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Correspondence and requests for materials should be addressed to G.J.B. (gbowen@biology.utah.edu).

Indirect reciprocity can stabilize cooperation without the second-order free rider problem

Karthik Panchanathan & Robert Boyd

Center for Behavior, Evolution, and Culture and Department of Anthropology, University of California, Los Angeles, California 90095, USA

Models of large-scale human cooperation take two forms. 'Indirect reciprocity'[1] occurs when individuals help others in order to uphold a reputation and so be included in future cooperation. In 'collective action'[2], individuals engage in costly behaviour that benefits the group as a whole. Although the evolution of indirect reciprocity is theoretically plausible[3–6], there is no consensus about how collective action evolves. Evidence suggests that punishing free riders can maintain cooperation[7–9], but why individuals should engage in costly punishment is unclear. Solutions to this 'second-order free rider problem' include meta-punishment[10], mutation[11], conformism[12], signalling[13–15] and group-selection[16–18]. The threat of exclusion from indirect reciprocity can sustain collective action in the laboratory[19]. Here, we show that such exclusion is evolutionarily stable, providing an incentive to engage in costly cooperation, while avoiding the second-order free rider problem because punishers can withhold help from free riders without damaging their reputations. However, we also show that such a strategy cannot invade a population in which indirect reciprocity is not linked to collective action, thus leaving unexplained how collective action arises.

To show that indirect reciprocity can stabilize collective action without the second-order free rider problem, we consider a large population subdivided into randomly formed social groups of size n. Social life consists of two stages. First, individuals decide whether or not to contribute to a one-shot collective action game at a net personal cost C in order to create a benefit B shared equally amongst the $n - 1$ other group members, where $B > C$. Second, individuals engage in a multi-period 'mutual aid game'[4], a form of indirect reciprocity that is well suited to a population structured into groups. The dynamics of the mutual aid game are very similar to other models of indirect reciprocity[3,6] so our results should generalize to other social exchange systems. In each period of the mutual aid game, one randomly selected individual from each group is 'needy'. Each of his $n - 1$ neighbours can help him an amount b at a personal cost c, where $b > c > 0$. Each individual's behavioural history is known to all group members. This assumption is essential because it is known that indirect reciprocity cannot evolve when information quality is poor[6]. The mutual aid game repeats with probability w and terminates with probability $1 - w$, thus lasting for $1/(1 - w)$ periods on average. Afterwards, individuals reproduce on the basis of payoffs accumulated over both stages, relative to the whole population, and then die.

Individuals are characterized by one of three heritable strategies: 'Defector', 'Cooperator', and 'Shunner'. Defectors do not contribute to the collective action, nor do they help during the mutual aid game. Cooperators contribute to the collective action and try to help all needy recipients during mutual aid. With probability e, however, Cooperators mistakenly fail to help recipients of good reputation in the mutual aid game owing to an implementation error[6] (See Box 1 for details). Shunners contribute to the collective action and then try to help those needy individuals who have good reputations during the mutual aid game, but mistakenly fail owing to errors with probability e just like Cooperators. Shunners never help needy recipients who are in bad standing.

All individuals begin their lives in good standing. Failure to contribute to the collective action results in a lifetime of bad standing. If an individual has contributed during the collective action stage, she temporarily loses her good standing if she fails to help a recipient of good reputation during the mutual aid game, either through intention or error. She can, however, restore her good standing by helping a needy recipient in some future period. Our results do not depend on the assumption that the reputations

Box 1
Errors in models of reciprocity and punishment

As in previous models of indirect reciprocity[3,5,6], errors play a crucial role in our analysis. These errors should not be thought of as part of an inherited strategy. Instead, they represent exogenous factors like sickness or accidents that prevent actors from helping despite an intention to do so. In our model, all group members, including the actor, know when an error has occurred. These 'implementation' errors are contrasted with 'perception' errors, in which individuals differ in their beliefs about who cooperated and who defected[6]. We have not analysed the effect of perception errors because these errors add sufficient mathematical complexity that analysis becomes intractable. As a result, it is unclear how perception errors affect the evolution of indirect reciprocity[3,6]. In addition, we do not consider errors in which individuals mistakenly help a recipient of bad reputation during the mutual aid game, nor errors during the collective action game, because both such errors complicate the model without qualitatively altering the results.

Previous models of collective action and costly punishment[10–12,18] have shown that implementation errors of the type we consider here undermine the evolution of collective action. To see why, suppose that there are no defecting strategies and that behaviour is error-free. In this case, selection cannot distinguish between strategies that cooperate and punish defectors and strategies that cooperate but do not punish. There is never a need to punish, so there is no second-order free rider problem. If actors occasionally defect by mistake, however, strategies that punish must do so at a personal cost. Selection will now favour strategies that cooperate but do not punish (second-order free riders). As a result, strategies that punish free riders decline and eventually defectors can invade and take over.

of collective action free riders are permanently damaged. Such an assumption does, however, simplify the analysis. The key assumption is that free-riding during the collective action stage has a more severe effect on reputation than failing to donate during a bout of reciprocity—if this were not the case, there would be little motivation to make costly contributions to the collective action. In modelling the Shunner strategy, we assume that reputation is linked across the collective action and mutual aid domains. In the next section, we examine under just what conditions selection will favour this linkage.

The model has two stable evolutionary equilibria[20] (Fig. 1; see Supplementary Information). Defector is always an evolutionarily stable strategy. When Shunners are common, the population resists invasion by rare Defectors if:

$$\left(\frac{n-1}{n}\right)\left(\frac{1-e}{1-w}\right)(b-c)(1-we) > C \qquad (1)$$

When condition (1) is satisfied, Defectors cannot invade because the long-term benefit from mutual aid is larger than the net private cost of contributing to the collective action. Shunners can resist invasion by rare Cooperators if $wec > 0$, a condition that is satisfied as long as mutual aid persists, is costly, and is prone to occasional error. Selection favours Shunners over Cooperators because the two strategies behave differently towards needy individuals who failed to help a recipient of good reputation owing to error in the previous period. Cooperators always try to help these individuals at a cost c, whereas Shunners withhold aid, which is socially sanctioned because the recipient was in bad standing. In previous models of collective action with costly punishment[10–12,18], errors undermine the evolution of punishment (see Box 1 for details).

In our model, errors actually stabilize punishment because Shunners punish defection by withholding costly aid, thereby increasing their own fitness. Strategies that do not punish, such as Cooperator, are at a selective disadvantage because they dole out help indiscriminately. Note that condition (1) is not affected by the magnitude of the group benefit created by the collective action. This means that any behaviour can be stabilized by linking it to a system of indirect reciprocity, as long as the cost of that behaviour is less than the benefits derived from indirect reciprocity. Thus this process can stabilize even maladaptive norms in which $B < C$.

Although punishment by exclusion is evolutionarily stable in this model, so is defection (as well as another strategy, which we will consider shortly, that supports mutual aid but not collective action). Why should we believe that Shunner is the likely evolutionary outcome? In their classic work on pair-wise reciprocity, Axelrod and Hamilton[21] suggest that a small amount of non-random assortment, such as interaction between relatives, destabilizes uncooperative, but not cooperative, equilibria. When pairs are formed non-randomly, a reciprocating strategy like 'tit-for-tat' more often channels cooperation to like types and this permits rare reciprocators to invade populations in which defecting strategies are common. To underscore the synergy between inclusive fitness and reciprocity, Axelrod and Hamilton[21] state that "the gear wheels of social evolution have a ratchet". For the same reason, as we demonstrate in the Supplementary Information, low levels of assortment allow reciprocating strategies, like Shunner, to invade less cooperative strategies, like Defector, but not the reverse. As long as the information available about the behaviour of others is accurate and widespread[6], there is a powerful synergy between small amounts of assortment and long periods of interaction, making increasing amounts of reciprocity the probable evolutionary outcome (Fig. 2a).

The same synergy does not, however, exist between reciprocity and collective action norms. Strategies that link the two behaviours through reputation cannot invade a population practising only indirect reciprocity. While we have demonstrated that indirect reciprocity can stabilize collective action, it is unlikely that the two behaviours evolve simultaneously as a complex. More probably, a population engaging only in indirect reciprocity (that is, mutual aid, no collective action) evolves first.

To demonstrate that mutant Shunners, who link collective action and indirect reciprocity, cannot invade a population engaged only in indirect reciprocity, despite assortment, we consider a fourth strategy, Reciprocator, which does not contribute to the collective action and also does not attend to the contributions of fellow community members. Thus, in the eyes of Reciprocators, all group members enter the stage two mutual aid game in good standing, regardless of their behaviour in the previous collective action game. Reciprocators help only good-standing recipients, assuming no error, during the mutual aid game. In their eyes, fellow group members remain in good standing as long as they help others in good standing (by their definition) during the mutual aid game. To allow for non-random interaction, we assume that the conditional probability that another individual in a group has the same strategy

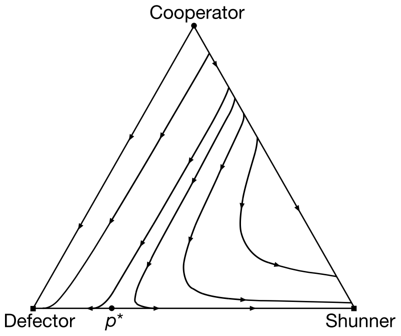

Figure 1 Evolutionary dynamics of the Shunner, Defector and Cooperator strategies, plotted in trilinear coordinates. The arrowheads depict evolutionary trajectories. Populations composed of all Shunners and all Defectors are both evolutionarily stable. When the initial frequency of Shunners is too low, the population evolves towards the asocial Defector equilibrium. When it is higher, the population reaches a stable equilibrium in which collective action is enforced by exclusion from the benefits of indirect reciprocity. The model parameters for this figure are: $B = 10$, $C = 5$, $b = 2$, $c = 1$, $n = 100$, $w = 0.95$, $W_0 = 100$ and $e = 0.05$.

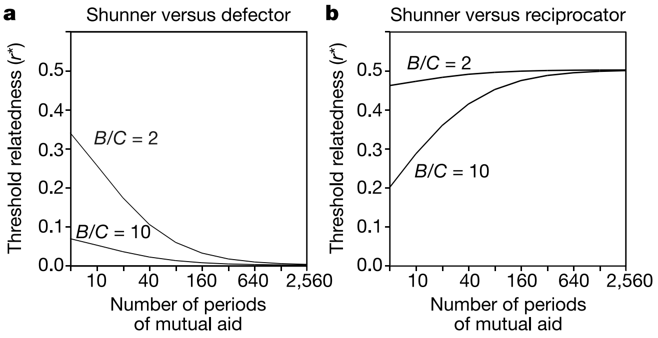

Figure 2 The threshold degree of assortment (r^*, derived in the Supplementary Information) necessary for rare Shunners to invade as a function of the number of mutual aid periods, $1/(1-w)$, for two different collective action benefit cost ratios, B/C. **a**, When Shunners compete against Defectors, the assortment threshold decreases as the number of mutual aid periods increases. For long-lasting groups even small amounts of assortment allow the cooperative strategy to invade. **b**, When Shunners compete against Reciprocators the assortment threshold increases as the number of mutual aid periods increases. Rare Shunners do best in one-shot interactions. However, as shown in the text (condition (1)), Shunners are unlikely to be evolutionarily stable against Defectors in one-shot interactions. For both **a** and **b**, the parameter values are $b = 2$, $c = 1$, $B = 10$, $n = 30$ and $e = 0.01$. The graph plotted in **b** is based on a compete condition derived in the Supplementary Information that does not depend on the assumption that r is small.

as a focal individual is given by $r + (1 - r)p$ where p is the frequency of that strategy in the population and $0 \leq r \leq 1$. Thus the parameter r is closely analogous to the familiar coefficient of relatedness[22]. When $r = 0$, groups are formed at random. Larger values of r mean that individuals tend to interact with others of the same strategy. Setting the frequency of Cooperator and Defector to zero, we can now ask whether rare Shunners can invade a population in which Reciprocators are common.

Small amounts of non-random assortment do not allow Shunner to invade a population in which Reciprocators are common, even if interactions go on indefinitely (Fig. 2b). When groups are formed at random ($r = 0$), both Shunner and Reciprocator are evolutionarily stable strategies. The basin of attraction for Shunner becomes smaller as the number of periods of mutual aid increases (Fig. 3b). As r is increased, a threshold value, r^*, is eventually reached; above this value Shunners always eliminate Reciprocators. However, increasing the number of mutual aid periods increases the value of r^* (Fig. 2b). This means that Shunners increase when initially rare only if collective action increases inclusive fitness in one-shot interactions[22] (that is, $w \approx 0$ and $rB > C$)—assortment and reciprocity now operate antagonistically. Axelrod and Hamilton's ratchet is nowhere in evidence.

To see why, consider condition (2) which must be met for Shunners to increase when rare:

$$r\left[B+\underbrace{\left(\frac{1}{1-w}\right)(2bw-c)}_{\text{Mutual aid from Shunners}}\right] > C+\underbrace{\left(\frac{1}{1-w}\right)(wb-c)}_{\text{Mutual aid from Reciprocators}} \qquad (2)$$

(In deriving this expression, we assume that $e = 0$, n is large, and r is sufficiently small that terms of order r^2 can be ignored. These simplifications have no qualitative effect.) Notice that there are terms that represent the benefits of mutual aid on both sides of the inequality. The term on the benefit (left) side gives the long-term benefits of mutual aid from other Shunners, whereas the term on the cost (right) side gives the forgone mutual aid benefits from Reciprocators. In the first stage of social interaction, Shunners contribute to the collective action whereas Reciprocators do not. On entering stage two, Reciprocators consider all others to be in good standing, whereas Shunners consider only other Shunners to be worthy. Shunners permanently impugn Reciprocators for their failure to contribute during stage one. Shunners therefore do not aid Reciprocators in the mutual aid game and in turn fall into bad standing in the eyes of Reciprocators. Thus, when a Shunner needs help in stage two, few Reciprocators oblige. As a result, Shunners lose out on most of the benefits of mutual aid. Differing opinions of good citizenship and impropriety have driven a moral wedge into the community. In the Supplementary Information, we also consider a situation, different from the one presented, in which a few individuals attempt to change an existing social norm. That is, we assume that the population is playing the Shunner strategy and a few mutants attempt to change from the current collective action to another one (for example, forest clearing to forest preservation). The results are similar to those just presented; assortment and reciprocity operate antagonistically.

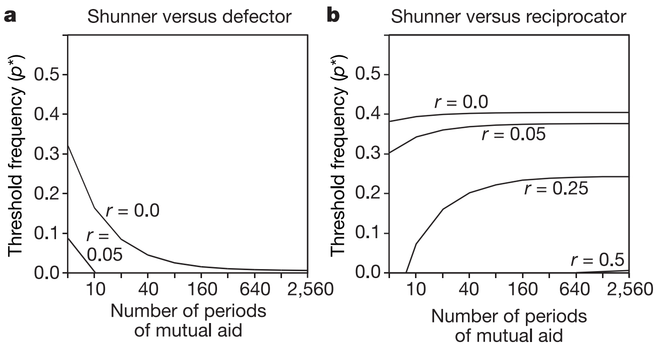

Figure 3 The threshold frequency at which Shunners increase (p^*) as a function of the number of mutual aid periods, $1/(1 - w)$, for different levels of assortment, r. If the initial frequency of Shunner is greater than p^*, Shunner increases in frequency, eventually eliminating the competing strategy. If the initial frequency of Shunner is less than p^*, Shunner is eliminated. Shunner cannot coexist with either Defector or Reciprocator in a stable polymorphic equilibrium state. **a**, When Shunner competes against Defector, the basin of attraction for Shunner becomes larger (that is, p^* decreases) as the number of periods of mutual aid increases. Increasing assortment amplifies this effect such that Shunner may become the only evolutionarily stable strategy (that is, $p^* \leq 0$). **b**, In contrast, when Shunner competes against Reciprocator, the basin of attraction for Shunner decreases as the number of mutual aid periods increases, for all levels of assortment. Increasing assortment increases the basin of attraction for Shunner. The Reciprocator equilibrium can be destabilized (that is, $p^* \leq 0$) when assortment is high and there are few bouts of mutual aid (for example, $r = 0.25$ and $w < 0.9$). Under such conditions, however, Shunner is not evolutionarily stable against Defector (see condition (1)). When mutual aid is long-lasting, the Reciprocator equilibrium can still be destabilized only if assortment is very high (for example, if $r = 0.5$). Further analysis indicates that when condition (1) is satisfied and the collective action is beneficial for the group ($B > C$), the Shunner strategy has a larger basin of attraction than Reciprocator ($p^* < 0.5$) which means that within-group equilibrium selection processes[23–27] will favour the Shunner strategy. The parameter values for both **a** and **b** are $b = 2$, $c = 1$, $C = 1$, $B = 10$, $n = 30$ and $e = 0.01$.

That indirect reciprocity can stabilize collective action is nonetheless significant. In other models[10,12,16,18], collective action is stabilized by direct punishment in which individuals pay a private cost in order to inflict a still greater cost on free riders. Such punishment is undermined by the presence of second-order free riders which ultimately destabilizes cooperation. When collective action free riders are indirectly punished through exclusion from ongoing social exchange (for example, indirect reciprocity) there is no second-order free rider problem. Instead of bearing a private cost, individuals benefit by withholding aid. The group pays the cost when individuals engage in such indirect punishment because withholding aid from one community member lowers mean fitness.

Where then does this leave us with respect to the evolution of collective action through indirect reciprocity? There are a number of equilibrium selection processes that could explain the transition from a population engaging in pure indirect reciprocity (such as Reciprocator) to one linking indirect reciprocity to a collective action (such as Shunner). Within-group processes based on random fluctuations[23–26] or individual calculation[27] typically pick out the equilibrium with the largest basin of attraction. Between-group processes that result from inter-group competition[12,28,29] or the diffusion of ideas from more successful groups to less successful ones[30] promote the systematic spread of strategies that lead to higher average group payoff. All of these processes favour the Shunner strategy over Reciprocator. ☐

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Correspondence and requests for materials should be addressed to K.P. (buddha@ucla.edu).

Physical performance and darwinian fitness in lizards

Jean-François Le Galliard[1]*, **Jean Clobert**[1] & **Régis Ferrière**[1,2]

[1] *Laboratoire Fonctionnement et Evolution des Systèmes Ecologiques, CNRS UMR 7625, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris cedex 05, France*
[2] *Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA*

* Present address: Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, P.O. Box 1050, Blindern, 0316 Oslo, Norway

Strong evidence for a genetic basis of variation in physical performance has accumulated[1,2]. Considering one of the basic tenets of evolutionary physiology—that physical performance and darwinian fitness are tightly linked[3]—one may expect phenotypes with exceptional physiological capacities to be promoted by natural selection. Why then does physical performance remain considerably variable in human and other animal populations[1,2,4]? Our analysis of locomotor performance in the common lizard (*Lacerta vivipara*) demonstrates that initial endurance (running time to exhaustion measured at birth) is indeed highly heritable, but natural selection in favour of this trait can be unexpectedly weak. A manipulation of dietary conditions unravels a proximate mechanism explaining this pattern. Fully fed individuals experience a marked reversal of performance within only one month after birth: juveniles with low endurance catch up, whereas individuals with high endurance lose their advantage. In contrast, dietary restriction allows highly endurant neonates to retain their locomotor superiority as they age. Thus, the expression of a genetic predisposition to high physical performance strongly depends on the environment experienced early in life.

Sporting events would be exceedingly boring were there no variation in human performance; fortunately, this is not the case. For example, the distribution of finish times at international marathons has a large variance and a long tail[1], due to a variety of factors affecting the performance of individual runners[5]. Although genetic variation in locomotor performance has been documented in human and other animal populations[1,2], questions remain as to how genetic and non-genetic factors would interact with each other and what effect selection has on the resulting individual variation[1,6]. We addressed these two questions using ground-dwelling lizards, a popular model system for studies of locomotor performance[2,4,7]. Our focus here is on the endurance capacity as assayed in the laboratory (see Methods). In lizards, endurance shows considerable interindividual variation that reflects differences in tight muscle mass, heart mass and aerobic metabolism[8].

Our study species is the common lizard (*Lacerta vivipara* Jacquin 1787) for which locomotor performance and life-history traits have been routinely studied[9]. We took advantage of the populations established at the Ecological Research Station of Foljuif (Nemours, France) in the semi-natural conditions of outdoor enclosures[10] to measure the heritability of initial endurance and the age-specific strength of natural selection on this trait. In these enclosures, endurance capacity could reflect social rank[2] and abilities to compete for and exploit basking sites and prey[4], and thus influence darwinian fitness[9]. Insights into proximate mechanisms underlying the observed pattern of selection have been gained experimentally by investigating how dietary conditions early in life influence the ontogeny of endurance and the relationship between survivorship and endurance.

In 2001, initial endurance was recorded in a cohort of 447 offspring (Fig. 1). Measurements spanned a 45-fold range, from 36 s to 1,677 s (mean = 222 s ± 153.7 s.d.). The distribution is typically skewed, with a few 'champions' displaying exceptional endurance. Initial endurance increased with offspring body size and body condition, decreased with maternal body size, and increased with behavioural motivation (Table 1). Accounting for all these factors, initial endurance was highly heritable ($h^2 = 0.40$), concurring with previous studies in this species and many other reptiles[2,11]. Even in the controlled conditions of our outdoor enclosures, high heritability might have been caused by maternal effects, but no such

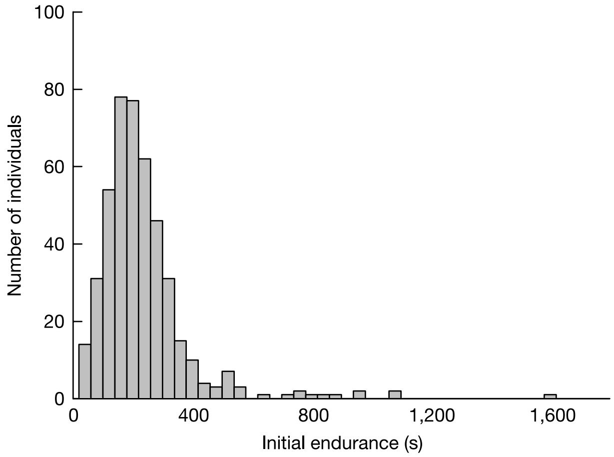

Figure 1 Individual variation in endurance capacity among 447 common lizard offspring.