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Reward inequity can promote both public goods production and free riding

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When animals in groups cooperate, individuals sometimes produce a ‘public’ good that benefits many or all group members and receive a ‘private’ reward (that is not shared with others). The rate at which rewards are given and how rewards are distributed among contributors is likely to affect the occurrence of public goods production, but empirical evidence is contradictory. Here, we develop a game-theoretic model to investigate how reward rate and distribution affect the production of a public good. Our model is applicable to various scenarios in which individuals can be rewarded for public goods contributions; for example, sentinel behaviour, intergroup contest participation and collective hunting. The model predicts that inequitable distribution of rewards results in higher public goods contributions by some individuals but free riding by others because it induces competition among potential contributors. We also find that a high reward rate promotes public goods contributions but only up to a point, after which further rewards suppress contributions. This suggests that social factors such as inequity and competition might interact to affect the outcome of common public goods scenarios.

1. Introduction

Animal cooperation, particularly in social species, sometimes takes the form of public goods production. Public goods can be produced by a single actor or many individuals, but always benefit many or all individuals in a group. For example: sentinel behaviour is a public good because other individuals can forage more efficiently in the presence of a guard looking for danger [1,2]; alarm calling can benefit any individual in hearing range (who may make up some or all of a caller’s group [3]); and participating in intergroup conflict is a public good because all group members (usually) benefit from winning a contest with rivals [4–6]. As long as a public good is produced, no individual can be excluded from receiving its benefits (i.e. public goods are non-excludable [7–9]). Similarly, the uptake of the benefits of public goods by one individual does not diminish the amount available to others (i.e. public goods are non-rivalrous or indivisible [9]). Because of these two characteristics, there is an opportunity for individuals who do not contribute to the production of a public good (or those who contribute a much lower amount) to benefit as much as those who do contribute, thus free-riding off the contributions of others. For public goods production to persist in nature, there must exist mechanisms allowing individuals in groups to inhibit such exploitation. While there is considerable literature on the use of punishment [10–12] in promoting public goods contributions, the potential role of different aspects of *rewards* remains relatively understudied, particularly in non-human animals [13]. Previous work exploring the effects of heterogeneity in benefits received from public goods focuses on wealth inequality—individuals with different capacities to contribute to public goods receive differential benefits [14]. Here, we use a game theoretic model to investigate how the rate and

distribution of rewards impact how individuals choose to contribute to a public good, regardless of their 'wealth'.

There is some theoretical evidence that the provision of rewards in exchange for public goods production can promote contributions to the public good [13,15], and this is supported by empirical evidence from human experimental scenarios [16]. A positive effect of reward on public goods contributions is also reported in vervet monkeys (*Chlorocebus aethiops sabaeus*), in which males are more likely to participate in subsequent intergroup contest bouts after receiving grooming rewards for previous participation [17]. However, there is some evidence that increasing the private benefit of contributing to a public good via rewards can sometimes negatively impact cooperative behaviour [13]. For instance, there are human studies showing that rewarding people who contribute to a monetary public good does not increase contributions in one-shot games [18]; similar experiments in repeated games show that while there is a temporary increase in contributions following reward, this is not sustained [19]. This is also apparent in some observations of blood donations in humans when monetary rewards have negligible or negative effects on donation [20,21] (but see [22]). In existing studies, rewards from public goods are often linked to initial wealth. Wealthy individuals (e.g. dominant individuals in the animal behaviour literature [14,23]) are generally found to contribute more than 'poorer' counterparts [14,24], as predicted by models of inequity aversion [25] (but see [26]). However, the effect of reward independent of initial wealth is less consistent: while rewarding contributors might often promote public goods production, there are scenarios in which rewards might be ineffective or even detrimental.

In addition to their magnitude, the *distribution* of rewards among contributors might influence individuals' decisions to contribute to a public good. In human experiments, wealth inequality—where individuals receive different base payments—can inhibit public goods production [27–29], and reward inequality—where individuals who contribute the same amount receive different rewards—can result in lower 'fitness' metrics [30]. Inequity in punishment can similarly lead to a reduction in group cooperation [31], suggesting that heterogeneity among individuals in the cost/benefit ratio of public goods contributions might drive the negative effect of inequity. In dyadic exchanges, inequity has been found to hinder helping behaviour in the short-changed partner (e.g. in experiments with corvids (*Corvus* spp.) [32] and capuchins (*Sapajus apella*) [33]). Inequity in the rewards that individuals receive based on their contributions to public goods might therefore also be expected to have a negative effect on public goods production. By contrast, inequity in the distribution of rewards might not always have a negative effect if, for example, the reward is related to the contribution made such that rewards for higher contributions out-weigh the costs of those additional contributions. However, little theoretical work has investigated the effect of reward inequity on contributions to public goods (but see studies by Wang *et al.* [34] and Ding *et al.* [35], who find that inequity aversion can promote contributions in some contexts).

In this study, we use a game-theoretic model to investigate the potential effects of the rate and inequity of private rewards on contributions to public goods. The reward that individuals receive depends on their own contribution and that of others such that individuals who contribute more receive greater reward; *how much* more reward individuals receive for additional effort depends on inequity and the average contribution of the group (illustrated in electronic supplementary material, figure S1). As such, individuals must make strategic decisions based on the behaviour of other group-members and the expected payoff from contributing (or not). While the benefits from public goods are available to all individuals, the rewards are privately given, meaning that only a single individual gains benefit from its reward. This allows us to manipulate how rewards are allocated and whether this is equitable (such that individuals receive rewards in proportion to their contribution) or inequitable (such that rewards are not proportional to contribution). Our model is general but is inspired by cooperatively breeding dwarf mongooses (*Helogale parvula*), in which individuals who act as a sentinel (providing vigilance for the group) later receive grooming as a reward [36].

In many species across taxa, sentinels watch for predators while the rest of the group forages (e.g. dwarf mongooses [37]; pied babblers, *Turdoides bicolor* [2]; vervet monkeys [38]). Sentinels provide a public good as groupmates can reduce their vigilance, thus increasing foraging efficiency [1,2,38]. Sentinels may or may not be at greater risk of predation because while they adopt a high vantage point that is likely more conspicuous [39], they are also likely to see predators quickly and escape [40]; indeed sentinel behaviour has been modelled as a 'selfish' behaviour in previous work [41]. However, one common cost is lost body mass and thus condition because a sentinel (by definition) does not forage while 'on duty'. One way such losses might be ameliorated is if individuals are later groomed by others. Grooming is common in both mammals and birds (e.g. [42–44]) and is important in both reducing parasite load (e.g. [45]) and strengthening social bonds that might provide future direct or indirect fitness benefits [42,46–49]. Grooming is used as a reward (or commodity 'traded') for helping behaviours in several contexts across taxa (e.g. in exchange for infant care [50]; tolerance and coalition support [51]; and participation in intergroup conflict [17]). For example, there is observational and experimental evidence in dwarf mongooses that individuals who do more sentinel duty during the day receive a greater proportion of the group's grooming in the evening [36].

In this study, we are interested in the effect of reward inequity on how individuals contribute to the public good. We do not, therefore, include any potential costs of *giving* rewards as this does not help us to understand how would-be contributors might respond to a particular value or distribution of reward; that is beyond the scope of the current model (though grooming typically occurs during rest and can therefore be considered to have negligible costs [42]). Our model structure reflects the private energetic costs and public benefits of sentinel behaviour, but can also be applied to other public goods scenarios such as participation in intergroup conflict and cooperative hunting in which individuals might gain different levels of reward (e.g. resources such as copulations or food). We can extrapolate our model in this way because we make no assumptions about *how* the reward inequity arises, thus extending previous models invoking social or physical dominance to reward inequity driven by other types of social interactions.

We first use our model to show how the rate of reward is predicted to affect public goods contributions when there is a single potential contributor. This scenario could occur, for example, in single-male primate groups in which the male often takes on a sentinel or alarm calling role (e.g. [52]). We then investigate the effect of the rate and distribution of reward when there is a

small group of potential contributors (e.g. sentinel behaviour in several species [2,36]). We discuss how our model can be used to make testable predictions in different systems involving the exchange of public and private goods.

2. Model

(a) Payoff to a potential public goods contributor

The payoff to a potential public goods contributor depends on the difference between the benefits that it receives from contributing and the cost of its contribution. We assume that an individual gains benefits from both its own and others' contributions as well as the benefits of receiving additional 'rewards' for its contribution equation (2.1). We make the assumption that the more reward that an individual receives, the lower the per-unit reward benefit of that reward—this makes the model tractable and allows for an interior solution (linearly increasing benefits cause contributions to 'run away'). Biologically, this is justified for, for example, a grooming reward, for which the benefit of reduced parasite load is greatest when parasite load is high and decreases as parasites are removed, meaning that the reward received by an individual likely has a diminishing effect (rewards of food and copulations would similarly diminish in this way); we represent this biological relationship using a diminishing function equation (2.2). More complex assumptions about the shape of the benefit function due to different biological factors (e.g. that a threshold reward is required before an individual will consider contributing) might affect predictions but here we show the simplest case to retain generalisability. Biologically, the primary cost of contribution to a public good is often lost foraging opportunities—for example, individuals cannot forage while on sentinel duty or during interactions with another group. The greater the contribution that an individual makes to the public good (e.g. the *longer* they are on sentinel duty or the more time or energy they give to intergroup conflict), therefore, the more body mass/condition an animal is likely to lose and the less time it has to forage subsequently; as such, the cost of lost foraging time might compound as contribution increases. We therefore assume that the per-unit-effort costs of contribution to a public good increase with contribution, this is represented by an accelerating function for the cost (equation (2.3)).

Here, we show the reward, benefit, cost and fitness functions for a rare mutant individual providing contribution s_m in a group of residents contributing with effort s_r (for figures illustrating these functions, see electronic supplementary material, figure S2). We model the amount of reward received by a mutant individual as a logistic function of its public goods contribution:

$$G(s_m, s_r) = v \cdot \left(\frac{s_m N}{1 + (N-1)e^{-k\left(\frac{s_m}{s_m + s_r(N-1)} - \frac{1}{N}\right)}} \right) + a, \quad (2.1)$$

where v is the reward rate, k is a shape parameter determining the steepness of the logistic function (thus the inequity of the reward distribution among contributors) and N is the number of individuals in the group—this is both the total group membership and the number of individuals who can potentially contribute to the public good (and provide rewards). A logistic function was chosen because this is the most parsimonious function that allowed us to manipulate the reward inequity, which we can do by changing the k parameter; k determines whether individuals receive reward *proportionally* to their contribution (i.e. equitably) or *disproportionately* (i.e. inequitably). In many social animals (including dwarf mongooses [36]), it is likely that even individuals who do not contribute at all to the public good still receive some reward because the reward is likely to be a common affiliative behaviour. For example, all individuals likely receive some grooming in most mammal groups or some share of a food reward in cooperative hunters. This is represented by the 'baseline reward' parameter, a , to represent how much reward the individuals get regardless of public good contribution.

Equation (2.1) simplifies to $G(s_m, s_r) = vs_m + a$ when $k = 0$ or $N = 1$ or $s_m = s_r$ so the reward increases linearly with the contribution of the mutant under these special cases. When $N \geq 1$ and $s_m \neq s_r$, as k increases, this function becomes steeper and thus the distribution of reward moves further from being proportional to an individual's contribution (i.e. it becomes less equitable). $\frac{1}{N}$ represents the 'fair' contribution that an individual would give in a group size N . When k is non-zero, an individual who gives just slightly more than the group average contribution—scaled by N and k such that higher N gives a higher inflection point and a higher k gives a lower inflection point—can receive disproportionately more reward than the others (electronic supplementary material, figures S1 and S2). This means that individuals who contribute more than average are overcompensated and those who contribute less than average are under-compensated. Individuals who contribute the same amount are rewarded equally so inequity is in how *contributions* are rewarded. Any given system (e.g. dwarf mongoose sentineling or vervet monkey intergroup encounters) can be assumed to take on particular values of the parameters described here. Each system will fall at a single point along this line of reward inequity, with contributors receiving rewards proportionately or any level of disproportionately to their contribution based on the selective processes that drive the evolution of traits that are represented by these parameters. To allow our model to remain general, we make no assumptions about how these selective processes might act to shape the parameters that any given system adopts, and instead show only the *effects* of these parameters on our quantity of interest: public goods contributions. We show values of k that illustrate the behaviour of our model across a range of slopes; see electronic supplementary material, figure S2 for an illustration of the shapes of the functions given the parameters that we show.

The reward received by an individual confers benefits on that individual. For example, grooming removes parasites, which are energetically costly to remove from oneself and could require an immune response, and improves social relationships, potentially allowing for more energetically efficient foraging and vigilance [46,48]. As such, when individuals receive a reward, this could allow for reduced energy expenditure on, for example, immunity and predator avoidance, improving overall energetic efficiency. Additionally, individuals receive collective benefits from both their own and others' contributions to the

public good. For example, sentinels might position themselves close to shelter (e.g. [40]), allowing a quicker (more energetically efficient) escape from potential predators. Foragers are required to spend less energy on being vigilant when there is a sentinel present, and consequently can forage more efficiently, improving energy intake. As such, the benefits conferred on a rare mutant can be given by:

$$B(s_m, s_r) = \frac{bG(s_m, s_r)}{1 + bG(s_m, s_r)} + p(s_m + s_r(N - 1)), \quad (2.2)$$

where b is a shape parameter giving the steepness of the slope describing the energetic benefits from reward received—or the 'benefit rate'—and p scales the energetic benefit that individuals gain from an individual (either self or other) contributing to the public good. The final term therefore represents the collective benefit of contributions by self and others. This was chosen as the most parsimonious function for our assumptions. To check that our model was robust to the assumption that an individual benefits from its own contribution (i.e. gains some 'selfish' benefit from contribution to the public good), we ran a version without this assumption and found qualitatively similar results (see sensitivity analysis in electronic supplementary material).

Individuals cannot forage while they are contributing to the public good (e.g. when they are on sentinel duty or engaged in intergroup interactions), and body condition declines over time when individuals are not foraging. Additionally, the more time that an individual spends contributing to a public good, the less time that individual has to forage later in the day; these costs are likely to compound, meaning that spending, for example, 30 min on sentinel duty is more than twice as costly as spending 15 min on duty. We therefore assume (again, using the simplest example of an accelerating cost function) that the energetic costs of contributing accelerate with contribution such that:

$$C(S_m) = cs_m^2 \quad (2.3)$$

where c is the cost rate of contributing to the public good, scaling the negative effects of contributing.

The net payoff to an individual given their and others' contributions can be written as the difference between the energetic benefits and cost of contribution:

$$W(S_m, S_r) = B(S_m, S_r) - C(S_m, S_r). \quad (2.4)$$

All parameters and their descriptions are given in electronic supplementary material, table S1, along with values used in figures.

With this model, we investigate the effect of the rate (v) and distribution (k) of rewards on optimal contributions to a public good. We assume that any reward for public goods contributions (e.g. grooming) is a divisible resource that is allocated either equitably or inequitably (determined by the free parameter, k) and in different amounts (determined by the free parameter, v). We do not include rewarders explicitly in our model because our question is about how the contributions of individuals should respond to the (average) contributions of others given different levels or distributions of reward for those public goods contributions. To explore the behaviour of this model, we present a variety of parameter sets (see electronic supplementary material for additional parameter values). All parameters used were chosen to illustrate the behaviour of the model across a broad parameter space (because there are several parameters it would be impractical to produce a grid-search of the entire parameter space). As an example, we choose to show $k = 0$, $k = 50$, $k = 200$ because these values produce a breadth of fitness function shapes when the group size is 10 (electronic supplementary material, figure S2). A group size of 10 was chosen largely arbitrarily, but is an ecologically relevant group size for many social mammal and bird species (e.g. dwarf mongooses [53]; vervet monkeys [54]; pied babblers [55]; chestnut-crowned babblers [56]).

(b) Evolutionarily stable contribution to public goods

The model could not be solved analytically so we found evolutionarily stable solutions numerically using a hill-climbing algorithm (detailed in electronic supplementary material).

3. Results

(a) A single potential contributor to the public good

To demonstrate model behaviour in the simplest case, we begin with a single contributor to a public good whose reward varies with the effort that it gives. This one-player scenario is potentially applicable to natural situations where there is division of labour; for example by sex, such that a single individual may be the sole provider of a public good (e.g. alarm calling behaviour in Diana monkeys, *Cercopithecus diana*, is primarily carried out by the sole male in the group [52]). When there is only one player, the amount of reward received increases linearly with contribution and the benefit from this reward increases, with diminishing returns, the higher the contribution (equation (2.2)); cost accelerates with contribution meaning that peak fitness occurs at an intermediate contribution (electronic supplementary material, figure S2).

Increasing the reward rate (v) for contributing (meaning that individuals receive more reward per unit contribution) usually increases optimal contribution because there is a greater benefit to contributing (figure 1). However, when the reward and direct benefits of contributing (determined by b and p) are high, further increasing the reward rate from an already high level can result in a *lower* optimal contribution because individuals do better to save on the costs when benefits are saturated. The benefits become saturated when b and p are high *and* an individual contributes at a high level because this is when it receives

most benefit. This is why this effect is particularly strong when the cost of the public goods contribution is low: initially counter-intuitive, this is because when the costs are low, only a small reward is required to give a very high contribution and further reward on top of already high benefits causes a steeper reduction in contribution (figure 1).

As there is only one contributor to be rewarded in this one-player scenario, there is no concept of reward inequity and so no effect of k .

(b) Multiple potential contributors to the public good

When there is more than one potential contributor to the public good, both inequity and group size (k and N) impact the shape of the reward function (equation 2.1), which has a downstream effect on the benefit function, and thus the fitness function (equations (2.2) and (2.4), electronic supplementary material, figure S2). For some parameter sets, there is a single evolutionarily stable strategy (ESS), which all individuals adopt, but for others there is a stable dimorphism in which some individuals give a high effort while others give little or no effort (they free ride). The values of all parameters interact to affect whether groups become monomorphic or dimorphic at equilibrium (see figure 2 for examples). Equitable reward distribution ($k = 0$; i.e. reward is proportional to contribution) results in a monomorphic stable strategy across all parameter values tested. The baseline level of reward (a) affects whether a monomorphic or dimorphic group emerges but only when the benefit rate from the reward is very high and there is inequity, when zero baseline reward results in a monomorphism and non-zero baseline reward results in dimorphism (figure 2). A high cost rate (c) leads to a dimorphic population when there is inequity, but a higher collective benefit (p) can increase the cost rate that is required for dimorphism (figure 2). In sum, for dimorphism to emerge such that some individuals always contribute while others free ride, there must be a way for individuals to benefit if they contribute nothing to the public good, either by gaining reward at its baseline level or avoiding the cost of contribution.

Reward inequity, while resulting in free riders when high, also increases the maximum contribution for some regions of the parameter space. In smaller groups (e.g. $N = 5$ or $N = 10$; figure 3a,b; and when the benefit rate of the reward for contributing is low; see electronic supplementary material, figure S4), the effect of inequity is non-monotonic with an intermediate level of inequity causing the highest maximum and group average contribution (figure 3a,b). In larger groups (e.g. $N = 20$; figure 3c), inequity causes a monotonic increase in the maximum and group-average contribution for this parameter range (figure 3c). In smaller groups, the effect of reward inequity is non-monotonic because at low inequity, the benefit function is approximately linear and so any additional effort an individual puts in to contributing to the public good results in a proportional increase in the payoff that they receive. However, when there is low to intermediate inequity, the benefit function becomes a slightly steeper logistic function (electronic supplementary material, figure S2); this means that large benefit increases can be gained from small increases in contribution. It also means that individuals who don't contribute a threshold amount to the public good receive little or no reward so there becomes little or no benefit from contributing just a small amount. This implicitly increases competition for the reward because now only individuals who invest a certain amount (which depends on the group-average contribution) receive any reward. As reward inequity continues to increase, the reward function comes to approximate a step function. This means that a threshold contribution must be made before an individual receives any reward as before, but now the upper asymptote of the logistic function is reached sooner, meaning that above a certain contribution there are no further rewards and fitness begins to decrease with further contributions. This non-monotonic effect of reward inequity is visible in smaller groups (or when the private benefits are low) but not in larger groups because in larger groups (or when the private benefits are high), the benefit function is stretched vertically, meaning that the upper asymptote may never be reached (electronic supplementary material, figure S2). This means that additional contributions made by individuals under these parameters result in increased benefits, pushing the maximum contribution up further even as k increases.

The effect of reward rate on the stable contribution(s) depends on the reward inequity. When inequity is lower, reward rate has a monotonic positive effect on stable contribution (figure 4a,b). However, when reward inequity is high, then increasing reward rate can result in a dimorphism such that some individuals give a high contribution and others—free riders—give a low contribution (figure 4b,c). Very high inequity can cause non-monotonicity in this effect: initial increases in reward rate cause a steep jump in the high contribution given but further increases cause this high contribution to fall slowly, having no effect on the contribution given by free riders (or the proportion of free riders; electronic supplementary material, figure S5). Once reward rate is very high (≥ 0.6), the group becomes monomorphic again and there is a step up in the contribution that all individuals stably give. This switch to monomorphism is because the benefits of contributing at a very high level outweigh the costs, and the concurrent increase in contributions is likely because more individuals are now competing for the very valuable reward, which pushes up the stable contribution.

When there is no inequity ($k = 0$), group size has no effect on the stable contribution because reward is dependent only on an individual's own contribution (figure 4d). Group size interacts with k such that for a higher group size, a higher k is required to give as steep a slope in reward (and consequently benefit and fitness functions); this means that k at a small group size will correspond to a steeper slope than the same value of k at a large group size (electronic supplementary material, figure S2). Because of this, the effect of group size is not straightforward. When inequity is low but non-zero (figure 4e), very small groups ($n < 4$) are predicted to be monomorphic and contribution increases with group size. However, at around four individuals, our model predicts that some individuals will begin to free-ride. Further increasing group size (to $N \sim 20$ for these parameters) again results in a monomorphic group and the stable contribution decreases with the addition of further individuals. When inequity is high ($k = 200$), we see a very similar (but more exaggerated) pattern, except that dimorphism remains as group size continues to increase (figure 4).

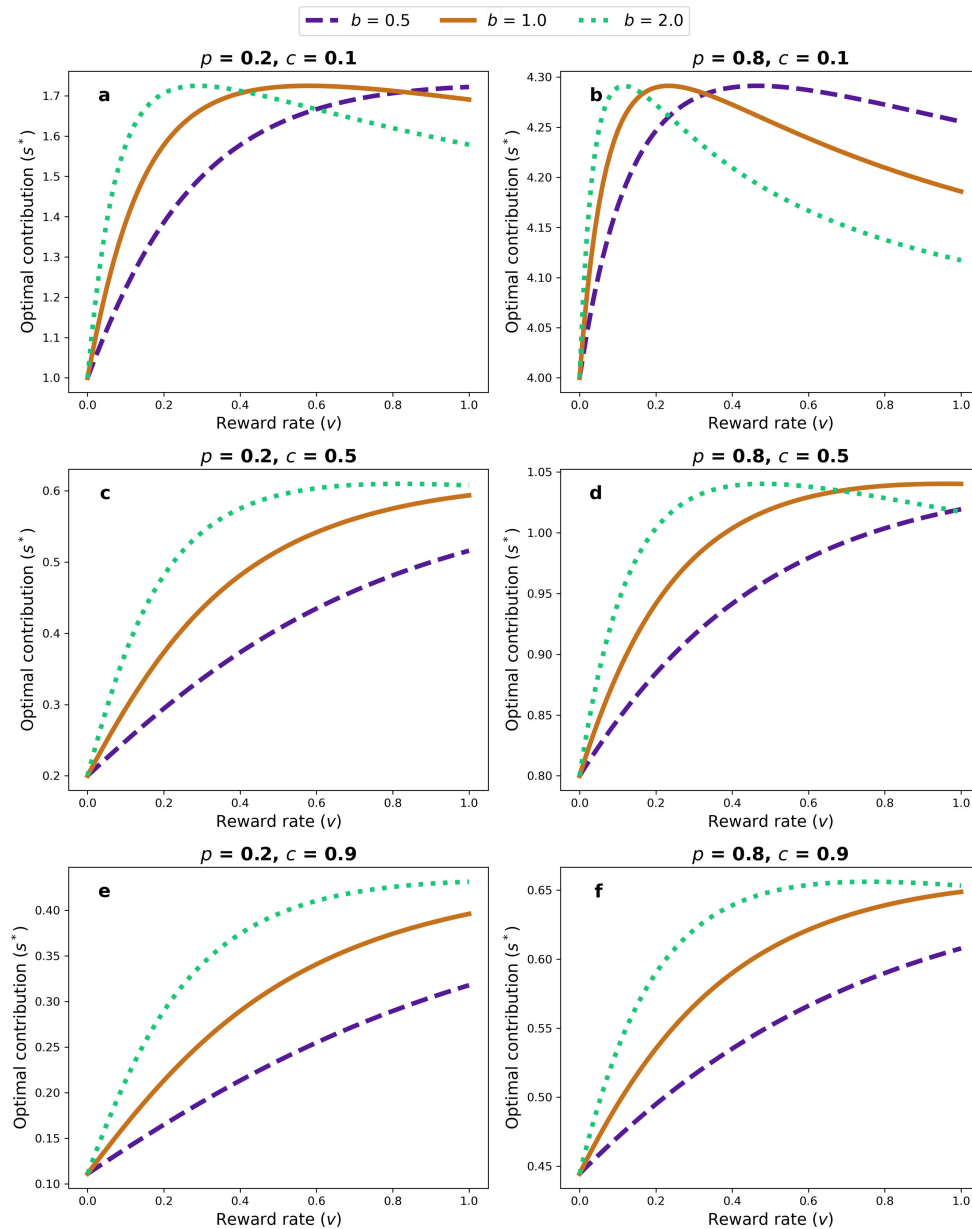


Figure 1. The effect of reward rate (v ; x axes) and benefit from public good contribution (b ; lines) on optimal contribution by a single contributor for different values of collective benefit (p ; columns) and cost (c ; rows). Increasing the reward rate generally increases the optimal contribution. However, when the other benefits (p and b) from contributing are high, reward rate can have a non-monotonic effect on contribution (right-hand column, green dotted lines). This effect is stronger and present for lower values of b (purple dashed lines) when the cost of contribution is low because this allows very high contributions to be reached at lower reward rates (panel b). Note the different y axis scales: high collective benefit and low cost also result in higher contribution. Other parameters: $a = 0$.

The apparent instabilities in figures 3 and 4 are a result of the small group size used. These regions of very rapid fluctuation are where the stable contribution for each individual is sensitive to the average contribution of others in the group because the payoff to a contributor and the payoff to a free rider are very similar. As such, small changes in parameter values can result in an individual or individuals being better off contributing the high amount or low amount (electronic supplementary material, figure S3 illustrates this). Because of the small group size, even a single individual choosing a different strategy can cause a relatively large change in the group average contribution, making these fluctuations appear relatively large. See electronic supplementary material, figure S6, which shows figure 3 but with a group size of 100 to illustrate that fluctuations are smaller for larger group sizes (note that the figures differ qualitatively because of the effect of group size).

Increasing the benefit rate of the reward (b) has a non-monotonic effect on the maximum contribution, with low-intermediate values causing the highest stable level of maximum contribution (electronic supplementary material, figure S7). Increasing the baseline level of reward (a) results in a lower maximum contribution but does not affect the free rider contribution (electronic supplementary material, figure S7). Increasing the collective benefit of contributing (p) increases the average individual contribution (electronic supplementary material, figure S8). Increasing the cost rate reduces the average individual contribution and can result in groups being dimorphic. A sufficiently high collective benefit can result in a monomorphic group but only when the cost is not very high. When the cost is very high, the free rider and 'provider' contribution increase linearly with collective benefit (electronic supplementary material, figure S8).

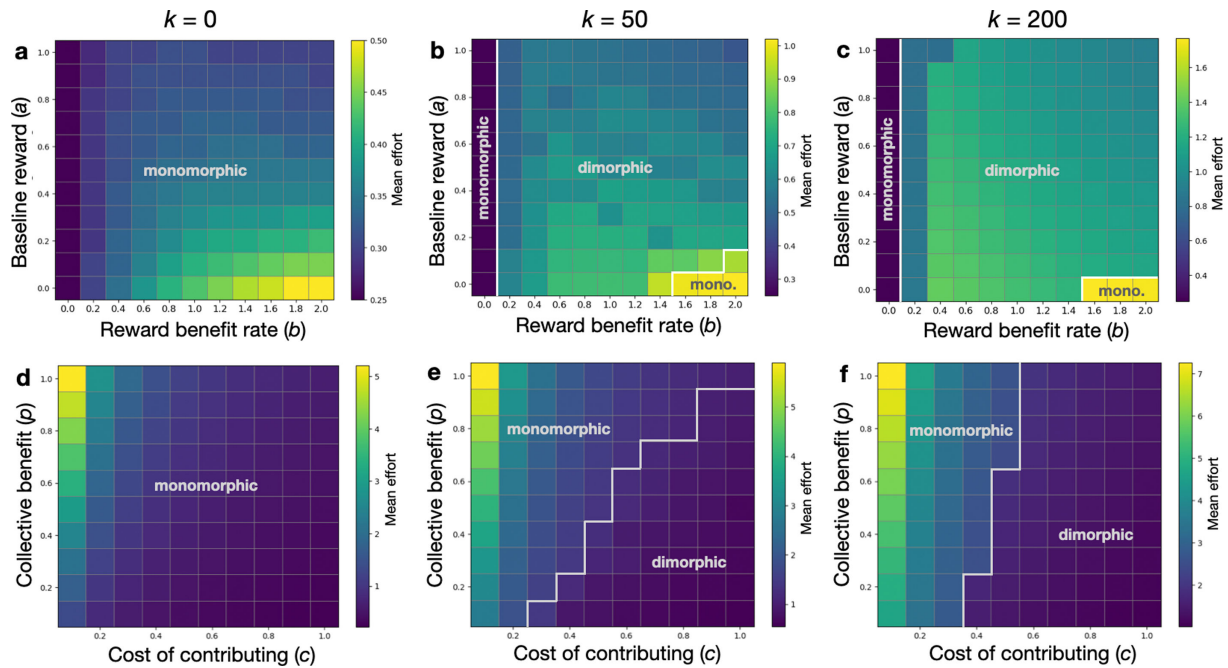


Figure 2. Regions of the parameter space that produce monomorphic or dimorphic populations (denoted by regions), and the average contribution of the group (colours). When there is no reward inequality (left column), populations are always monomorphic, with higher public goods contributions when the benefits are higher and baseline rewards are lower (panel a), and when costs are lower and the collective benefit is higher (panel d). When there is an intermediate value of inequality (middle column), dimorphism emerges at intermediate reward benefit rate (b) when there is some baseline level of reward (a , panel b), and when there is a high cost (c)/benefit rate (b) ratio (panel e). At high inequality (right column), the relationship between the benefit rate of the reward (b) and the average effort given by individuals in the group changes (panel c); while a low reward benefit still produces the lowest average efforts, an intermediate benefit rate produces the highest average contributions, with contribution declining faster at higher baseline reward. A high collective benefit cannot prevent free riding at high costs when inequality is very high (panel f). Note that we do not show when the cost of contributing is zero because this produces extremely high contributions. Other parameters: $c = 0.8$, $p = 0.4$ (top row); $a = 0$, $b = 1$ (bottom row); $v = 0.4$, $N = 10$.

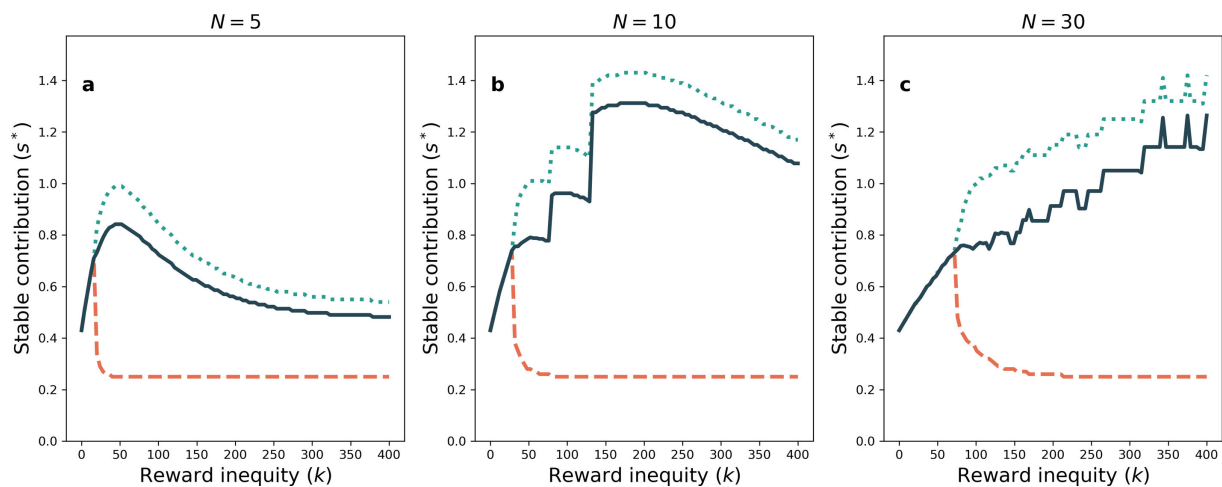


Figure 3. The effect of reward inequality (k , x axis) for different group sizes (N , panels). Lines show the mean high effort (given by contributors; green dotted), the mean low effort (given by free riders; red dashed) and total group average (navy solid). Increasing reward inequality increases the maximum stable contribution for larger group sizes and has a non-monotonic effect on maximum contribution for small groups. While inequality increases the maximum contribution, it also causes free riding. Free riding occurs at lower inequality values for lower group sizes likely because similar values of k cause a steeper benefit function at low group sizes. Discontinuities are due to model sensitivity in this region of the parameter space. Other parameters: $a = 0$, $b = 1$, $c = 0.8$, $p = 0.4$, $v = 0.4$.

4. Discussion

We used a game-theoretic model to investigate the effect of varying reward distribution and rate on contributions to a public good. We found that contributions increased when rewards were inequitably distributed among contributors, although inequality could also lead to free riding. Additionally, increasing the reward rate generally increased the contribution that individuals should make to the public good but could have a non-monotonic effect when private benefits of contribution were high or the cost of contribution was low. Our results suggest that increasing competition among individuals within a group for rewards can increase public goods contributions but also encourage free riding: in our model, greater inequality implicitly resulted in greater competition for rewards because it introduced a threshold contribution below which individuals would not receive rewards, and the location of this threshold depended on the contributions made by others, allowing individuals to ‘outbid’ each other for

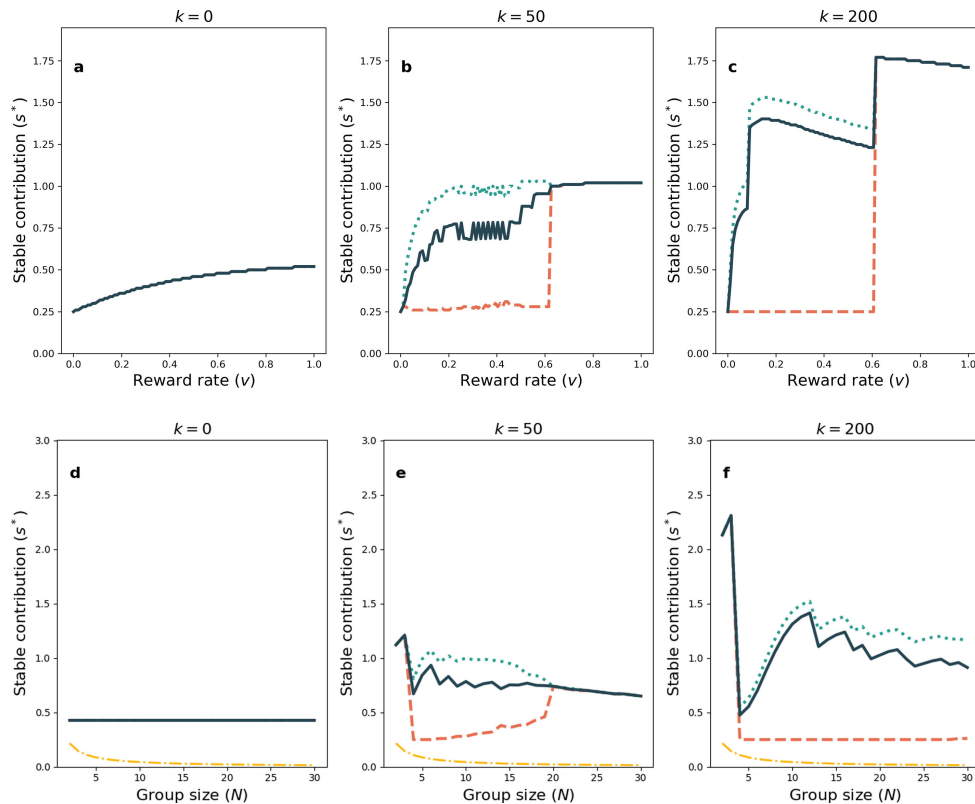


Figure 4. The effect of reward rate (v) and group size (N) on the stable contribution for zero, low and high values of reward inequity (k , panels). Lines show the group mean contribution (navy solid), the high contributor effort (green dotted), the low contributor (free rider) effort (red dashed) and the ‘null’ expectation for the effect of group size (yellow dot-dashed; d,e,f), which is an individual’s one-player optimum divided by N . For low inequity, there is a positive monotonic relationship between reward rate and contribution, and no effect of group size. At low inequity, reward rate has a positive effect on high contributor effort but free riders persist until reward rate is high enough (around 0.6) when the group becomes monomorphic. Group size has a generally negative effect on mean contribution at low inequity (except for very small groups), but has a non-monotonic effect on high contributor effort with intermediate group sizes resulting in the highest efforts. The effect of group size on free rider contribution is also monotonic, almost cancelling out the positive effect of group size on high contributor effort. Both reward rate and group size have a non-monotonic effect on stable contribution when there is high inequity. Reward rate primarily impacts the high effort, causing it to increase to a point and then fall slowly before stepping up again at a very high reward rate when there are no longer free riders. At high inequity, free riders are present at all group sizes above $N = 3$ and increasing group size causes the high effort to slowly fall. Other parameters: $a = 0$, $b = 1$, $c = 0.8$, $p = 0.4$, $v = 0.4$.

greater rewards until equilibrium was reached. The results also suggest that increasing the magnitude of the reward itself can have different effects depending on the other benefits of the public good.

While increased competition via partner choice can promote cooperation [57–60], inequity is often found to be detrimental to cooperative behaviour in both humans [27,30,31] and non-human animals (e.g. domestic dog, *Canis lupus familiaris* [61]; Norway rat, *Rattus norvegicus* [62]; capuchin, *Cebus apella* [63]; but see a recent meta-analysis that finds no evidence for inequity aversion in non-human animals [64]). In our model, increasing reward inequity could result in *greater* average contributions to the public good. This was because increasing reward inequity implicitly increased competition among individuals for the reward by both reducing the reward received by those contributing less than the group average, and increasing the reward received by those contributing more than the group average. This extends previous modelling work firstly by showing that there can be a link between inequity and competition that can actually *promote* cooperation, and secondly by showing that assumptions about initial state (or wealth, e.g. dominance status) are not required to produce polymorphism in public goods contributions. Furthermore, these results do not rely on competition *between* groups (e.g. [14]), showing instead that within-group competition can promote contributions to public goods in the same way that biological market dynamics can promote contributions to pair-wise exchanges [65–67].

Rewards were not fixed in our model, but depended on an individual’s contribution. Therefore, even when rewards were inequitably distributed, individuals could improve their reward by contributing more; this differs from some experimental tests of reward inequity (and fundamentally from wealth inequity models) in which reward is entirely independent of contribution (e.g. [27]). Because reward in our model depended (albeit unfairly) on the contributions that individuals made, at equilibrium in monomorphic groups, all individuals received the same reward because all individuals contributed the same. However, in dimorphic groups, disproportionately more reward was received by the ‘high contributors’ that emerged than the ‘low contributors’. That our model predicts that some individuals do not entirely *free ride* but contribute much less than others is also in contrast to classic models of public goods/snowdrift game scenarios, which find that some individuals are expected to not contribute at all. Further theoretical work to capture the effect of reward inequity independent of contribution could give additional insight into the likely connected roles of inequity and competition in promoting contributions to public goods.

To test predictions from our model relating to reward inequity will require data about contributions to public goods and the rewards that individuals receive. In the dwarf mongoose system, there is evidence that reward is relatively equitable and

individuals are rewarded in proportion to their sentinel contributions [36]. Given that the direct benefit of sentineling is likely to be high (in the dwarf mongooses [68]; and other species [40,69]), our model predicts that sentinel contribution should be a monomorphic trait in dwarf mongooses. This prediction could be tested through future empirical investigation of the distribution of sentinel effort: a monomorphic population would exhibit a unimodal distribution in sentinel effort, while for a dimorphic population the distribution would be bimodal. Empirical data from scenarios in which the reward for contribution to a public good is highly monopolizable would be appropriate to test our model predictions for when inequity is *high*. For example, mating coalitions where there is high reproductive skew despite investment by multiple males (e.g. manakins, *Chiroxiphia* spp. [70]) or contributions to collective hunting efforts, which result in an often inequitably (or at least, unequally) shared food reward (e.g. [71,72]).

That a high reward *rate* can reduce contribution to public goods suggests a mechanism by which rewards for contributions might be constrained even if they are effectively costless for the reward-givers (as a grooming reward might be [42]). The non-monotonic effect of reward rate was present when the benefits of the public good were very high and the costs low. One potential natural scenario that might approximate these parameters is sentinel and grooming exchange in dwarf mongooses. Sentinel effort is state-dependent [68] and likely provides direct benefits to the sentinel [40], as well as large benefits from the grooming reward. Additionally, the benefits of having a sentinel are likely high for other group members as they can forage more efficiently [1,2,38] and are less likely to be predated (as is the sentinel itself [40]). We might therefore expect that in the mongooses and other systems with high private benefits from public goods contributions (e.g. predator inspection and mobbing [73,74]; or blood donations in humans [20,75], reviewed in [21,22]), an extreme high level of reward is detrimental to contributors. Large rewards might only promote public goods provision if contributing provides few other benefits for contributors. Such scenarios might include intergroup conflict in which participants have little to gain from winning the conflict in itself. For example, in vervet monkeys, females direct grooming towards males who have participated in intergroup conflict, apparently as a reward [17] though it is often females who instigate this conflict, suggesting that they might have more to gain. To test the effect of reward rate in public goods systems, rewards (or their outcomes) could be experimentally manipulated; for example, experimentally provisioning food or treating parasites (though this could disrupt or fail to account for the social benefits of such behaviours).

For most of the parameter space, our model output agrees with many previous public goods models that larger group sizes result in individuals making lower public goods contributions. However, for very low group sizes, additional group members caused an increase in contributions. This is likely because of the interaction between group size and the reward distribution parameter (k), which affects how much reward an individual receives for the effort that it gives relative to the group average, thus competition for rewards. While most theoretical work finds a negative effect of group size on cooperation [76,77], empirical evidence is much less clear-cut. Depending on the payoff structure of an experimental game, humans in larger groups can contribute more or less to a public good [78,79]. In non-human animals, negative, nonmonotonic and positive relationships have been reported for the effect of group size on contributions to public goods [40,80–82], while some studies find no effect [37,83]. In dwarf mongooses, group size does not appear to have an effect on the duration of individual sentinel bouts [37]. In our model, this occurred when there was low or no inequity, predicting that dwarf mongooses distribute their grooming rewards equitably. This prediction is compatible with data showing that mongooses receive grooming proportional to their sentinel effort [36]. To understand fully the effect of group size on cooperation and public goods production, we need to identify how it interacts with other factors such as reward, punishment and competition.

Our model is intentionally general, thus likely represents a range of systems of public goods contribution for which individuals receive differential rewards. Future modelling of specific systems could allow for empirically informed cost and benefit functions to be explored. For example, some systems might exhibit a threshold level of reward required before individuals will contribute to the public good; individual heterogeneity in this threshold could produce interesting dynamics. Our model maintains reward as a free parameter, allowing us to investigate the effects of reward structure directly. As such, we make no limiting assumptions about how or why a particular reward structure comes about. This means that our model can capture reward inequity driven by any factor such as informational asymmetries, spatial effects on how reward is delivered, social dominance, or stochasticity [84,85]. By making no assumptions about the mechanism underpinning reward inequity, we are able to investigate how public goods production might change directly in response to changes in inequity without making assumptions about external factors that might impact the causal relationship between reward inequity and public goods contributions (thus making it impossible to parse out a direct relationship). We have therefore provided a foundation for understanding how rewarding behaviour and public goods contributions may co-evolve and co-adapt under social and environmental selective pressures.

Competition for rewards in our model can be considered analogous to competition for better partners in two-player biological market models [59,86–88]. In such models, individuals compete for better *partners* by increasing their own cooperativeness [59,89]; in our model, individuals compete for better *rewards* by increasing their own cooperativeness. Our model builds on previous work by removing the assumption that exchanges are between pairs of individuals, thus extending the biological market paradigm to the exchange of *public* goods for private goods. The presence of rewards for public goods in nature suggests that a market involving public goods can be stable under the forces of supply and demand, and the stability of trade in public goods has been shown theoretically [90]. Additionally, there is empirical evidence that supply and demand drive rewards for public goods providers [91]. It could be useful in the future to think about exchanges of public goods contribution and rewards as a type of biological market. While such models would make some different assumptions than classic market models in economics, extending market models to incorporate public goods could provide insight into how public goods producers avoid catastrophic exploitation in the absence of top-down regulation. For now, our model shows that social factors— specifically,

inequity and competition—and their interactions are likely to be important for determining the production of public goods and the presence of free riders in social groups.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Supplementary material is available online [92].

Declaration of AI use. Code for some figures was developed with assistance from large language models.

Authors' contributions. R.F.B.P.: conceptualization, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; A.N.R.: conceptualization, funding acquisition, investigation, methodology, writing—original draft, writing—review and editing; A.D.H.: conceptualization, funding acquisition, investigation, methodology, writing—original draft, writing—review and editing.

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Conflict of interest declaration. We declare we have no competing interests.

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