used the term "public goods game," we use the term common-pool resource game to align with research in economics. Economists reserve the term "public good" to mean

something that is nonrivalrous, i.e. consumption by one person does not detract from consumption of the same by any other person, and nonexcludable, i.e. nonpayers cannot be prevented from consuming. The models we build in this current research, and that build on the work by Hooper et al. (10) and Kohler et al. (12), do not adhere to the first property yet do adhere to the second. Thus, to align with work in economics as well as developing work on common-pool resources in anthropology (16, 17) we use the term common-pool resource game.

In our research, we find that while global/despotic leadership may lead towards high prosociality and high returns it does not exceed the effects of a local individual who can exert positive influence in the community. This may suggest that greater individual gains can be had by cooperating and that global hierarchical leadership may not be essential as long as influential individuals exert their influence for public good and not for public ill.

Executive summary of results

In this work, we first build a formal mathematical model to examine the game-theoretic approach for achieving cooperation in a group of heterogeneous agents. We find that monitoring is essential to ensure cooperation for individuals who self-regulate sensu Madeo and Mocenni (15) since there will be a spectrum of pure cooperators to reluctant cooperators to pure defectors. We find that there is an optimum for detection of defection; with 100% reliable detection, monitors can ensure a prosocial society, yet this is not a realistic level of detection. Thus, we sweep across different values of detection, showing that as detection decreases, defection will increase, causing prosociality to decrease as a whole.

We then examine these findings within an agent-based model of a heterogeneous population. We report the full sensitivity analysis in the Supplementary Material in which we examine all combinations of all variables, but for ease of narrative we report the most germane results below.

We first examine a base model built on the idea of a heterogeneous population of agents, a percent of whom always cooperate, a percent of whom either reluctantly cooperate or defect, a percent of whom always defects, and a percent of whom not only cooperate but monitor their neighbors for cooperation in a common-pool resource game. We find that a stable state can be achieved over time in the model as long as monitors are able to effectively detect and punish a large portion of reluctant defectors.

We then build on this model to see if a leader "setting the tone" similar to Yilmaz and Bahçekapili (14) would lead to high cooperation. We find a stable evolutionary state where there are fewer defectors and more cooperators over time. We then examine a strategy similar to that analyzed by Madeo and Mocenni (15) where an influential individual will recruit neighbors within a specified radius to behave prosocially if the influential individual finds that cooperation results in higher individual gains than defection does. Interestingly, we find that the influencer governance strategy performs similarly to the strategy of leaders setting the tone, and better than the mutual monitoring scenario, suggesting that spheres of influence can have similar impacts to group-level prosociality sensu Madeo and Mocenni (15) as does fear of reprisal sensu Yilmaz and Bahçekapili (14).

The mathematical model

To examine the effects of prosocial behavior and different governance strategies in a common-pool resource game, we begin with a mathematical model. This numerical approach formally examines the game-theoretic model to establish the difficulties of achieving a cooperative outcome for a community's overall benefit. We then build an agent-based model that alters some of the key assumptions responsible for the mathematical outcome, showing how some of the mutual benefit can be realized without resorting to centralized control of all activity.

In the mathematical model, we consider a population of N individuals, each of whom acts in their own personal interest. Each owns an amount R of some resource (for example, money or labor). Each can consume all of this directly, or can contribute 1 to a common resource pool q. Suppose k people make such a contribution. The resulting k units of contributions get multiplied by a factor M > 1, resulting in a total quantity k M of the common-pool. This is divided equally among all N people, regardless of whether a person had made a contribution. Thus each person gets kM/N units of consumption from the common-pool.

Each person has the choice of whether or not to contribute. If (k-1) others are contributing, this individual will get

$$total\ consumption = \left\{ \begin{array}{ll} (R-1) + k\,M/N & \ \ by\ contributing, \\ R + (k-1)\,M/N & \ \ by\ not\ contributing \end{array} \right.$$

$$(R-1) + kM/N > R + (k-1)M/N$$
 if and only if $M/N > 1$

Thus, if M > N, that is, the multiplier on each person's contribution is so huge that each gets back more than the contribution even when the magnified amount is divided up among the whole population, each will find it selfishly optimal to contribute. But if M < N, it is selfishly optimal for each not to contribute (i.e. to exhibit no prosociality). This is true regardless of how many others are contributing, so it is the dominant strategy for each.

Barring miracles, M > N is very unlikely in a society of any nontrivial size, and we assume it away. Therefore in our analysis such a society with pure selfish behavior and no other mechanism to induce cooperation is fated to end up without any contributions to the common resource pool. In technical terms, the noncooperative Nash equilibrium of their game has zero contributors, and each member of the population consumes R.

But if k people contribute, each consumes (R-1) + kM/N. This steadily increases in k, so it is socially optimal for everyone to contribute, when each would consume (R + M - 1) > R.

The game is a multi-person Prisoners' Dilemma, with the strategy of contributing corresponding to cooperation, and not contributing is defection, which corresponds to the different strategies we examine below in the agent-based model—cooperators, defectors, and reluctant cooperators/defectors who contribute only once punished for defection. In a single play with purely selfish behavior and no other institutional modification or enforcement in the game, pure defection is the only, and socially suboptimal, equilibrium. Many methods attempting to achieve, or work toward, this optimum have been proposed, and studied in the research literature (4, 6, 8, 18, 19).

At one extreme, a central planner could require and force everyone to make the contribution. Yet, in practice this is likely unrealistic. Even in the highly simplistic model above, where all individuals are identical and have equal resource endowments, detecting whether a person has contributed, and enforcing the requirement if they have not, is costly, and this cost must be subtracted from the total benefit. Whether the net social value is positive or not is unclear. In reality, individuals differ in their resource endowments and needs, so who should contribute how much and get what share of the resulting total are difficult questions. Moreover, although individuals know their own

resource endowment and the need, the social planner does not. Individuals do not have the incentive to reveal their information; instead it is selfishly optimal to strategically manipulate the information transmission so as to conceal resources (thereby reducing the contribution the planner would assess for them) and exaggerate their needs (thereby increasing the share of the final output that the planner would give them). Indeed, in the real world most attempts at central planning have failed for such reasons. Therefore, we must explore alternative institutions and organizations that work their way toward the optimum.

In this section, we examine two solutions of this kind using game-theoretic methods. They find Nash equilibria or stationary states of such interactions. In the rest of the paper, we turn to an agent-based version of the interaction, where different individuals in the society exhibit different behaviors analyzed here, and the dynamics where these agent behaviors change over repeated plays of the game in response to their experiences in previous plays.

1. Prosociality (or altruism):

Many people have some regard for others and internalize their benefit to some extent in their own calculation. Consider one such person who gets a mental payoff equivalent to α of the resource endowment for each unit that each other person in the society received as a share of the common resource pool. If this person contributes the 1 unit to the pool that is being asked of them, each of the other (N-1) people gets M/N, which creates the mental payoff α M/N to the donor. To that we must add the M/N the donor gets directly. The overall result is a net benefit to the donor if

$$M/N + \alpha(N-1)M/N > 1$$

or

$$\frac{1 + \alpha \left(N - 1\right)}{N} M > 1 \tag{1}$$

For a purely selfish person ($\alpha = 0$), this reduces to M > N as above, which we are assuming to be false. For $\alpha = 1$, this reduces to M > 1, which we are assuming to be true. Therefore, there is a critical value α^* such that the social optimum will be attained if all members of the society have $\alpha > \alpha^*$.

The more likely scenario is one where individuals are heterogeneous in their levels of altruism.^a Then the fraction with $\alpha > \alpha^*$ will find it optimal to contribute, and that remains true regardless of how many others are contributing. In the agent-based model to come, we postulate the existence of some individuals who are pure cooperators (contributors) in this way.

2. Monitoring:

Suppose some members of the society spend time and effort to check whether others have contributed. Some people may do this purely out of a sense of social duty, or a vengeful attitude of "I am contributing; others should too, and I will ensure they do." Others may have to be compensated to monitor. Such monitoring is not perfect. Suppose that in the society of N people, the probability that any one individual gets checked is a decreasing function p(N). If checked and found not to have contributed, that person is fined F. This may be monetary, or a mental penalty arising from social disapproval or shaming.

If (k-1) others are contributing, a selfish person gets

expected payoff =
$$\begin{cases} (R-1) + k M/N & \text{by contributing,} \\ R + (k-1) M/N - p(N) F & \text{by not contributing} \end{cases}$$

Therefore, contributing is the preferred strategy if

$$M/N + p(N) F > 1 \tag{2}$$

To satisfy this, we need p(N)F > 1 - M/N. That can be done either by making p(N) or F sufficiently large, or some combination of the two. The former requires real resource costs; in our context monitoring. These monitors may be volunteers motivated by, e.g. a sense of social justice, but even then they have to spend time and effort that could have been used instead to produce goods or services for their own or others' consumption. This argues for keeping p(N) small. As for F, fines are transfers—from the offender to the government's coffers, or as restitution to any identifiable victims when someone fails to make their contribution to sustaining or improving the common-pool resource. Fines don't necessarily carry any resource cost; the gain of the receiver roughly balances out the loss of the payer. To the extent that taxes distort effort, if the proceeds of the fines are used for reducing the rates of other taxes like general income or sales taxes, that is an even better secondary benefit, as people like Nordhaus (20) have argued. This argues for making F as large as possible. However, there are limits; for example you cannot fine anyone more than would reduce them to total penury. But the optimum is to push F up to such a limit, and then choose p(N) only just large enough to satisfy Eq. 2.b

In the agent-based model, we make some choices of specification for sake of definiteness, although alternatives are worth exploring in future work. We postulate that a few agents take on the task of monitoring their neighbors without direct compensation. We also assume that the "fine" can take the form of coercing the future behavior of a defector who has been caught, perhaps even deducting these contributions from their resource endowment. Thus, we assume the existence of an agent type called "reluctant cooperators": they contribute only after they have been once detected. (We also allow for a pure defector type, who will not contribute even after a detection and payment of a fine in the form of social shame).

The agent-based model

The mathematical model helps us understand that the social optimum of everyone contributing to a public good requires enforcement by monitors since individuals will act on their self-interest and will likely defect if it can lead to greater individual gains. To account for how the formal mathematical model would behave over time as well as under different governance strategies for monitoring, we built an agent-based model (ABM) in NetLogo 6.2.2 (21). This ABM allows us to examine how the dynamics of a heterogeneous population would evolve over time, and how different governance strategies and different values for parameters impact the results found in the mathematical model.

The ABM proceeds according to a population of agents N playing a common-pool resource game in a classical game-theoretical model. Here agents play a game at each time step and then adjust their strategies for the next round based on their state as cooperators or defectors. In the ABM, k agents pay into a common resource pool g that is collected centrally. This common resource pool is then multiplied by a common-pool resource game multiplier M. Once the game is played, the common resource pool, M((q)k), is then equally redistributed among all agents N regardless of participation or defection, as in the mathematical model above.

Within each iteration of the agent-based model, there are multiple individual strategies comprising the agents in the population N; in this we follow precedent by Kohler et al. (12) and Hooper et al. (10). First there are individuals who always cooperate and pay into the common resource pool (q)k; these we call "always cooperate." Second there are agents who always defect—they never pay into the common resource pool but will always be counted in the redistribution, representing N - k above; these agents we call "always defect." Next there are monitors who, each time step, look to see if there have been defectors and choose to punish one defector per time step, extracting a fine from the defector; these agents we call "monitors." The fine is then deposited in (q) and counted in the redistribution of the common resource pool. Monitors have to pay a small resource cost for monitoring, as it is costly to monitor other agents; in this we follow work by Hooper et al. (10). Finally, there are agents who will reluctantly cooperate in the next turn if they are caught defecting and are punished; we call these agents "reluctant cooperators," and depending on the governance strategy (below) they may return to defecting after they have been sanctioned or they may keep cooperating. This heterogeneous agent population reflects our results from the mathematical model-monitors need to enforce cooperation to ensure the social optimum—while also building on the work by Hooper et al. (10) and reflecting the well-established feature of human cooperation (22), that many individuals will look to their own self-interest over group interest in common pool resource games.

Next, we examine three distinct leadership strategies that guide the common-pool resource game: mutual monitoring (10), global leadership (14), and local influencing (15). In each of these governance strategies, all of the above agent-types are present at initialization, though in some experiments certain agents can die out over time due to unfavorable conditions. In this, we can examine how different governance strategies can attain or approach or approximate to the optimum of everyone contributing to the common-pool resource as identified in the mathematical model. Of note, the common-pool resource game is played in public, so agents have access to the wealth and defection status of any agent at any point. However, only monitors act on this knowledge by imposing sanctions at a resource cost to their own wealth. For more information on how the agent-based model proceeds see the Supplementary ODD Protocol.

Mutual monitoring governance strategy

In Hooper and colleagues' original paper, they called the task of watching one's neighbor and sanctioning them if they defect "mutual monitoring." We take this as our baseline governance strategy such that a certain proportion of the population will not only always cooperate by paying their share of the common-pool resource game cost into the common resource pool, but they will also pay a personal cost to ensure that their neighbors are not defecting. This is reflected in the above mathematical model. This base governance strategy examines how well neighbors monitoring one another can lead to prosocial behavior.

Global leadership governance strategy

Layered on top of the mutual monitoring scenario, global leadership prevents agents who have already defected from defecting again after they have been punished. In this strategy, we can imagine a leader who "sets the tone," and via fear of reprisal, those reluctant cooperators who are punished for defection will rarely defect again. In this way, we explicitly examine the work by (14). While the agent-based model does not use capital punishment, for example, the global leadership strategy leverages the idea that "'tone" can influence people's decision of whether or not to defect again. To keep the ABM more parsimonious we establish that reluctant cooperator agents will not defect again after

punishment once; this follows logic in the common-pool resource game in the agent-based model by Kohler et al. (12) where they examine the development of general leadership. In the current work, mutual monitors still monitor defectors in this scenario and pay a small resource cost to monitor as before. Always defect agents continue to defect regardless of the punishment consistent with the work by Kohler et al. (12).

Local influencing governance strategy

In this scenario, the ABM again begins with the baseline mutual monitoring governance strategy. When reluctant cooperators defect, the simulation then compares the mean wealth of currently cooperating agents versus noncooperating agents. If the mean cooperating wealth is greater, a random noncooperating reluctant agent is converted to be a local cooperating "influencer." The influencer will then convince, with a probability P, their neighbors in a radius R to cooperate in the common-pool resource game to increase their own fitness. This governance strategy examines the work by (15) that an influential individual can promote prosociality. This is the only part of the ABM that is explicitly spatial, as conversion occurs only within a specified spatial radius and, in subsequent time steps, additional influencers can only be converted from outside of that spatial radius—there will not be two influencers in the same sphere, though there may be a slight overlap of agents they try to recruit if their radii overlap.

Running the Agent-Based Model

We begin the agent-based model by creating a population of agents who interact in a common-pool resource game and setting the number of each agent type by percentages of the overall population. In Table S1, we report the agent population size and type proportions at initialization; populations increase or decrease over time, as this paper examines the evolution of a pluralistic society that has different strategies within it acting with and/or against each other in a game theoretic way. We keep these initial proportions of agent types constant for each subsequent experiment of the four governance scenarios, yet in our Supplementary Materials describe how we varied all of the possible parameters to examine their effects on model output. Of particular note, we examine how different tax levels can lead to the death of monitors, which leads to a rebound of defection, as we describe in the Supplementary Material. Any set parameter in the final results reported in the main text are set from a wide sensitivity analysis, as reported in the Supplementary Material.

We then examine the simulation according to parameter values identified in the mathematical model. By keeping the common-pool resource game multiplier at 1 and running the simulation for a minimum number of timesteps, we see that monitors are critical to ensure prosociality in the short term, verifying the results from the mathematical model. In the Supplementary Material, we demonstrate that when monitors die off that defection rebounds. Beginning with the simple model of monitoring enables us to build up in complexity from the mathematical model to examine other governance strategies, leveraging the benefits of an agent-based model, which allows for examining heterogenous populations and how they interact through time.

In the agent-based model, there are several parameters that we vary to examine the effects of returns to the common-pool resource and the impact of fines on defectors. To establish which parameters should remain fixed for the subsequent governance strategies, we ran a parameter sweep on the baseline mutual monitoring scenario focusing on sanction fines and on the common-pool resource game multiplier. Table S2 reports the parameters we varied in our sweep. Several parameters were held constant in the sweeps for this scenario, but can be varied to ask other questions. To account for the effects of stochasticity, we ran each parameter combination 50 times, and the results below represent the central tendencies of these runs. Additionally, each of these parameters are described in more detail within the supplement following the ODD Protocol (23).

In the ABM, M is multiplied by the quantity of pennies in the common resource pool, reflecting M((q)k), suggesting that the whole resource pool will be greater than individual contributions, and following logic from Kohler et al. (12). We assess both an increase of 50% (M of 1.5) and an increase that doubles the common resource pool (M of 2.0).

We also assess different quantities of pennies for a sanction fine for defectors. While the base fine is parameterized, in each scenario the fine is adjusted depending on wealth as a "progressive tax":

- If <10 pennies, only 25% of the base fine is paid;
- If ≥10 but <20, 50% of the base fine;
- If ≥20 but <40, 75% of the base fine;
- If ≥40 but <60, all of the base fine;
- If ≥60, 125% of the base fine.

This ensures that very poor agents are not overly penalized, while wealthy agents are penalized proportionally.

Finally, we add a simple population dynamic such that, while our ABM does not allow for sexual reproduction, if an agent has below 0 pennies, they are removed from the simulation and are replaced by a new agent that may be either cooperating or defecting depending on the currently dominant agent strategy as determined by the summed wealth of all cooperating vs. defecting agents. Thus, the population size of each agent type can evolve to roughly reflect current conditions, and whether it is optimal to cooperate or to defect. This replication dynamic is thus proportional to reproductive success in the form of wealth (pennies) and mirrors reproductive dynamics in the agent-based model by Premo (24).

While there are many parameters that can be varied, we kept them fixed after the initial sensitivity analysis (see Supplementary Materials); this allows us to reduce parameter space and target specific effects of variable combinations. In Table S3, we see that there is a cost of 1 unit of wealth (termed "penny" in the ABM) to pay into the common resource pool, that sanctions only begin at timestep 50 to allow for a "burn in" time, as is common in simulations, and that monitors spend 0.5 pennies as a resource cost to punish a defector. Again, each parameter combination was run 50 times to account for stochasticity and we report mean and standard deviation in the figures below.

Results

To track the success of the various strategies under the three governance scenarios, we focus on reporting average agent wealth as a proxy for fitness. Within these we decompose the reluctant agents into those agents currently cooperating versus currently defecting, which can be an indicator for whether cooperation or defecting is currently the most winning strategy. In the Supplementary Materials, we report populations for each of the experiments as well, since replacement occurs when an agent dies due to lack of wealth. Since reluctant cooperator agents can either be currently cooperating or currently defecting, we report those as separate populations. We report these for each of the governance scenarios allowing comparability among the different scenarios to help determine which scenarios lead to prosocial outcomes. Below we

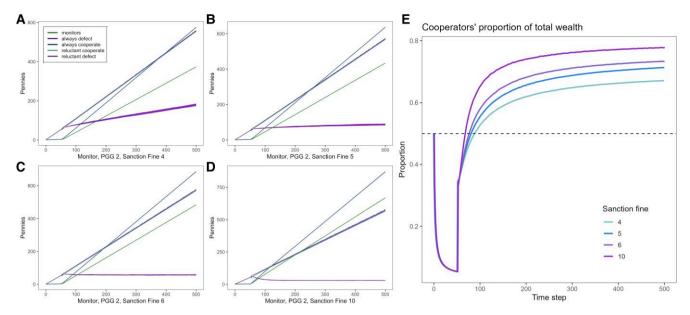


Fig. 1. Sanction fines have a large effect on the ability of prosociality or defection to gain and maintain wealth, as can be seen from the central tendencies of four different monitor outputs with a common resource pool multiplier of 2. Panels A-D depict full 500 timesteps of the simulation and the central tendencies of wealth for each of the agent types. Panel E shows the proportion of wealth that cooperators versus defectors have. A) Simulation with a monitoring governance strategy with a base sanction fine of 4. B) Simulations with a monitoring governance strategy with a base sanction fine of 5. C) Simulations with a monitoring governance strategy with a base sanction fine of 6. D) Simulations with a monitoring governance strategy with a base sanction fine of 10. E) All four of the results from A-D, but with relative proportions of cooperators versus defectors wealth; when the lines are below the 50% line defectors have more wealth, while when lines are above the 50% line cooperators hold more wealth. Note that in A. defect scenarios perform better than in D, reflecting the impact of high fines on the simulation.

focus on only the most germane results for each of the experiments; full sensitivity analyses for each variable as well as other figures can be found in the Supplementary Materials.

Common-pool multiplier and mutual monitoring

To recap, the Mutual Monitoring scenario is the base scenario on top of which each other governance strategy is built, so we examine how each parameter combination interacts in this scenario before setting parameters in subsequent scenarios. To assess how the common-pool multiplier M interacts with the common-pool resource game and agent wealth, we ran a parameter sweep of the simulation with the multiplier set at both 1.5 and at 2. We coupled these with fines for defection from 4 to 10 pennies, adjusted based on stored wealth of the defecting agents as described above.

A common-pool multiplier M of 1.5 always led to defectors winning—both always defect and reluctant defect were the winning strategies in these simulations. The results from these experiments are reported in Figure S10. Within these scenarios, cooperate strategies monotonically approach zero and do not recover. This suggests that a low common-pool multiplier would be impossible for promoting prosociality in a heterogeneous population of defectors and cooperators.

In Figure 1, we see those scenarios with a common-pool multiplier M of 2. In this figure, we graph the full 500 timesteps in A-D where we specify the accumulated wealth of each of the agent-types. Additionally, we add a simplified panel, Panel E, to show the relative proportion of accumulated wealth for all pooled defecting agents (always defect, and reluctant defect) and all pooled cooperating agents (always cooperate, reluctant cooperate, monitors) which acts as a simplified way to easily examine which strategy currently has the higher fitness. In panel A, we see that while defectors initially outperform other agents, that at step 50 when sanctioning begins we see cooperating strategies (both reluctant and always cooperate) gain wealth. When sanction fines begin, we see that it takes until

step 350 for always cooperate agents to begin to outperform defecting strategies; monitors, while increasing their wealth, never outperform reluctant defectors, though do begin to outperform pure defectors by timestep 200. In panel B where sanction fines are set at 5 we see similar trajectories to A, though wealth for defectors is slightly dampened from 4. In panel C, we see that a sanction fine of 6 begins to level out wealth accumulation for each of the strategies except for pure defectors, who maintain a steady amount of wealth but do not gain. Cooperators start to perform well even right by about timestep 80, and by timestep 200 pure cooperators are performing well. We do see that reluctant cooperators and reluctant defectors still perform rather similarly, though cooperation seems to lead toward more wealth in the long run. When we look to a fine of 10 in Panel D we see that cooperation is by far the most winning strategy and that there is not much variance around the means.

When we examine the simplified figure in Panel E, which shows central tendencies for the proportion of wealth for each of the four sanction fines, we can see that sanction fines have a critical importance on the ability of cooperators or defectors to accumulate wealth. With a sanction fine of 4 defectors perform better than they do with a sanction fine of 10, where cooperators hold almost all the wealth by the end of the simulation. Yet compared to Figure S9 we can see that a common pool resource game multiplier of 2 is critical for cooperators to be able to exist at all. Juxtaposing panels A through D, which show how each of the agent-types fares in the scenario, with panel E that shows on average how cooperation or defection fares as an evolutionary strategy for fitness in the form of wealth is critical to evaluate how prosociality fares in a mutual monitoring scenario.

In each of these, we see the agents with the strategy "always defect" become the most wealthy relatively quickly before sanctioning begins at timestep 50, followed by reluctant defectors and cooperators, mirroring results from the mathematical model—sanctioning is critical for the social optimum. Moreover, we see

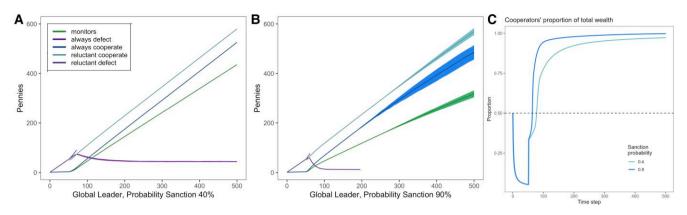


Fig. 2. Global leadership tends to lead toward a reduction in defection over time with a cooperation leading to highest wealth, although sanctioning influences the ability of defection to maintain being a viable strategy (A) or fizzle out (B). Panels A-B depict the central tendencies of each strategy for the full 500 timesteps of the simulation. A) Simulation with a Global Leadership governance strategy with a probability of sanctioning at 40%. B) Simulations with a Global Leadership governance strategy with a probability of sanctioning at 90%. C) Both results from A-B, but with relative proportions of cooperators versus defectors wealth; when the lines are below the 50% line defectors have more wealth, while when lines are above the 50% line cooperators hold more wealth. Note the impact of high detection for the ability of defectors to perform more poorly in the simulation.

that near perfect perception (90% probability sanction) and relatively high sanctioning (6 or 10) is critical in a mutual monitor scenario. In Supplementary Materials, we find that overall, when sanctioning rates are high, agent populations evolve strongly toward cooperation, while when sanctioning is low, defection tens to perform better. While there is not a dramatic population difference between the sweeps (e.g. S11 or S12), we can still see effects of nonperfect perception and sanctioning on the full population and how reluctant agents will move toward defection. To account for a certain amount of stochasticity, we fixed the parameters of the common-pool resource game multiplier at 2 and the sanction fine at 6 for subsequent experiments in governance strategies, though continue to explore how high versus low sanctioning impacts wealth and populations. Setting the base fine at 6 and a common-pool multiplier M at 2 allows for the variability in the model to explore whether or not governance strategies can lead toward prosocial behaviors. In the Supplementary Material, more information on each of the individual scenarios can be explored.

Global leadership

To examine the impacts of a global leader "setting the tone" and not allowing reluctant cooperator agents to defect again, we ran a simulation with the above-fixed parameters to understand the impacts of global leadership on wealth; populations are reported in the Supplementary Material. While wealth in this scenario does differ from results in the mutual monitoring scheme they are rather similar; first defectors flourish due to not paying in to the common-pool resource game, but as sanctions occur, reluctant defectors switch to reluctant cooperators and do not defect again. This can be seen with the relative increase in cooperative pennies and the slight but present decrease in defecting pennies. The leftmost graph (Fig. 2A) shows probability of sanction at 40%, while the middle graph shows probability of sanction at 90% (Fig. 2B). As with 1 we also graph the relative wealth of cooperators versus defectors. In the rightmost graph (Fig. 2C), we can see that cooperation becomes dominant regardless of if the probability of sanction is 40% or 90%. In the Supplementary Materials, we explore wider ranges of the probability of sanction. In the Supplementary Materials (e.g. Figure S16), the populations reflect similar effects to the wealth; the increase in cooperators and decrease in defectors is due to population replacement as described in the Supplementary Materials.

Influencing

As above, we explore both a probability of sanctioning at 40% and 90% while maintaining a sanction fine of 6 pennies and M of 2; we report a full sensitivity analysis in Figures S20 and S21. In Figure 3, we focus on the probability of sanctioning at 90%. We further focus the discussion on the scenarios with a probability of influencing one's neighbors at either 50% or 90% and the radius of influence at 5 and 10 cells. We pair the full wealth output with the proportion of wealth figure for these simulations as well. In Figure 3 we see that, as with the above scenarios, defection begins as the best strategy until sanctions begin. At the point when defection starts to be punished (timestep 50) we see that cooperation starts gaining in wealth, which eventually become the highest performing strategy in each of the four experiments.

In Figure 3, we see that in each of the four experiments that pure defectors are quickly eliminated from the simulation. Interestingly, for all four experiments we see that reluctant defectors continue holding wealth for many timesteps beyond when monitoring begins. We see that the sphere of influence impacts whether or not reluctant defectors return to the simulation, with panels A and B showing that stochastic population rebounds occur when the probability of influence is at 50%. When the probability of influence is at 90% we see much higher variance around the wealth for cooperators over time. We further see in panel E that a probability of influence of 90% leads to higher cooperative gains than a probability of influence of 50% (also see Figure S20). However, cooperators still hold a higher proportion of wealth than defectors. We also see that in Figures S17 and S18 while there is variation around the mean, populations of cooperators stay larger than those of defectors throughout the influencer scenario simulation.

To more readily compare results from each experiment, in Figure 4, we combine the wealth proportion plots for the mutual monitoring scenario, the global leadership scenario, and the influencer scenario. Here we plot in the mutual monitoring scenario a sanction fine of 6, in the global leadership scenario a sanction fine of 6 and a probability of sanction at 90%, and in the influencer scenario a sphere of influence of 10 and a probability of influence of 90%. These results are discussed below.

Discussion

In our mathematical model, we demonstrate that it is selfishly optimal for individuals playing the common-pool resource game to

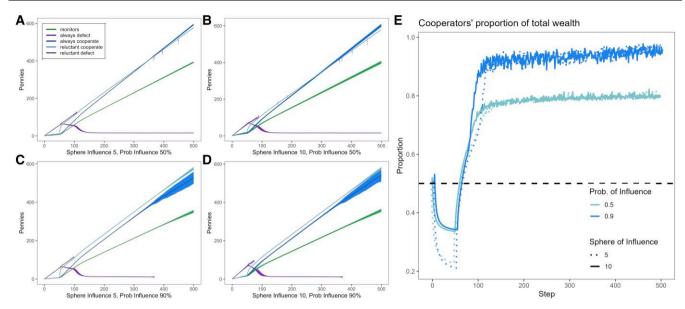


Fig. 3. Influencing leads to prosocial behaviors despite the radius of the sphere of influence or the probability of influence. Yet, the probability of influence has greater effect on the variance of wealth and the ability for reluctant defectors to return to the population, as can be seen in panels A and B. Here we display the central tendencies of two different outputs with a common resource pool multiplier of 2 within the Influencer strategy when the probability of detection is at 90%. Panels A-D depict full 500 timesteps of the simulation. A) Simulation with a sphere of influence of 5 and a probability of influencing one's neighbors at 50%; note that while reluctant defectors die out by step 100 they stochastically return around step 300, demonstrating that defection can be viable, albeit for short times. B) Simulations with a sphere of influence of 10 and a probability of influencing one's neighbors at 50%; as with A, reluctant defectors die out by early, yet they stochastically return periodically throughout the simulation, demonstrating that defection can be viable, albeit for short times. C) Simulation with a sphere of influence of 5 and a probability of influencing one's neighbors at 90%; reluctant defectors leave by step 100 and do not return long enough to be seen on the graph of central tendencies. D) Simulations with a sphere of influence of 10 and a probability of influencing one's neighbors at 90%; as with C, reluctant defectors leave by early, this time by step 80 and do not return long enough to be seen on the graph of central tendencies. Pure defectors survive past step 300 but then die out completely in both C and D. E) Results from A-D, but with relative proportions of cooperators versus defectors wealth; when the lines are below the 50% line defectors have more wealth, while when lines are above the 50% line cooperators hold more wealth.

defect on contribution. However, it is in the interest of society to ensure defectors are detected and punished, thus requiring monitoring to ensure continued contributions to the common resource pool. It is also increasingly costly to detect defectors as societies grow in size. An immediate implication of the mathematical model is that resource-rich economies are able to maintain larger groups with universal common-pool resource contribution as long as there are sufficient enough monitors to enforce sanctioning of defectors. To the extent that the common-pool resource has any investment or growth benefit for the future (e.g. education, health care, infrastructure etc.), they will get even richer due to the compounding effects of common resources.

Detection costs resources for society as a whole. Fines, however, are transfers among individuals. So a given expected cost of deterring anti-social behavior is best achieved by having as low a probability of detection and as high a fine as feasible (25). We see this in the formal model and also reflected in the results of our agent-based model.

In our simulations, a common-pool multiplier of 2 leads to gains in wealth for cooperative strategies, while lower multipliers are more beneficial for defectors, suggesting that incremental gains for public goods projects may not be viable for situations with large amounts of defection which we demonstrate in Figure S9. We see that in the mutual monitoring governance strategy that cooperators can accumulate more wealth with high sanction fines for those who defect. From the results from Figure 1 we were able to determine those parameters to fix for future governance strategy experiments.

When we introduced global leadership we see that defection becomes a lower performing strategy. Both pure defection and reluctant defection have rapid declines in wealth as can be seen in Figure 2. Interestingly, in Panel C of Figure 2 we can see impact of sanction probability on the ability of cooperators to retain wealth. However, we do see in Panels A and B of Figure 2 that reluctant cooperators hold the most wealth over time. This is likely due to the fact that they made rapid gains as defectors before they became cooperators; by defecting and having a greater payout and then switching to a cooperating strategy they are able to compound the most wealth throughout the simulation.

When we compare the wealth output results for each of the agent types in Figures 2 and 3 we see that all prosocial strategies perform the best, with reluctant cooperators achieving the most wealth over time in 2A and 2B as well as 3C and 3D; always cooperate perform marginally better than reluctant cooperate in 3A and 3B. Interestingly, pure defectors all lose their wealth in both the Global Leadership and the Influencer strategies, likely due to the need for monitors to punish someone and only pure defectors are left after many reluctants are already sanctioned, causing them to be punished regularly and thus lose their wealth quickly. Overall we may suggest that what is critical is high probability of punishment and any leadership scenario that skews cooperation towards greater fitness.

When we examine Figure 4, we see a similar trajectory of cooperators' accumulated wealth among the governance strategies of mutual monitoring, for global leadership, and for influencing, though with greater fluctuation for influencing, though with much less wealth for cooperators in the mutual monitoring scenario. This is not altogether surprising, for Hooper et al. (10) suggest that leadership is needed to maintain prosociality when populations grow. Within global leadership, agents who reluctantly cooperate very rarely return to defection for fear of reprisal. In the influencing scenario, however, those who are influenced self-

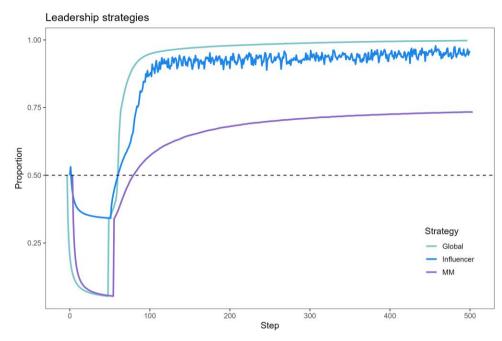


Fig. 4. Central tendencies of each of the three leadership strategies for comparative purposes. Here we plot in the mutual monitoring scenario a sanction fine of 6, in the global leadership scenario a sanction fine of 6 and a probability of sanction at 90%, and in the influencer scenario a sphere of influence of 10 and a probability of influence of 90%. We see that leadership, whether global leadership or influencing, leads to higher prosocial outcomes than mutual monitoring alone. Remarkably, we see that influencing performs almost as well as global leadership.

regulate (15) and more frequently return to defection. Yet even with the greater variance, the trajectory towards increased prosociality remains similar when comparing the overall wealth of cooperation versus defection. As wealth in the population accumulates over time, we can see in Figure 4 that defectors perform increasingly poorly. While early defection may be beneficial, over time the gains to cooperation outpace that of defection. This may have implications for short-term common-pool resource games, where defection can be beneficial for certain individuals for short amounts of time, but over time would have decreasing payoffs.

Global leadership could be seen as a type of despotic leadership, since we assume that fear would prevent agents from defecting again (14). In Kohler et al. (12), this is exactly the case for their leadership strategy; they assume that with a leader, once an agent is sanctioned for not playing the common-pool resource game the defectors do not defect again. We see in our results that global leadership leads to reluctant cooperators performing well, followed eventually by cooperators. Defectors still perform well enough to persist under the global leadership strategy, though they do marginally better when the probability of sanctioning is at 40% than when it is at 90%.

One possible implication for the results of both the agent-based models and the mathematical model lies in comparing the outcomes to those seen in real systems. Anthropologists, such as von Rueden et al. (26) have found that individual differences, as we explored within the agent-based model herein, can influence the overall trajectory of the system as a whole. This can generate dynamics of which leader to follow and how stringently, and can impact group selection of prosocial collective action, as seen above. Key individuals have been found to be essential in promoting prosociality (27) in diverse and disparate contexts by increasing benefits for others and helping beget cooperation via the act of cooperating. Finally, cultural group selection favors institutions that benefit the group and reduce defection (28). Via the

mechanisms that lead toward the inheritance of traits that benefit the group, such as competition between groups with different levels of prosociality, we can examine the trajectory of prosociality and the ways that adaptation to cooperation has arisen over time.

Several extensions to this model can be envisioned to examine how prosociality can spread in societies. First, the generation of influencers in this model is created when one defecting individual notices that cooperation is out-performing defection on average. One defecting individual is then changed to an "influencer" who then finds defectors in their neighborhoods, telegraphs the winning strategy, and changes defectors to cooperators (with a certain probability of failure). However, we could imagine a scenario in which influencers are more actively responding to a given social context. In that case, we could envision examining the magnitude of defection or prosociality impacting the influencer strategy, which could fluctuate depending on current conditions.

We could also envision how spatial structure impacts the way prosociality would change in a society. In this model, while influencers will influence those in their radius, our agents do not move and stay on their fixed location, which enables us to examine the simplest possible model. Yet we could build on the current simple version to allow simple movement, similar to Schelling's segregation model (29). We then would need to examine the benefits of neighbors, and see how different neighborhoods would perform according to their wealth, which itself is a proxy of fitness. Neighbors could then decide to "vote with their feet" to join other defecting or cooperating neighborhoods, as explored by Wu et al. (30) who found that migration can help in the evolution of cooperation.

Agent-based models provide a way to examine how heterogenous individuals interact over time and enable the examination of different strategies. Our agent-based model reports the overall wealth of individual agents over the course of 500 timesteps, allowing us to see how different strategies behave over time and how different individuals can impact the prosociality of the group.

Our results provide an "emergent property of social interaction in context" (31) to be able to see how different governance strategies can lead to prosocial gains. Ultimately, as seen from Figure 4, prosociality can be achieved via a multitude of methods, although punishment of defection is always key to ensuring prosocial gains.

Conclusions

The results of our mathematical model and agent-based model taken together suggest that influencing one's neighbors can be as effective in the long run as top-down despotic leadership. While despotic leadership—and forcing cooperation—does indeed lead to high gains for cooperators in our model, this can come at a cost. While our simulation does not take into account agent wellbeing, despotic leadership rarely comes from a "benevolent dictator" and often can breed resentment over time. In mobile societies, high amounts of fission and "voting with ones feet" (32) can lead to the leveling of hierarchies-the reduction of the hold of leaders over a society. In more complex societies, voting out the ruler or open rebellion can ultimately have similar consequences.

In cross-cultural work among eight case studies worldwide, Moritz et al. (16) show that sustainable solutions with high prosociality can and do emerge from bottom-up processes. In these eight societies they demonstrate that top-down despotic leadership is not necessary to have high gains to common-pool resources. In fact, in those areas where there has been top-down intervention, often the results are not as beneficial as they are from bottom-up action. While on average global leadership and influencer strategies may perform similarly, within specific runs of the leadership scenarios we see such great variance to suggest the possible benefits to society on a whole of the influencer strategy.

Yet others, such as Henrich et al. (33), have suggested that copy-the-prestigious dynamics, as explored in our influencer strategy, will only be possible when groups are small. As groups get larger they find that influential individuals may stop having enough influence. Here we see that the size of the radius of influence matters, as does the ability for defectors to defect again once recruited into prosociality.

What these results may suggest is that the promotion of prosocial behaviors from influential individuals can lead to greater prosocial gains in society. In the spring of 2020, these prosocial behaviors were seen by individuals and corporations who donated unused N-95 and homemade cloth masks to hospitals (Supplementary File C). In the case of individuals, donation of masks could have a fitness cost to the individual because they would not have use of those masks themselves. However, donating them helped the public good of a functioning hospital system, and may have paid off to the individual if they were hospitalized later. The donation of these prosocial goods were covered in the media, potentially leading to more donations and to more groups of people donating their time in making cloth masks.

However, what is strikingly different between our agent-based model and the above scenario is the immediate payoff. In the simulations, agents could see an immediate benefit to being prosocial, as they were rewarded with greater wealth. Others have suggested that immediate payoffs in happiness or positive well-being do not sustain prosocial behaviors (34). The giving up of something to lead to prosocial behaviors can, according to Falk and Graeber, lead to a decrease in well-being over time. To counter this impact, rewards for prosocial behavior may be necessary to promote prosocial behavior (35).

What our work shows, however, is there may not be an ultimate trade-off in outcome for society between promoting prosocial behaviors in influential individuals and by having global despotic leadership enforcing prosocial behaviors. The mean outcome in the simulation is the same, though there is more variance in those simulations that employed influencer leadership. Taken in tandem with the work by Wu et al. (35) and Falk and Graeber (34) our work may suggest that prosocial behaviors can be promoted in society, if they are properly rewarded and sustained.

Ultimately, our mathematical model shows that enforcement is needed to stop defection and promote prosocial behaviors in society. The agent-based model shows that there are multiple paths to prosocial societies, but promoting bottom-up strategies where influential individuals can promote the benefits of prosocial behaviors at the local-scale—and be properly rewarded—can lead to more consistently optimal outcomes for individuals and societies as a whole.

Notes

- ^a In a large society (i.e. for large N), (1) becomes $\alpha M > 1$ or $M > 1/\alpha$ approximately. This is in practice somewhat unlikely to be true for all members, but may be true for some individuals with α close to 1.
- ^bThis is very similar to Becker's (25) analysis of the optimal combination of detection and punishment strategies to deter crime.
- ^cTechnology could effectively enable high levels of monitoring due to a public record, making p(N)=1 no matter how large N is, and enable F to be automatically collected. Surveillance like this would likely fall under a "global monitoring" scheme as explored below

Acknowledgments

We would like to thank Iza Romanowska for feedback on ideas that led to this draft, M. Matteo Paz Soldan whose work was essential for enabling the completion of this paper, as well as three anonymous reviewers who greatly improved this work. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the funding agencies.

Supplementary Material

Supplementary material is available at PNAS Nexus online.

Funding

This research was supported by the Army Research Office Grant Masson-Marmot W911NF-18-1-0325, the Fund Archaeological Research, and the Coalition for Archaeological Synthesis.

Author Contributions

A.D. and S.A.L. developed the mathematical model; S.A.C. and C.D.W. developed the agent-based model and ran all simulations. All authors worked on developing the models, writing the paper, and analyzing the results.

Data Availability

The agent-based model and all outputs from the model as well as R code for analyses is fully available on GitHub. Please find it here: https://github.com/stefanicrabtree/Prosocial

References

- Mackay M. 2022 Aug. Volunteers help Left Bank Books recover after flooding. KSDK St Louis. https://www.ksdk.com/article/ news/local/volunteers-help-st-louis-bookstore-recover-fromflood-missouri/63-b0ea0aa5-a7e4-4ef7-a395-828f35e70743.
- O'Grady C. 2017 Feb. In New Jersey, neighbors helping neighbors recover from hurricane sandy. USDA. https://www.usda.gov/ media/blog/2012/11/16/new-jersey-neighbors-helping-neighborsrecover-hurricane-sandy.
- Westervelt E. 2020 Mar. Can the U.S. Crowdsource its way out of a mask shortage? no, but it still helps. National Public Radio. https:// www.npr.org/2020/03/25/820795727/can-the-u-s-crowdsourceits-way-out-of-a-mask-shortage-no-but-it-still-helps.
- Tilman AR, Dixit AK, Levin SA. 2019. Localized prosocial preferences, public goods, and common-pool resources. Proc Natl Acad Sci USA. 116(12):5305-5310. https://doi.org/10.1073/pnas. 1802872115.
- Akçay E, Van Cleve J, Feldman MW, Roughgarden J. 2009. A theory for the evolution of other-regard integrating proximate and ultimate perspectives. Proc Natl Acad Sci USA. 106(45): 19061-19066. https://doi.org/10.1073/pnas.0904357106.
- Dixit A, Levin S. 2017. Social creation of pro-social preferences for collective action. In: Buchholz W, Rübbelke D, editors. The theory of externalities and public goods. Springer International Publishing, Cham. p. 127-143. ISBN 978-3-319-49441-8 978-3-319-49442-5. https://doi.org/10.1007/978-3-319-49442-5_7.
- Fehr E, Gintis H. 2007. Human motivation and social cooperation: experimental and analytical foundations. Annu Rev Sociol. 33(1): 43-64. https://doi.org/10.1146/annurev.soc.33.040406.131812.
- Gintis H. 2003. Solving the puzzle of prosociality. Rationality Soc. 15(2):155-187. https://doi.org/10.1177/1043463103015002001.
- Szabó G, Szolnoki A. 2012. Selfishness, fraternity, and otherregarding preference in spatial evolutionary games. Evol Coop. 299:81-87. https://doi.org/10.1016/j.jtbi.2011.03.015.
- 10 Hooper PL, Kaplan HS, Boone JL. 2010. A theory of leadership in human cooperative groups. J Theor Biol. 265(4):633-646. https:// doi.org/10.1016/j.jtbi.2010.05.034.
- 11 Hooper PL, Kaplan HS, Jaeggi AV. 2021. Gains to cooperation drive the evolution of egalitarianism. Nat Hum Behav. 5(7):847-856. https://doi.org/10.1038/s41562-021-01059-v.
- 12 Kohler TA, Cockburn D, Hooper PL, Bocinsky RK, Kobti ZIAD. 2012. The coevolution of group size and leadership: an agent-based public goods model for prehispanic pueblo societies. Adv Complex Syst. 15(01n02):1150007. https://doi.org/10.1142/S0219525911003256.
- 13 Sigmund K, De Silva H, Traulsen A, Hauert C. 2010. Social learning promotes institutions for governing the commons. Nature. 466(7308):861-863. https://doi.org/10.1038/nature09203.
- 14 Yilmaz O, Bahçekapili HG. 2016. Supernatural and secular monitors promote human cooperation only if they remind of punishment. Evol Hum Behav. 37(1):79-84. https://doi.org/10. 1016/j.evolhumbehav.2015.09.005.
- 15 Madeo D, Mocenni C. 2020. Self-regulation versus social influence for promoting cooperation on networks. Sci Rep. 10(1): 4830. https://doi.org/10.1038/s41598-020-61634-7.
- 16 Moritz M, et al. 2018. Emergent sustainability in open property regimes. Proc Natl Acad Sci USA. 115(51):12859-12867. https://doi. org/10.1073/pnas.1812028115.
- 17 Ostrom E. 1992. Institutions and common-pool resources. J Theor Polit. 4(3):243-245. https://doi.org/10.1177/0951692892004003001.

- 18 Fischbander U, Simon G. 2010. Social preferences, beliefs, and the dynamics of free riding in public goods experiments. Am Econ Rev. 100(1):541-556. https://www.jstor.org/stable/27804940.
- 19 Bowles S. 2008. Policies designed for self-interested citizens may undermine "the moral sentiments": evidence from economic experiments. Science. 320(5883):1605-1609. https://doi.org/10.1126/ science.1152110.
- 20 Nordhaus WD. 1993. Optimal greenhouse-gas reductions and tax policy in the "DICE" model. Am Econ Rev. 83(2):313-317. URL https://www.jstor.org/stable/2117683.
- 21 Wilensky U. 1999. NetLogo. Center for Connected Learning and Computer-Based Modeling. http://ccl.northwestern.edu/netlogo/.
- 22 Melis AP, Semmann D. 2010. How is human cooperation different? Philos Trans R Soc B Biol Sci. 365(1553):2663-2674. https:// doi.org/10.1098/rstb.2010.0157.
- 23 Grimm V, et al. 2020. The ODD protocol for describing agentbased and other simulation models: a second update to improve clarity, replication, and structural realism. J Artif Soc Soc Simul. 23(2):7. https://doi.org/10.18564/jasss.4259.
- 24 Premo LS. 2014. Cultural transmission and diversity in timeaveraged assemblages. Curr Anthropol. 55(1):105-114. https:// doi.org/10.1086/674873.
- 25 Becker GS. 1968. Crime and punishment: an economic approach. J Political Econ. 76(2):169-217. https://doi.org/10.1086/259394.
- 26 von Rueden C, Gavrilets S, Glowacki L. 2015. Solving the puzzle of collective action through inter-individual differences. Philos Trans R Soc B Biol Sci. 370(1683):20150002. https://doi.org/10. 1098/rstb.2015.0002.
- 27 McAuliffe K, Wrangham R, Glowacki L, Russell AF. 2015. When cooperation begets cooperation: the role of key individuals in galvanizing support. Philos Trans R Soc B Biol Sci. 370(1683):20150012. https://doi.org/10.1098/rstb.2015.0012.
- 28 Richerson P, et al. 2016. Cultural group selection plays an essential role in explaining human cooperation: a sketch of the evidence. Behav Brain Sci. 39:e30. doi: 10.1017/S0140525X1400106X.
- 29 Schelling TC. 1969. Models of segregation. Am Econ Rev. 59(2): 488-493. http://www.jstor.org/stable/1823701.
- 30 Wu T, Fu F, Wang L. 2011. Moving away from nasty encounters enhances cooperation in ecological prisoner's dilemma game. PLoS ONE. 6(11):e27669. https://doi.org/10.1371/journal.pone. 0027669.
- 31 Iles P, Preece D. 2006. Developing leaders or developing leadership? the academy of chief executives' programmes in the North East of England. Leadership. 2(3):317-340. https://doi.org/ 10.1177/1742715006066024.
- 32 Boehm C, et al. 1993. Egalitarian behavior and reverse dominance hierarchy [and comments and reply]. Curr Anthropol. 34(3): 227-254. https://doi.org/10.1086/204166.
- 33 Henrich J, Chudek M, Boyd R. 2015. The big man mechanism: how prestige fosters cooperation and creates prosocial leaders. Philos Trans R Soc B Biol Sci. 370(1683):20150013. https://doi.org/10.1098/ rstb.2015.0013.
- 34 Falk A, Graeber T. 2020. Delayed negative effects of prosocial spending on happiness. Proc Natl Acad Sci USA. 117(12): 6463-6468. https://doi.org/10.1073/pnas.1914324117.
- 35 Wu J, Luan S, Raihani N. 2022. Reward, punishment, and prosocial behavior: recent developments and implications. Curr Opin Psychol. 44:117-123. https://doi.org/10.1016/j.copsyc.2021. 09.003.