

Dominance Hierarchies Induce a Population's Full Cooperation

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Abstract Evolution of cooperation is still a puzzle in evolutionary and socio biology. Based on the asymmetric interactions in a dominance hierarchy system, a simple theoretical framework is developed to reveal the effect of “induced cooperation” (i.e., the cooperative behavior of subordinate individuals to dominant individuals) on the evolution of cooperation. Extending the classic Prisoner's Dilemma (PD) game, we define the concept of the defection cost of subordinate individuals to measure the effect of induced cooperation, i.e., a subordinate defector will incur a cost when it plays against a dominant defector. The analysis of the repeated PD game with linear dominance hierarchy and with cyclic dominance hierarchy shows clearly that induced cooperation of subordinate individuals may lead to a population's full cooperation, and that the coexistence of cooperation and defection in a population with hierarchy dominance is possible. Our results are the first step to develop a new theoretical approach for understanding the emergence of cooperation; namely, that induced cooperation is one of the most important forces driving the evolution of cooperation as pointed out by May (in May R, McLean A (eds) *Theoretical ecology* 3rd edn., (2007)).

Keywords Evolution of cooperation · Asymmetric interaction · Dominance hierarchy · Induced cooperation · Defection cost

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1 Introduction

Altruistic cooperation means that a donor pays a cost, c , for a recipient to get a benefit, b . Recently, Nowak and Sigmund [26] (see also ref. [22]) reviewed the five rules for the evolution of cooperation using the classic Prisoner's Dilemma (PD) game with $b > c$, which are kin selection [8, 10–12], direct reciprocity [3, 4, 21, 33], indirect reciprocity [24, 25], graph selection [27], and group selection [32], respectively. In their review, it was pointed out how each of these five rules can promote cooperation if specific conditions are fulfilled. These five rules are all based on symmetric interactions between individuals in a single population (i.e., payoffs depend only on the strategies used by these interacting individuals and not on their designation in a particular subpopulation). Furthermore, a common mechanism behind each rule is the collective advantage of cooperators through non random interactions (i.e., if the chance that an interaction between two cooperators occurs is higher than it would be for random interactions, then cooperation may be favored by natural selection).

Asymmetric interactions between individuals are also common in nature and human society. For example, interactions may occur between a male and a female, between old and young, between small and large individuals, or between the owner of a resource and a non-owner [30, 40]. In a population with a dominance relation (also called dominance hierarchy or social hierarchy [40]), the asymmetries between individuals may depend on differences in resource holding power (RHP) such as size, strength, or fighting ability [13, 19, 30]. In general, if the difference in RHP between opponents is consistent and detectable, then the better competitor should consistently win each contest and the other competitor should defer to its opponent and thereby establish the dominance relationship [16, 40]. The simplest form of a dominance order is called the linear hierarchy, in which individual A is dominant to the rest of group, B dominates all but A, C dominates all but A and B, and so on [16, 39, 40]. However, the structure of a dominance hierarchy can be more complicated, for example, the triangular structure, in which individual A dominates B, B dominates C, and C dominates A [16, 40].

It is recognized that one of the most important mechanisms for establishing dominance hierarchies in nature and human society is the fact that dominated individuals (also called subordinate individuals) behave cooperatively in asymmetric interactions. For example, on the fundamental theoretical question concerning the evolution and maintenance of cooperative behavior within human and other animal communities, May [17] pointed out: “it may even be that, over the millennia since agriculture was invented, the answer shaped by evolutionary processes to the problem of building complex but stable human societies was to favor acquiescence in authoritarian hierarchies.”

The evolutionary significance of subordinates exhibiting cooperative behavior in establishing dominance hierarchy has been studied by many authors (see refs. [16, 40]). For convenience, we call this behavior “induced cooperation” (of subordinate individuals). We are interested in the effects of induced cooperation on the evolution of cooperation from the perspective of evolutionary games [14] where it is populations that are in a dominance hierarchy and pairs of individuals from these subpopulations are drawn at random to interact. However, the effects of induced cooperation on interactions involving only dominant individuals or only subordinate individuals (i.e., on interactions between individuals in the same subpopulation) are not clear. For the evolution of cooperation, a challenging question is then whether the induced cooperation of subordinate individuals will promote cooperation in symmetric interactions between individuals in the same subpopulation (and whether this will lead to full cooperation in the total population).

In this paper, a theoretical framework is developed as a base model to study the effect of induced cooperation on the evolution of cooperation in a population with dominance hierarchy. In our model, pairs of individuals play a PD game (either one-shot or repeated) where subordinate individuals incur a “defection cost” if they defect against a dominant defector.

Our analysis is based on several simplifying assumptions including that the relative sizes of the subpopulations are fixed [14,29,30] and that, in the repeated PD game, individuals either always defect in a given interaction or else play the tit-for-tat strategy (but see Sect. 2.1 where the other common strategy in the repeated game literature [3,21] to always cooperate is also considered). We also assume that an individual will use the same strategy in both symmetric and asymmetric interactions (e.g., if an individual Cooperates (Defects) in one-shot symmetric interactions, then he will also use Cooperate (Defect) in asymmetric interactions). In game-theoretic terms, this last condition is equivalent to assuming that players must choose their strategy without knowing the type of their opponent (i.e., without knowing the subpopulation of their opponent), a common condition in extensive form games of complete but imperfect information [2,6]. The condition also models situations where the player cannot change his behavior based on the type of opponent (for example, behaviors may be genetically programmed). Although these assumptions are clearly not true of every real system with a dominance hierarchy based on a PD game, our model is a reasonable place to start the analysis of how such structures affect the evolution of cooperation.

The emergence of cooperative behavior through dominance relations has also been studied in other sociobiology contexts. For instance, (reproductive) skew theory examines the allocation of reproductive shares among members of a group [28] whereby either the dominant breeder offers a share of communal reproduction to the subordinate as an incentive for the recipient to stay as a cooperative member of the group or a compromise is reached with reproductive shares determined by the competitive abilities of individuals [20,34]. Models of skew theory also consider conditions for the stability of a particular group size exhibiting cooperative behavior, whereas we are more interested in conditions on the defection cost that imply the emergence and maintenance of full cooperation when (relative) group sizes are fixed.

Asymmetric hierarchical structures based on order of moves have been analyzed in other game contexts as well. For instance, in Stackelberg games, the hierarchy is formed by designating one player as the first mover (or leader), and any subsequent mover knows this player’s choice [36,38]. The resulting Stackelberg equilibrium is different than the outcomes found in our model where players choose their strategies simultaneously in any PD game [18].

2 Models and Results

2.1 Two-Subpopulation Model with Linear Dominance

Consider first a system consisting of two subpopulations, called A_1 - and A_2 -populations (or groups), respectively. We assume that A_1 -individuals are better competitors than A_2 -individuals in interactions between an A_1 - and an A_2 -individual. From this assumption, interactions between A_1 -individuals and between A_2 -individuals should be considered to be symmetric, while interactions between A_1 - and A_2 -individuals are asymmetric. The proportion of A_1 -individuals (or A_2 -individuals) in the total population is denoted by z (or $1 - z$), where z is a fixed constant.

Suppose that all individuals in both A_1 - and A_2 -populations display only two phenotypes, one is cooperation (C) and the other defection (D). According to the PD game based on costs and benefits [26], let b_{ij} be the benefit an i -individual receives if its opponent in the j -population cooperates and c_{ij} be the cooperation cost of an i -cooperator for $i, j = 1, 2$. Thus, for the symmetric interactions between i -individuals ($i = 1, 2$), the payoff matrix is

$$\Pi_{ii} = \begin{matrix} & \begin{matrix} C & D \end{matrix} \\ \begin{matrix} C \\ D \end{matrix} & \begin{pmatrix} b_{ii} - c_{ii} & -c_{ii} \\ b_{ii} & 0 \end{pmatrix} \end{matrix},$$

where the entry in row k and column ℓ is the payoff to the row player using strategy k (i.e., C for $k = 1$ and D for $k = 2$) when interacting with the column player using strategy ℓ [21]. Note that the C and D strategies are indicated in this PD game but not in subsequent ones. Since $b_{ij} > c_{ij}$ in the PD game, if an individual only interacts within its own population, rational players must defect even though their payoff is higher when everyone cooperates.

For the asymmetric interactions between A_1 - and A_2 -individuals, we assume that when a A_2 -defector plays against an A_1 -defector, the A_2 -defector will incur a cost β imposed by the dominant A_1 -individual. Here, we call β the defection cost to a A_2 -defector when interacting with an A_1 -defector. A further assumption is that when an A_2 -defector plays against an A_1 -cooperator, the A_2 -defector will not pay any defection cost. The payoff matrix of an A_2 -individual when it plays against an A_1 -individual is then given by

$$\Pi_{21} = \begin{pmatrix} b_{21} - c_{21} & -c_{21} \\ b_{21} & -\beta \end{pmatrix}$$

since $-\beta$ is the payoff of an A_2 -defector when it plays against an A_1 -defector. To model induced cooperation, we assume that, when a A_2 -individual meets an A_1 -defector, the A_2 -individual's defection cost, β , is larger than its cooperation cost, c_{21} (i.e., $\beta > c_{21}$). Thus, the subordinate individual is better off to cooperate (respectively, defect) against a dominant defector (respectively, cooperator).

On the other hand, similar to the payoff matrix Π_{ii} for symmetric interactions, the payoff of an A_1 -individual when it plays against a A_2 -individual is given by the payoff matrix

$$\Pi_{12} = \begin{pmatrix} b_{12} - c_{12} & -c_{12} \\ b_{12} & 0 \end{pmatrix}.$$

To simplify the analysis, we take $b_{ij} = b$ and $c_{ij} = c$ for $i, j = 1, 2$. The one-shot game is then characterized by the parameters z, β, b , and c . As shown in the Supporting Information (SI), the only rational choice (and also the evolutionary outcome) of the A_1 -population in this one-shot PD game is to defect. However, if $z\beta > c$, then the advantage to the A_2 -population to cooperate in their asymmetric interactions is greater than the net benefit of defecting in symmetric interactions and so the subordinate population plays C. That is, the dominance hierarchy has induced cooperative behavior where it would not have existed otherwise.

It is straightforward to extend the above payoff matrices for the one-shot PD game to model the repeated PD game [4, 21] when all individuals in both A_1 - and A_2 -populations display only two phenotypes, tit for tat (TFT) and always defect (ALLD), and the expected number of repeated interactions between two individuals is \bar{m} . Recall that, an individual using TFT cooperates in the first round of the repeated game and then, in subsequent rounds, plays the strategy his opponent used in the previous round. Specifically, for the symmetric

interactions between i -individuals ($i = 1, 2$) [21], the payoff matrix becomes

$$H_{ii} = \begin{matrix} & \text{TFT} & \text{AllD} \\ \text{TFT} & \left(\begin{matrix} \bar{m}(b-c) & -c \\ b & 0 \end{matrix} \right) \\ \text{AllD} & & \end{matrix}.$$

Again note that the TFT and AllD strategies are indicated in this repeated PD game but not in subsequent ones.

For asymmetric interactions, when an A_1 -individual plays against an A_2 -individual, the payoff matrix of the A_1 -individual equals H_{ii} ($i = 1, 2$) (i.e., $H_{12} = H_{ii}$), while the payoff matrix of the A_2 -individual is

$$H_{21} = \left(\begin{matrix} \bar{m}(b-c) & -c - (\bar{m}-1)\beta \\ b - (\bar{m}-1)\beta & -\bar{m}\beta \end{matrix} \right).$$

For the remainder of this section, we will assume that the repeated PD game has at least two expected rounds in addition to the above condition that the defection cost β is larger than the cost c of cooperation, i.e., $\beta > c$ and $\bar{m} \geq 2$. The one-shot PD game (i.e., $\bar{m} = 1$) is considered in the SI.

First consider the situation where there are only asymmetric interactions. This is the two-strategy (with strategies TFT and AllD for both populations) bimatrix game [14] given by the payoff matrices H_{12} and H_{21} . Since TFT strictly dominates AllD in the A_2 -population (i.e., since $\bar{m}(b-c) > b - (\bar{m}-1)\beta$ and $-c - (\bar{m}-1)\beta > -\bar{m}\beta$ in the payoff matrix H_{21}), the A_2 -population plays TFT in the evolutionary outcome. Given that the A_2 -population will all play TFT, the evolutionary outcome will also be TFT in the A_1 -population when $\bar{m}(b-c) > b$ in H_{12} , leading to mutual cooperation in all rounds of the repeated PD game. That is, the strategy pair (TFT, TFT) is the only Nash equilibrium (NE) and the globally asymptotically stable evolutionary outcome. Full cooperation is induced in both populations by the dominance hierarchy when $\bar{m} > b/(b-c)$. On the other hand, if $\bar{m} < b/(b-c)$, the globally asymptotically stable evolutionary outcome is the NE (AllD, TFT). Both of these predictions are clear from the stability analysis of the corresponding evolutionary dynamics in the SI. The effect of including the strategy that always cooperates (i.e., AllC) is also considered there. For the resulting three-strategy bimatrix game, the SI shows that (AllD, AllC) is locally asymptotically stable whenever there is more than one expected round in the repeated game and that mutually cooperative behavior is only locally asymptotically stable once $\bar{m} > b/(b-c)$. That is, allowing individuals to always cooperate cannot induce full cooperation in both populations (or, to rephrase, TFT is more effective than AllC in driving the system to full cooperation). Since the same conclusion holds (see SI) when there are symmetric interactions as well, from now on we will restrict the strategy choices in the repeated PD game to TFT and AllD.

When there are only symmetric interactions, the two populations can be considered separately. It is then well known [21] that (i) AllD is always locally asymptotically stable for both populations and (ii) TFT is never globally asymptotically stable for either population but that it is locally asymptotically stable if and only if $\bar{m} > b/(b-c)$. In contrast, the induced cooperation in the above asymmetric interactions always leads the A_2 -population to TFT and this is sufficient to yield cooperative behavior in both populations (i.e., the global asymptotic stability of (TFT,TFT)) when \bar{m} is above the threshold value of $b/(b-c)$.

Now consider the situation where there are both symmetric and asymmetric interactions and suppose that these occur between random individuals in the entire population. As mentioned in the Introduction, we assume that a given individual in either population will use the

same phenotype in both symmetric and asymmetric interactions. Thus, if an individual displays TFT (AllD) in symmetric interactions, then he will also use TFT (AllD) in asymmetric interactions.

Let x be the frequency of TFT in A_1 -population and y the frequency of TFT in A_2 -population. Since the proportion of A_1 -individuals is z , the expected payoffs of TFT and AllD in the A_1 -population are $F_{TFT} = z[x\bar{m}(b-c) - (1-x)c] + (1-z)[y\bar{m}(b-c) - (1-y)c]$ and $F_{AllD} = zx b + (1-z)y b$, respectively, and the expected payoffs of TFT and AllD in the A_2 -population are $G_{TFT} = (1-z)[y\bar{m}(b-c) - (1-y)c] + z[x\bar{m}(b-c) - (1-x)(c + (\bar{m}-1)\beta)]$ and $G_{AllD} = (1-z)y b + z[x(b - (\bar{m}-1)\beta) - (1-x)\bar{m}\beta]$, respectively. The standard evolutionary dynamics known as the replicator equation [22] becomes

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) \left[(zx + (1-z)y)(\bar{m}-1)(b-c) - c \right], \\ \frac{dy}{dt} &= y(1-y) \left[(zx + (1-z)y)(\bar{m}-1)(b-c) - c + z\beta(1+x(\bar{m}-2)) \right]. \end{aligned} \tag{1}$$

Since $\bar{m} \geq 2$, there is no equilibrium in the interior of the unit square (i.e., $\dot{x} = 0 = \dot{y}$ has no solution for $0 < x, y < 1$). Every interior trajectory converges to a NE on the boundary (see Fig. 1 as well as Fig. S3 in SI). In fact, almost all interior trajectories converge to a strict NE, which vary among (TFT,TFT), (AllD,TFT), and (AllD,AllD) depending on the parameters of this game. Here, we report the results from SI in the special case $z = 1/2$ (i.e., the sizes of A_1 - and A_2 -populations are assumed to be same). It is again the threshold number of rounds $b/(b-c)$ that is central to characterize the level of cooperation expected in this game. The following two cases summarize the outcome.

Case 1 ($\bar{m} > \frac{b}{b-c}$). (TFT,TFT) is locally asymptotically stable. That is, if the populations are sufficiently cooperative initially, the induced cooperation in the A_2 -population also produces cooperative behavior in the A_1 -population. Furthermore, if $\beta > 2c$ and $\bar{m} > (b+c)/(b-c)$, then (TFT,TFT) is globally asymptotically stable (i.e., the dominance hierarchy induces full cooperation). On the other hand, if $\beta < 2c$ (respectively, $\bar{m} < (b+c)/(b-c)$), then (AllD,AllD) (respectively, (AllD,TFT)) is also locally asymptotically stable. The sample trajectories for this case are shown in Fig. 1.

Case 2 ($\bar{m} < \frac{b}{b-c}$). Now, AllD always has higher payoff than TFT in the A_1 -population [i.e., x is always decreasing from the first equation in (1)]. Thus, evolution leads them to AllD just as occurred when there were only asymmetric interactions or only symmetric interactions. If $\beta > 2c$, the A_2 -population evolves to TFT since the advantage of induced cooperation in their asymmetric interactions outweighs the combined benefit of defection in their symmetric and asymmetric interactions. On the other hand, if $\beta < 2c$, the A_2 -population evolves to AllD if $\bar{m} < (b+c-\beta)/(b-c)$ and to either AllD or TFT if $\bar{m} > (b+c-\beta)/(b-c)$. The sample trajectories for this case are shown in Fig. S3 in SI.

Case 1 shows clearly that, for combined symmetric and asymmetric interactions, linear dominance induces full cooperation when the cost of defection is high and there are a large number of rounds (specifically, if $\beta > 2c$ and $\bar{m} > (b+c)/(b-c)$, then the corner (1, 1) of the unit square corresponding to full cooperation is globally asymptotically stable). This means that, although the local stability of (1, 1) depends only on the expected number of rounds \bar{m} (i.e., (1, 1) is locally asymptotically stable if $\bar{m} > b/(b-c)$), its global stability also depends on the defection cost β compared to the cost of cooperation c . For lower defection costs and/or a smaller number of rounds, other locally stable outcomes emerge as summarized by Cases 1 and 2. It is important to note that, in all these cases, the subordinate population will be at least as cooperative as the dominant population at the evolutionary outcome. The added

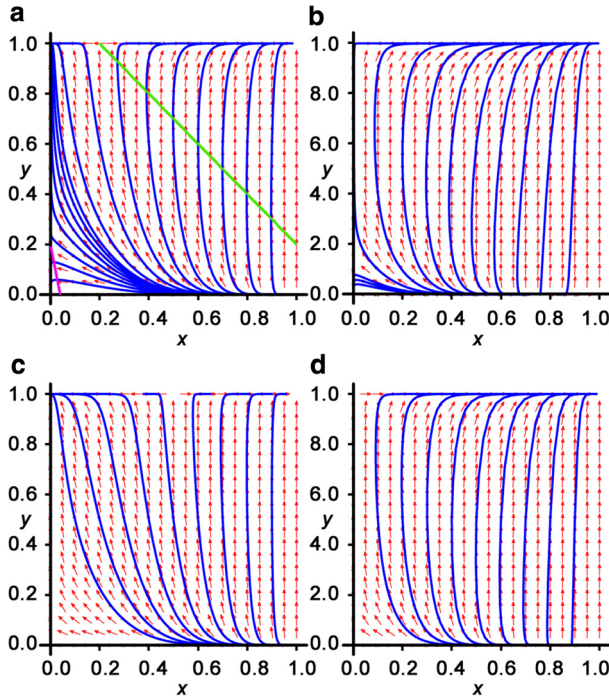


Fig. 1 Dynamic trajectories of the replicator equation (1) for the two-population repeated PD game with linear dominance. The four panels illustrate all possibilities in Case 1 since \bar{m} is large ($\bar{m} > b/(b - c) = 4$) enough that (TFT, TFT) is locally asymptotically stable. (AllD, AllD) is locally asymptotically stable in panels **a** and **b** ($\beta = 5 < 2c$) but not in panels **c** and **d** ($\beta = 7 > 2c$). (AllD, TFT) is locally asymptotically stable in panels **a** ($\bar{m} = 6$) and **c** ($\bar{m} = 5$) but not in panel **b** ($\bar{m} = 9$) or **d** ($\bar{m} = 8$). Panel **a** also includes the isoclines (see SI) with the *green* (respectively, *cyan*) line where $dx/dt = 0$ (respectively, $dy/dt = 0$). Other parameters: $b = 4, c = 3, z = 1/2$

cost of defection for these subordinate players gives them an extra incentive to cooperate. This contrasts with the evolutionary outcome of AllD for the A_2 -population and TFT for the A_1 -population when there are only symmetric interactions and $\bar{m} > b/(b - c)$.

It is also instructive to compare the results of the replicator equation (1) to those when there are only asymmetric interactions. The general conclusion is that, for combined symmetric and asymmetric interactions, linear dominance leads to at least as much cooperative behavior as when there are only symmetric interactions but no more cooperation than when there are only asymmetric interactions.

Remark The threshold stability values for the repeated game found in Cases 1 and 2 (as well as elsewhere in the article) can be expressed in terms of how costs and benefit ratios compare to the degree of relatedness between interacting individuals. For instance, the threshold $\bar{m} = b/(b - c)$ is the same as $(\bar{m} - 1)/\bar{m} = c/b$ where the left-hand side is the proportion of one-shot games played by individuals who know each other (called the degree of relatedness here). That is, by Case 1, (TFT, TFT) is locally asymptotically stable if and only if relatedness exceeds the cost to benefit ratio in the standard one-shot PD game (an intuitive result similar to those found for other mechanisms that promote cooperation [22, 26]). Furthermore, global asymptotic stability requires relatedness exceeds the higher ratio $2c/(b + c)$. Similarly, the threshold $\bar{m} = (b + c - \beta)/(b - c)$ in Case 2 is the same as $(\bar{m} - 1)/\bar{m} = (2c - \beta)/(b + c - \beta)$

which adjusts both terms in the previous ratio $2c/(b + c)$ by the cost of defection when the A_1 -population plays ALLD.

Clearly, the two-subpopulation model with linear dominance can be extended to the multi-subpopulation model with linear dominance. A three-subpopulation model with linear dominance is investigated in the SI, in which we denote the subpopulations as A_i for $i = 1, 2, 3$ and assume that A_j -individuals are better competitors than A_i -individuals in interactions between an A_j -individual and an A_i -individual with $i > j$. Let β_{21} be the cost of defection in the A_2 -population in interactions with the A_1 -population. Similarly, let β_{3j} be the cost of defection in the A_3 -population in interactions with the A_j -population (for $j = 1, 2$). From the one-shot PD game, a particularly interesting result is that the linear dominance does not always imply that the cooperative populations are the ones at the end of the dominance chain. That is, the A_2 -population may be cooperative while the A_3 -population defects. A necessary condition for this to occur is that the cost of defection in interactions with the dominant A_1 -population must be higher for the intermediate A_2 -population than for the last population in the dominance chain (i.e., $\beta_{21} > \beta_{31}$). These results for the one-shot PD game can be extended to the general n -population model (see the second half of Sect. 2.1 in SI). For the repeated PD game, the conditions for global asymptotic stability of full cooperation are less stringent for three subpopulations with linear dominance than for two subpopulations. This is shown in Sect. 2.2 of the SI where it is pointed out that the intuitive reason for this is that each individual now has more asymmetric interactions which encourages cooperative behavior from the subordinate ones.

2.2 Three-Subpopulation Model with Cyclic Dominance

In order to obtain a deeper understanding of the effect of induced cooperation on the evolution of cooperation, a three-subpopulation model is considered with a more complicated dominance hierarchy. In this model, A_1 -individuals dominate A_2 -individuals, A_2 -individuals dominate A_3 -individuals, and A_3 -individuals dominate A_1 -individuals, and, for simplicity, we assume that in all asymmetric interactions, the subordinate individuals have the same defection cost. This cyclic dominance is reminiscent of the triangular hierarchy structure of the rock–scissors–paper game [14]. We examine whether this induces corresponding cyclic behavior in the evolutionary outcome.

The one-shot PD game with cyclic dominance. In the one-shot game, all individuals in the A_1 -, A_2 - and A_3 -populations display only two phenotypes, cooperation (C) and defection (D). The payoff matrices for symmetric interactions are

$$\Pi_{ii} = \begin{pmatrix} b - c & -c \\ b & 0 \end{pmatrix}$$

for $i = 1, 2, 3$, and for asymmetric interactions are $\Pi_{12} = \Pi_{23} = \Pi_{31} = \Pi_{ii}$ and

$$\Pi_{21} = \Pi_{32} = \Pi_{13} = \begin{pmatrix} b - c & -c \\ b & -\beta \end{pmatrix}.$$

Recall that z_i is the proportion of the A_i -population and x_i is the frequency of cooperation in A_i -population. When there are random pairwise interactions between individuals in the entire population, the expected payoffs of C and D in A_i -population are $F_C^{(i)} = \bar{x}(b - c) - (1 - \bar{x})c$ and $F_D^{(i)} = \bar{x}b - z_j(1 - x_j)\beta$, respectively, for $i = 1, 2, 3$, where $j = 3$ if $i = 1$ and $j = i - 1$ if $i = 2$ or 3 . Here, \bar{x} is the average frequency of C in the total population

(i.e., $\bar{x} = \sum_{i=1}^3 z_i x_i$). Thus, the replicator dynamics on the unit cube has the form

$$\frac{dx_i}{dt} = x_i(1 - x_i) [-c + z_j(1 - x_j)\beta] \tag{2}$$

for $i = 1, 2, 3$, where $j = 3$ if $i = 1$ and $j = i - 1$ if $i = 2$ or 3 .

If $\beta z_i < c$, then the cost of defection for individuals dominated by A_i is too small to offset the combined disadvantage of cooperation by these individuals in their three symmetric and asymmetric interactions. Thus, the only rational behavior in the population dominated by A_i is defect since D strictly dominates C. This result is reflected in the analysis of the dynamics (2). For example, if $\beta z_3 < c$, the frequency of cooperation in the A_1 -population is strictly decreasing in the interior of the unit cube (i.e., $\dot{x}_1 < 0$). A corollary of this result is that, if $\beta z_i < c$ for all $i = 1, 2, 3$, then (D,D,D) strictly dominates every other strategy triple and so the evolutionary outcome is mutual defection in all interactions.

On the other hand, if $\beta z_i > c$ for some i , the system does not evolve to mutual defection. For instance, if $\beta z_1 < c$, $\beta z_2 < c$ and $\beta z_3 > c$, the A_2 and A_3 populations both play D (i.e., x_2 and x_3 both evolve to 0) since these populations are dominated by A_1 and A_2 respectively. Given this behavior, it is then beneficial for the A_1 -population to exhibit induced cooperation due to the large number of interactions with the third subpopulation. This translates into the A_1 -population becoming fully cooperative (i.e. the corner $(1, 0, 0)$ is globally asymptotically stable). Similarly, if $\beta z_1 < c$, $\beta z_2 > c$ and $\beta z_3 > c$, the corner $(0, 0, 1)$ is globally asymptotically stable. Now the A_2 -population must defect (i.e., x_2 evolves to 0) and then the third subpopulation becomes fully cooperative (i.e., x_3 evolves to 1), after which the first subpopulation takes advantage of this induced cooperation and everyone in it defects. Thus, if $\beta z_i > c$ for some A_i -populations but not for others, exactly one subpopulation becomes fully cooperative (and the other two defect).

The most interesting case is when $\beta z_i > c$ for all $i = 1, 2, 3$ since no pure strategy triple is then a rational choice for the system (i.e., none is a NE). There is still a unique NE but it is now in the interior of the unit cube; namely, $\mathbf{x}^* \equiv (x_1^*, x_2^*, x_3^*)$ where $x_i^* = (\beta z_i - c)/(\beta z_i)$ for $i = 1, 2, 3$. However, it cannot be the expected outcome of this game since it is an unstable rest point of the evolutionary dynamics (2). In particular, the linearization at \mathbf{x}^* has one negative eigenvalue and two complex conjugate eigenvalues with positive real part. From the SI, this interior equilibrium is attracting on an invariant curve through \mathbf{x}^* (i.e., on its stable manifold) that connects the unstable nodes (i.e., sources) $(0, 0, 0)$ and $(1, 1, 1)$ corresponding to full defection and full cooperation, respectively. The only other rest points of (2) are the six remaining corners of the unit cube and each of these is an unstable saddle point with two negative eigenvalues and one positive. The global dynamics on the unit cube follow from the special properties of system (2) (see SI), especially that it is a competitive system (i.e., $\partial \dot{x}_i / \partial x_j \leq 0$ for all $i \neq j$) that is volume preserving. In fact, all interior trajectories (except those initially on the invariant attracting curve through \mathbf{x}^*) converge to the *heteroclinic cycle* which is formed by the six edges on the boundary of the unit cube that connect these unstable saddle points in the order $(1, 0, 0), (1, 0, 1), (0, 0, 1), (0, 1, 1), (0, 1, 0), (1, 1, 0)$ (and then back to $(1, 0, 0)$). That is, in the limit, the system has at least one and at most two fully cooperative subpopulations at any particular time (the same is true for the fully defective subpopulations) as the heteroclinic cycle follows the sequence of pure strategy best replies.

Sample trajectories are plotted in Fig. 2 for this last case and for two parameter sets. In panel a, all z_i are equal (i.e., $z_i = 1/3$ for $i = 1, 2, 3$) (for which the invariant curve through \mathbf{x}^* is the line segment joining $(0, 0, 0)$ to $(1, 1, 1)$) and payoffs are chosen so that $x_i^* = 1/2$. This special case corresponds to Jordan’s [15] example and the dynamic analysis given by Gaunersdorfer and Hofbauer [9]. There is a smooth two-dimensional invariant surface that

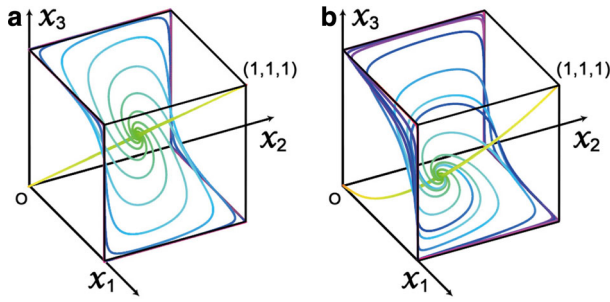


Fig. 2 Dynamic trajectories of the replicator equation (2) for the one-shot three-population PD game with cyclic dominance. The parameters are chosen $b = 3, c = 1,$ and $\beta = 6$. In panel **a**, $z_i = 1/3$ and $x_i^* = 1/2$ for all $i = 1, 2, 3$. In panel **b**, $z_1 = 1/2$ and $z_2 = z_3 = 1/4$ with $x_1^* = 2/3, x_2^* = x_3^* = 1/4$. In both panels, all trajectories are evolving outward from \mathbf{x}^* to the boundary of the cube except for those on the curve through \mathbf{x}^* connecting $(0, 0, 0)$ to $(1, 1, 1)$

extends the local unstable manifold at \mathbf{x}^* to the boundary of the cube and that divides the interior of the cube into two regions symmetric in \mathbf{x}^* . These regions are invariant under (2) and all trajectories in them are attracted to this invariant surface. In panel b, the z_i are not all equal. The stable and unstable manifolds at \mathbf{x}^* are no longer symmetric but the qualitative behavior of the dynamical system remains as described in the preceding paragraph.

In all these cases for the one-shot game, mutual cooperation for the three populations is never the evolutionary outcome. That is, cyclic dominance cannot induce full cooperation since, for example, if two subpopulations behave cooperatively, it is always advantageous for the other subpopulation to defect with no fear of incurring a cost of defection. For small defection costs, it remains disadvantageous for any individual to cooperate and so mutual defection evolves. For high defection costs, cyclic dominance leads to the subpopulations which are fully cooperative oscillating over time, unlike the result for linear dominance where only the subordinate subpopulations can cooperate. For intermediate defection costs, exactly one subpopulation can be fully cooperative depending on model parameters. With β and c fixed as in our model, this last situation can only arise if subpopulations have different sizes. For instance, a subpopulation that is substantially larger than the other two will defect since its expected defection cost in a random interaction is negligible, perhaps contributing to the potential of large crowds becoming less cooperative. We will now investigate the effect that repeated interactions have on these predictions.

The repeated PD game with cyclic dominance. If all individuals in A_1 -, A_2 -, and A_3 -populations display only two phenotypes, TFT and AllD, then the symmetric payoff matrices are

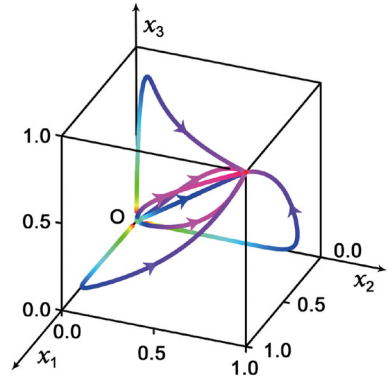
$$H_{ii} = \begin{pmatrix} \bar{m}(b - c) & -c \\ b & 0 \end{pmatrix}$$

for $i = 1, 2, 3$, and the asymmetric payoff matrices are given by $H_{12} = H_{23} = H_{31} = H_{ii}$ and

$$H_{21} = H_{32} = H_{13} = \begin{pmatrix} \bar{m}(b - c) & -c - (\bar{m} - 1)\beta \\ b - (\bar{m} - 1)\beta & -\bar{m}\beta \end{pmatrix}.$$

If x_i denotes the frequency of TFT in A_i -population, then the expected payoffs of TFT and AllD in the A_i -population are $F_{TFT}^{(i)} = \bar{x}\bar{m}(b - c) - (1 - \bar{x})c - z_j(1 - x_j)(\bar{m} - 1)\beta$ and

Fig. 3 Trajectories of the replicator equation (3) for three-population repeated PD game with cyclic dominance. For the parameters chosen ($b = 3$, $c = 1$, $\beta = 4$, $\bar{m} = 3$, and $z_i = 1/3$ for $i = 1, 2, 3$), the corner $(1, 1, 1)$, corresponding to the strategy triple (TFT, TFT, TFT), is globally asymptotically stable



$F_{AllD}^{(i)} = \bar{x}b - z_j(\bar{m} - x_j)\beta$, respectively, for $i = 1, 2, 3$, where $\bar{x} = \sum_{i=1}^3 z_i x_i$ is the average frequency of TFT in the entire population, and $j = 3$ if $i = 1$ and $j = i - 1$ if $i = 2$ or 3 .

To simplify the analysis of this model, we will assume that each subpopulation is of the same size (i.e., $z_i = 1/3$ for $i = 1, 2, 3$) and also continue to assume that the expected number of rounds is at least two (i.e., $\bar{m} \geq 2$). Clearly, if $\beta > 3c$, TFT is the only rational choice in each subpopulation since $F_{TFT}^{(i)} > F_{AllD}^{(i)}$ for every value of x_i and all $i = 1, 2, 3$. This result is also clear from the replicator equation which becomes

$$\frac{dx_i}{dt} = x_i(1 - x_i) \left[\bar{x}(\bar{m} - 1)(b - c) - c + \frac{\beta}{3} (1 + (\bar{m} - 2)x_j) \right] \tag{3}$$

for $i = 1, 2, 3$, where $j = 3$ if $i = 1$ and $j = i - 1$ if $i = 2$ or 3 . When $\beta > 3c$, x_j is monotonically increasing. Thus, the system evolves to mutual cooperation when the defection cost incurred by subordinates is larger than the cost of cooperation in the combined symmetric and asymmetric interactions. An example is plotted in Fig. 3, in which the corner $(1, 1, 1)$ is globally stable.

For the remainder of this section, assume that $\beta < 3c$. Then (AllD, AllD, AllD) is locally asymptotically stable since it is a strict NE. The global stability of (AllD, AllD, AllD) depends on the expected number of rounds in the repeated PD game. From the following two cases, the result here is also different than in the linear dominance situation where the threshold number of rounds was $b/(b - c)$. For cyclic dominance, this threshold is replaced by the smaller quantity $(3b + \beta)/(3b - 3c + \beta)$ as summarized in the following two cases.

Case 1 ($\bar{m} < \frac{3b + \beta}{3b - 3c + \beta}$). The system evolves to mutual defection (AllD, AllD, AllD) since this strategy triple strictly dominates any other strategy profile. Thus, x_i is monotonically decreasing for all $i = 1, 2, 3$ and so $(0, 0, 0)$ is globally asymptotically stable (Fig. 4, panels a and a').

Case 2 ($\bar{m} > \frac{3b + \beta}{3b - 3c + \beta}$). Both (AllD, AllD, AllD) and (TFT, TFT, TFT) are rational outcomes since they are both strict NE. That is, both $(0, 0, 0)$ and $(1, 1, 1)$ are locally asymptotically stable for the dynamics (3) (Fig. 4, panels b and c). Furthermore, there is an interior equilibrium of (3) of the form $\mathbf{x}^* = (x_1^*, x_2^*, x_3^*)$ where $x_i^* = (3c - \beta) / (3(\bar{m} - 1)(b - c) + \beta(\bar{m} - 2)) = x^*$ for $i = 1, 2, 3$ (i.e. $x_1^* = x_2^* = x_3^* \in (0, 1)$). If $\bar{m} = 2$, there is a plane of equilibria through \mathbf{x}^* given by $\bar{x} = x^*$ (this case is analyzed in the SI). Otherwise (i.e. $\bar{m} > 2$), \mathbf{x}^* is the unique interior equilibrium whose linearization has one positive eigenvalue and two complex conjugate eigenvalues with non-positive real parts (see SI). In particular, \mathbf{x}^* is an unstable equilibrium with a two-dimensional stable manifold. By symmetry, the unsta-

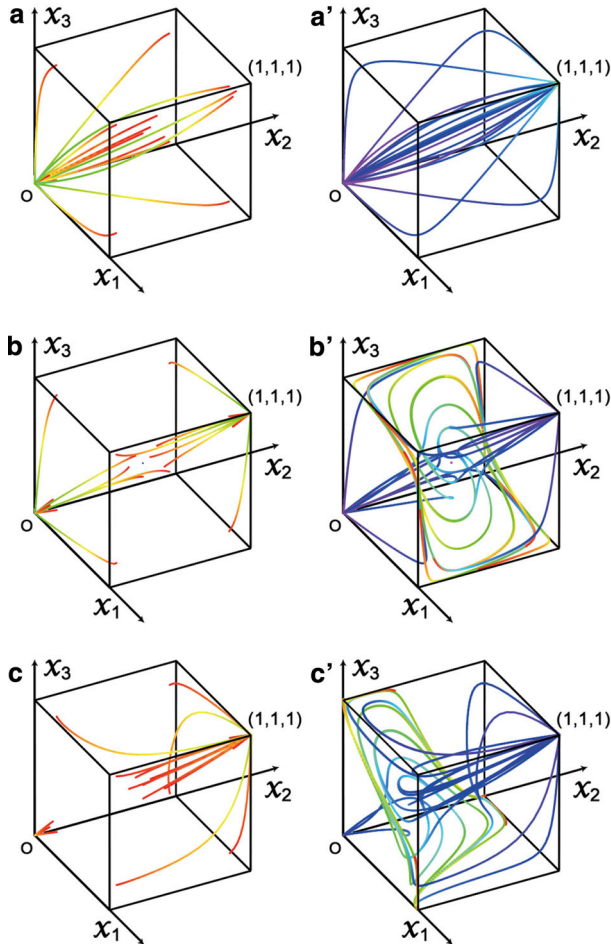


Fig. 4 Trajectories of the replicator equation (3) for the three-population repeated PD game with cyclic dominance and different choices of \bar{m} ($\bar{m} = 2$ in top panels, $\bar{m} = 3$ in middle panels, $\bar{m} = 4$ in bottom panels). The left panels show the trajectories in forward time (specifically, for $t = 0$ to 5) from various interior initial points and the right panels show the trajectories in backward time (specifically, for $t = -10$ to 5) from the same initial points. Parameters are chosen ($b = 10, c = 7, \beta = 8$) so that (A1LD,A1LD,A1LD) is locally asymptotically stable (i.e., $\beta < 3c$). In panels **a** and **a'**, it is globally asymptotically stable since $\bar{m} < (3b + \beta)/(3b - 3c + \beta)$ (Case 1) but not in the other four panels (Case 2) where both $(0, 0, 0)$ and $(1, 1, 1)$ are clearly locally asymptotically stable. In the middle panels, with interior rest point $x_i^* = 1/2$ for all i , the dynamics (3) is symmetric in \mathbf{x}^* and its stable two-dimensional manifold that separates the domains of attraction is also symmetric in \mathbf{x}^* . In backward time (panel **b'**), trajectories converge to the heteroclinic cycle along the edges of the unit cube that joins the other six corners as in Fig. 2. In the bottom panels with $x^* = 13/43, \mathbf{x}^*$ is much closer to $(0, 0, 0)$ than $(1, 1, 1)$ and so $(0, 0, 0)$ has a much smaller domain of attraction (panel **c'**). Moreover, the attracting heteroclinic cycle in backward time (panel **c'**) is no longer exclusively along the edges of the unit cube but includes some portions in the interior of three of the faces

ble manifold (corresponding to the positive eigenvalue) is the invariant line $x_1 = x_2 = x_3$ joining $(0, 0, 0)$ to $(1, 1, 1)$.

The global dynamics in Case 2 can be understood by analyzing the stable manifold of \mathbf{x}^* for the time-reversal of system (3) (i.e., the trajectories of (3) in backward time). Since the

dynamics (3) is a cooperative system (i.e., $\partial \dot{x}_i / \partial x_j \geq 0$ for all $i \neq j$), the time reversal of (3) is again a competitive system which turns out to be volume contracting (see SI). In particular, there are no nontrivial periodic orbits in the interior of the unit cube (either for the dynamics (3) or its time-reversal). Moreover, \mathbf{x}^* is the unique interior rest point of this time-reversed system whose linearization has the same qualitative behavior as the interior rest point of the dynamics (2) for the one-shot PD game with cyclic dominance; namely, one negative eigenvalue and two complex conjugate eigenvalues with positive real part. It is shown in the SI that the local two-dimensional unstable manifold of the time-reversed system extends to the boundary of the unit cube, dividing the cube into two regions, each of which contains exactly one of the corners $(0, 0, 0)$ or $(1, 1, 1)$. In backward time, all interior trajectories of (3) (except those on the line joining $(0, 0, 0)$ to $(1, 1, 1)$) converge to a heteroclinic cycle on the boundary of the unit cube (see Fig. 4, panels b' and c'). Thus, in forward time, all interior trajectories of (3) initially in the region containing $(0, 0, 0)$ (respectively, $(1, 1, 1)$) converge to $(0, 0, 0)$ (respectively, $(1, 1, 1)$). That is, these regions are the domains of attraction of the two locally asymptotically stable rest point of the dynamics (3).

3 Conclusion and Discussion

The cooperative behavior exhibited by subordinate individuals to dominant individuals (which we call “induced cooperation” of subordinate individuals) is one of the most important characteristics of any population in nature and human society that has a dominance hierarchy [16, 30, 40]. Based on this fact, we developed a theoretical framework to investigate whether this induced cooperation will also promote cooperation in symmetric interactions between dominant individuals and between subordinate individuals, and whether this will lead to full cooperation in the total population.

In our model, we defined the concept of defection cost of subordinate individuals, denoted by β , to measure the asymmetric interactions between subordinate and dominant defectors (i.e., a subordinate defector will incur a cost β when it plays against a dominant defector), and we assumed that this defection cost of a subordinate individual is larger than its cost of cooperation (i.e., $\beta > c$). Using the standard repeated PD game based on strategies TFT and ALLD [3, 33] our main theoretical results show that full cooperation in the total population can indeed be the expected outcome from the perspective of rational decision making as well as from the evolutionary perspective in the sense that this outcome is globally asymptotically stable. These results are summarized as follows.

For the two-subpopulation repeated PD game with linear dominance, the local stability of the strategy pair (TFT, TFT) depends only on the expected number of repeated interactions, \bar{m} , in that (TFT, TFT) is locally asymptotically stable if and only if $\bar{m} > b/(b - c)$. This result is identical to that for the repeated game without a dominance structure [21]. However, TFT is never globally asymptotically stable when there is only one population, whereas it can be in the two-population model depending not only on the expected number of repeated interactions but also on the defection cost β of the subordinate individual. Specifically, if the two subpopulations have the same size, then the strategy pair (TFT, TFT) is globally asymptotically stable if and only if $\beta > 2c$ and $\bar{m} > (b + c)/(b - c)$.

These global stability results for full cooperation can be extended to three populations. For example, for the three-subpopulation repeated PD game with linear dominance, if the three subpopulations have the same size and $\bar{m} > b/(b - c)$, then the strategy triple (TFT, TFT, TFT) is globally asymptotically stable if and only if $\beta > 3c/2$ and $\bar{m} > \max \{ (b + 2c - \beta)/(b - c), (2b + c)/2(b - c) \}$. Finally, for the three-subpopulation

repeated PD game with cyclic dominance and all three subpopulations of the same size, the strategy triple (TFT, TFT, TFT) is globally asymptotically stable if and only if $\beta > 3c$. All of these results show clearly that the induced cooperation of subordinate individuals to dominant individuals in a dominance hierarchy system can lead to full cooperation in the total population.

The above discussion shows that defection costs must be high relative to the cost c of cooperation in order for dominance hierarchies to induce full cooperation in repeated PD games. This is often the case in real systems. For instance, Wilson [40] pointed out that the dominance relationship among bumblebees is orderly and predictable, with punishment “sometimes so rough that the poor creature is seriously wounded or even killed.” In fact, it is well known that subordinates will defer to dominant individuals in a hierarchy. However, the effect this induced cooperation has on the behavior of the dominant subpopulation is not so clear. Our theoretical model reveals that full cooperation in a hierarchical system can be induced by the cooperation exhibited by the subordinates. Although this is only a theoretical result, it does provide an insight into understanding the emergence of cooperation in nature.

Our results also show that coexistence of cooperation and defection is possible in hierarchical systems (e.g., in repeated games, evolutionary outcomes can lead to mutual cooperation in interactions between certain subpopulations and mutual defection in others). Specifically, for the two- and three-subpopulation repeated PD models with linear dominance, (AllD, TFT) (for two-subpopulation model) and the three-strategy triples (AllD, AllD, TFT) and (AllD, TFT, TFT) (for three-subpopulation model) can also be rational outcomes for some choices of model parameters in the sense that they are strict Nash equilibria and so locally asymptotically stable. The notation for these ordered tuples lists the outcome for the most dominant species first, followed by the next most dominant and so on (e.g., (AllD, AllD, TFT) means the least dominant subpopulation plays TFT while the other two play AllD). For the one-shot PD game (i.e., $m = 1$) with either linear or cyclic dominance, cooperation in the total population (i.e., all subpopulations play C) is never the expected outcome (in fact, it is not even locally asymptotically stable). A particularly interesting result for linear dominance is that the expected outcome may be (D,C,D), showing that the cooperative populations are not necessarily those that are least dominant. Moreover, for the one-shot PD game with three-subpopulations and cyclic dominance, high defection costs will lead to the subpopulations which are fully cooperative oscillating over time.

The evolution of cooperation is still a puzzle in evolutionary biology [22,26]. Hamilton’s [10,11] theory of kin selection provides a theoretical explanation for cooperation between relatives. The basic idea behind kin selection appeals to common sense, i.e., cooperation can emerge more easily among closely related individuals [23]. According to Hamilton’s Rule, cooperation among relatives can be favored by natural selection if the coefficient of genetic relatedness between the donor and the recipient exceeds the cost/benefit ratio of the altruistic act (i.e., the logic behind Hamilton’s model is that the relatives tend to help each other because they may inherit genes of a common ancestor with high probability [10,11]). This intuitive reasoning is formalized through the idea that individuals strive to maximize their inclusive fitness [37]. Indeed, many cooperative acts among animals occur between close kin [8,12], including the increased reproductive share given to subordinate individuals by dominant breeders as the degree of relatedness increases [28].

It is also widely acknowledged that dominance hierarchies are prevalent among kin [16,40]. Our model, which is based on the fact that subordinate individuals should behave cooperatively to dominant individuals in a dominance hierarchy system, offers an alternative, non genetic, argument to show that full cooperation in the total population is possible under natural selection. The theoretical results of this model provide one of the first steps

in studying the evolution of cooperation in a hierarchical population. In fact, most animal populations as well as human society should be considered to be a dominance hierarchy system [40]. Wilson [40] summarized some special properties of dominance hierarchy systems for promoting cooperation, which are the xenophobia principle, peace of strong leadership, the will to power, social inertia, and nested hierarchies. For example, he pointed out that dominant animals of some primate societies utilize their power to terminate fighting among subordinates (e.g., this phenomenon has been found in rhesus and pig-tailed macaques [5,31] and in spider monkeys [7]) and that species organized by despotism (e.g., bumblebees, paper wasps, hornets, and artificially crowded territorial fish and lizards) also live in relative peace owing to the generally acknowledged power of the tyrant. All of these phenomena not only align with May's [17] statement but also provide possible evidence for our theoretical results.

The model of induced cooperation developed in this paper has certain simplifying assumptions discussed near the end of the Introduction. Cooperative behavior can also emerge when the relative sizes of subpopulations evolve over time according to the differences in their expected payoffs, although this often leads to the extinction of one subpopulation [35]. An important question in the corresponding extension of our model is then conditions that imply the subpopulations persist over time. Other extensions of interest allow model parameters (e.g., the cost (c), the benefit (b) or the subordinates's defection cost (β)) to depend on the interaction or vary with time. We also assumed that individuals cannot condition their strategy choice on the subpopulation of their opponent, perhaps due to a lack of information. Since imperfect information has been shown to affect the evolution of cooperation in models of reproductive skew [1], another important question is to analyze informational effects on cooperative behavior in hierarchical models based on the PD game. Although all these extensions are beyond the scope of this paper, they are important topics of future research to gain a better theoretical understanding how dominance hierarchies affect the emergence of cooperation.

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