

# Evolutionary Stability of Discriminating Behaviors With the Presence of Kin Cheaters

Jiawei Li and Graham Kendall

**Abstract**—Discriminating altruism, particularly kin altruism, is a fundamental mechanism of cooperation in nature. Altruistic behavior is not favored by evolution in the circumstances where there are “kin cheaters” that cannot be effectively identified. Using evolutionary iterated prisoner’s dilemma, we deduce the condition for discriminating strategies to be evolutionarily stable and show that the competition between groups of different discriminating strategies restrains the percentage of kin cheaters. A discriminating strategy (DS) manages to cooperate with kin members and defect against non-kins by using an identification mechanism that includes a predetermined sequence of cooperation and defection. The opponent is identified as a kin member if it plays the same sequence. Otherwise, it is identified as non-kin, and defection will be triggered. Once the DS forms the majority of the population, any strategy that does not play the same sequence of moves will be expelled. We find that the competition between a variety of discriminating strategies favors a stable rate of cooperation and a low frequency of kin cheaters.

**Index Terms**—Discriminating strategy, evolutionary stability, game theory, iterated prisoner’s dilemma.

## I. INTRODUCTION

COOPERATION is not uncommon in even the most aggressive species, and numerous costly and fitness-reducing behaviors remain stable in evolution. Among the many explanations of cooperation in nature, kin altruism is by far the most incontrovertible as evidenced by the significant body of scientific literature [1]–[4]. Hamilton’s rule depicts the condition of kin altruism by  $rb - c > 0$ , where  $r$  is the relatedness between two individuals,  $b$  and  $c$  are the benefit to the recipient and the cost to the altruist, respectively [1], [2]. Even though the altruist may reduce their own fitness, the behavior increases the fitness of their relatives with which they share the same gene. As altruistic behavior has developed among the individuals that may share the same gene, the species as a whole receives significantly higher fitness in evolution than that it would have been if there was no kin altruism.

Hamilton’s model of kin selection assumes that kin altruism is independent of kin recognition and altruistic behaviors occur

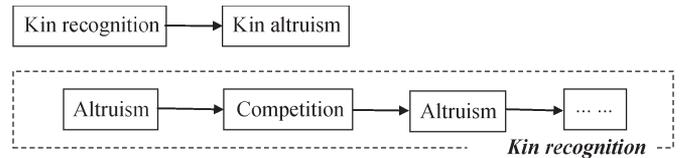


Fig. 1. Two models of kin selection. (a) Kin altruism is independent of kin recognition. (b) Kin altruism is part of the process of kin recognition.

after the beneficiaries have been identified as kin members (as shown in Fig. 1(a)). It is hard to maintain the stability of kin altruism with the presence of kin cheaters. Kin cheaters are those who are identified as kin and derive benefit from the altruistic behaviors of others but never reciprocate. Experiments have shown that the frequency of kin altruism, as well as the fitness of the species, significantly decreases in the presence of kin cheaters [5], [6]. How could kin altruism be evolutionarily stable when kin cheaters are present in the population?

There are competitions, as well as altruistic behaviors, between individuals of the same species. They may fight for the rights of mating and dominance, while cooperate in hunting for food and feeding their young. Note that most of these combat and cooperative behaviors do not occur between individuals of different species. It is reasonable to assume that kin recognition is accomplished by sequences of behavioral interactions [7]. If altruistic behaviors are considered to be part of the process of kin recognition (as shown in Fig. 1(b)), it is possible for these behaviors to be evolutionarily stable.

In this paper, we study a special type of altruistic behaviors, which we call it discriminating behavior. An instance of discriminating behavior is the so-called discriminating strategy (DS) in iterated prisoner’s dilemma (IPD)[8], [9]. A DS identifies the opponent and then only cooperates with its kin members and defects against any non-kin members.

Our main motivation is to show that discriminating behaviors could be evolutionarily stable even in the environment where there are kin cheaters. Since kin altruism is hard to persist with the presence of kin cheaters, we are motivated to investigate the conditions on which cooperation among kin members persists.

The contribution of this paper is twofold. First, we deduce the conditions for discriminating strategies to be evolutionarily stable in evolutionary IPD. Second, we show that the competition between various discriminating strategies restrains the ratio of kin cheaters so that the discriminating strategies could be dynamically stable in a heterogeneous population.

The rest of the paper is organized as follows. In Section II, we present related work. Next, the condition of IPD strategies to be evolutionarily stable strategy (ESS) is discussed in Section III. In Section IV, we deduce the conditions of evolutionary stability for discriminating strategies and give an example.

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Section V describes the effect of kin cheaters on discriminatory behaviors and competition of different discriminating strategies via a series of simulation tests is presented. Section VI concludes the paper with a summary of the significance of the obtained results and suggestions for possible future research directions.

## II. RELATED WORK

In the prisoner’s dilemma, two players choose between “cooperate with the other side” and “defect against the other side,” and the payoffs can be expressed as the following matrix,

		Player II	
		Cooperate	Defect
Player I	Cooperate	$(R, R)$	$(S, T)$
	Defect	$(T, S)$	$(P, P)$

where  $R, S, T,$  and  $P$  denote, respectively, Reward for mutual cooperation, Sucker’s payoff, Temptation to defect, and Punishment for mutual defection, and  $T > R > P > S$  and  $R > (1/2)(S + T)$ . The two constraints motivate each player to play non-cooperatively and prevent any incentive to alternate between cooperation and defection. The dilemma faced by the players is that, whatever the other does, each is better off choosing to defect than to cooperate. However, the payoff when both defect is worse for each player than the outcome they would have received if they had both cooperated. In the IPD, two players have to choose their mutual strategies repeatedly and have the option to retain a memory of the previous behaviors of both players.

The IPD is an ideal experimental platform for evolutionary algorithms and strategies [10]–[25]. Since Axelrod’s famous IPD tournaments and the success of the Tit-For-Tat strategy, much research on novel IPD strategies, for example adaptive strategies [26], evolved strategies [27, 27]–[29], strategies with multiple objectives [30], group strategies [31]–[34], and discriminating strategies [8], [9], has been carried out. A DS only cooperates with its kin members and defects against any non-kin members. This is different from other strategies that aim to maximize their own payoffs. The discriminating strategies are designed to maximize the average payoff of their species, which makes them particularly strong in maintaining a stable population.

In the evolutionary IPD, a population of strategies plays IPD against one another, and each strategy has the opportunity to produce a number of offspring proportional to its fitness (payoff) received in game playing [35]. The strategies with higher fitness reproduce and replace those with lower fitness at each time step. The population converges to strategies with higher fitness.

In evolutionary IPD, the agents do not have a priori information about the strategies of other agents, and no tag is available to identify a strategy. The identity of a strategy is associated with the choices it makes during the interaction with the opponents. Each agent has a memory that stores the past

moves and the payoffs received in past rounds, from which the past moves of the opponent can be deduced. The historical moves are the only information that can be used for an agent to identify the strategy of the opponent.

Discriminating strategies have the most potential to be ESS, although it has been proven that no IPD strategy is ESS when there is long-term interaction between the players [36], [37]. Discriminatory strategies manage to minimize the average payoff of other species while keeping a certain ratio of cooperation among kin members so that a homogeneous population of discriminating strategies could resist invasions from other strategies.

## III. ESS

One of the objectives of studying strategies in IPD is to find an ESS.

An ESS is a strategy such that, if all the members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection [38]. Suppose that there are two types of strategies in the population,  $A$  and  $B$ . Let  $E(B, A)$  denote the payoff strategy  $B$  receives in interacting with strategy  $A$ . The strategy  $A$  is evolutionarily stable if (1) is true for all  $B$

$$E(A, A) \geq E(B, A) \text{ and } E(A, B) > E(B, B). \quad (1)$$

The concept of an ESS considers those situations when a single mutant invades an infinite population of homogeneous strategies. It is not concerned with the structure of the population, the selection scheme, and other parameters of evolutionary dynamics.

It is possible that some strategies remain evolutionarily stable only if some restrictions on the structure of population are added. For example, “always defect” (AIID) could be ESS in IPD if the number of iterations is small ( $n < (T - P/R - P) + 1$ ) or there are only a very limited number of strategies.

When the population structure is taken into consideration, it is possible for a strategy to maintain a stable population in evolution even if it is not ESS. Assume that there are two species of agents in the population,  $A$  and  $B$ . Let  $\rho (1 \geq \rho \geq 0)$  denote the frequency of  $A$  in the population, and  $1 - \rho$  the frequency of  $B$ . The expected payoff of  $A$  and  $B$ ,  $E_A$  and  $E_B$ , can be expressed by

$$\begin{aligned} E_A &= \rho E(A, A) + (1 - \rho)E(A, B) \\ E_B &= \rho E(B, A) + (1 - \rho)E(B, B) \end{aligned}$$

where  $E(A, B)$  denotes the payoff  $A$  receives in interacting with  $B$

$$\begin{aligned} E_A - E_B &= \rho (E(A, A) - E(B, A)) \\ &\quad + (1 - \rho) (E(A, B) - E(B, B)). \quad (2) \end{aligned}$$

Obviously, if there are  $E(A, B) > E(B, B)$  and  $E(A, A) > E(B, A)$ ,  $E_A - E_B > 0$  always hold for any  $\rho (1 \geq \rho \geq 0)$ . Then,  $A$  is an ESS.

When the population structure  $\rho$  is taken into consideration, it is possible for a population of  $A$  to be evolutionarily stable even if  $A$  is not ESS. If there exists a value of  $\rho$  such that (2)

holds for any  $B$ ,  $A$  will always receive higher fitness than its opponents in evolution

$$\rho (E(A, A) - E(B, A)) + (1 - \rho) (E(A, B) - E(B, B)) > 0$$

or

$$\begin{cases} E(A, A) - E(B, A) - E(A, B) + E(B, B) > 0 \\ \rho > \frac{E(B, B) - E(A, B)}{E(A, A) - E(B, A) - E(A, B) + E(B, B)}. \end{cases} \quad (3)$$

This means that a group of  $A$  can defeat any other strategies in evolution if the frequency of  $A$  is greater than a threshold in the population. Therefore, a population of  $A$  strategies can maintain stability if (3) holds for any  $B$ .

In the following sections, we analyze the mechanisms for the discriminating strategies to identify kin members and deduce the conditions for the discriminating strategies to be evolutionarily stable.

#### IV. EVOLUTIONARY STABILITY OF DISCRIMINATING STRATEGIES

Each IPD strategy plays specific moves in the interactions with other strategies. The action of a strategy can be identified although there is no information exchange between strategies. With the information of past behaviors, a DS manages to identify the opponent and adopt discriminatory behaviors.

##### A. Discriminating Strategies

A DS adopts an identification mechanism to distinguish between kin members and other strategies, and it cooperates with its kin and defects against others. Thus, the fitness of the group of DSs is maximized while the fitness of other strategies is minimized by means of kin recognition and discriminatory behaviors.

The identification mechanism of DS constitutes a deterministic sequence of *Cooperate* ( $C$ ) and *Defect* ( $D$ ) in  $n$  moves. The opponent is identified according to its actions in  $n$  rounds. If the opponent plays the same sequence of  $C$  and  $D$  moves, it is identified as a kin member, and cooperation will be achieved. Otherwise, it is identified as a non-kin member, and defection will be triggered. The effectiveness of an identification mechanism depends on the special sequence of  $C$  and  $D$  moves. In the worst case, it takes  $n$  rounds for an opponent to be identified as non-kin.

The order of the sequence of moves has a crucial effect on the efficiency of the identification mechanism. For example, an identification mechanism with the sequence of “ $DC\dots$ ” can identify most well-known strategies in two rounds because these strategies seldom play “ $DC$ ” in the first two rounds. If a random sequence is adopted, the probability that a non-kin strategy is identified in  $n$  rounds is  $1 - (1/2^n)$ .

DSs are particularly strong in maintaining a stable population compared with other IPD strategies. Li and Kendall [8] use an invasion barrier to compare IPD strategies and show that a simple DS is evolutionarily stronger than any cooperative and defective strategies such as Tit-For-Tat and AllD. If the majority of a population adopts a DS, any mutant strategy that does not play the deterministic sequence of moves will be defected against and expelled.

A population is in an evolutionarily stable state if its genetic composition is restored by selection after a disturbance, providing that the disturbance is not too large. We use evolutionary IPD to deduce the conditions for a homogenous population of DSs to be in an evolutionarily stable state. In the evolutionary IPD, the agents are randomly paired, and each pair plays an  $n$ -round prisoner’s dilemma. Then, each agent is given the chance to reproduce with probability equal to its aggregated payoff.

##### B. Conditions of Evolutionary Stability

When there are “tags” that denote any heritable indicators of relatedness between kin members, it is possible for a mutant strategy to be recognized before the IPD game. In this circumstance, the condition for a population of a DS to be evolutionarily stable is that its frequency is not less than 0.5.

Assume that there are two types of strategy in the population,  $A$  and  $B$ .  $A$  is a DS, that is, it cooperates with its kin members and defects against any non-kin strategies. Because  $A$  will always cooperate with  $A$  and defect against  $B$ , we have  $E(A, A) = nR$ ,  $E(A, B) \geq nP$ ,  $E(B, A) \leq nP$ , and  $E(B, B) \leq nR$  for any  $B$ . According to (2), we have

$$E_A - E_B \geq (2\rho - 1)n(R - P).$$

Thus,  $E_A > E_B$  always holds if  $\rho > 0.5$ , and there is  $E_A = E_B$  only if  $B$  is also a DS.

When there is no tag, an identification mechanism is needed for a DS to distinguish kin members from non-kin, and the condition of evolutionary stability depends on the effectiveness of the identification mechanism. Let  $A$  denote the DS that cooperates with its kin members and defects against any non-kin strategies. Its mechanism of kin recognition takes  $n$  rounds. Let  $\rho$  denote the frequency of  $A$  in the population. If it takes  $l+m$  ( $1 \leq l+m \leq n$ ) rounds for  $A$  to identify  $B$  as a non-kin where  $l$  denotes the number of  $A$ ’s cooperate choices and  $m$  the number of  $A$ ’s defect choices, the fitness of  $A$  and  $B$  can be expressed by

$$\begin{aligned} E_A &= \rho E(A, A) + (1 - \rho)E(A, B) \\ &\geq \rho(lR + mP + (n - l - m)R) + (1 - \rho)((l - 1)R \\ &\quad + S + mP + (n - l - m)P) \\ E_B &= \rho E(B, A) + (1 - \rho)E(B, B) \\ &\leq \rho((l - 1)R + T + mP + (n - l - m)P) \\ &\quad + (1 - \rho)((l - 1)R + P) \end{aligned}$$

We have

$$E_A - E_B \geq \rho(2(n - l - m)(R - P) + R + P - T - S) - P + S - (n - l - m)(R - P).$$

The condition for  $E_A \geq E_B$  is that

$$\begin{cases} \rho \geq \frac{(n-l-m)(R-P)+P-S}{2(n-l-m)(R-P)+R+P-T-S} \\ n-l-m > \frac{T+S-R-P}{2(R-P)}. \end{cases} \quad (4)$$

This shows that the payoff DS receives is not less than the payoff of the opponent if the opponent can be identified within limited rounds and the frequency of DS is not less than a threshold. The fitness of DS depends on its identification mechanism

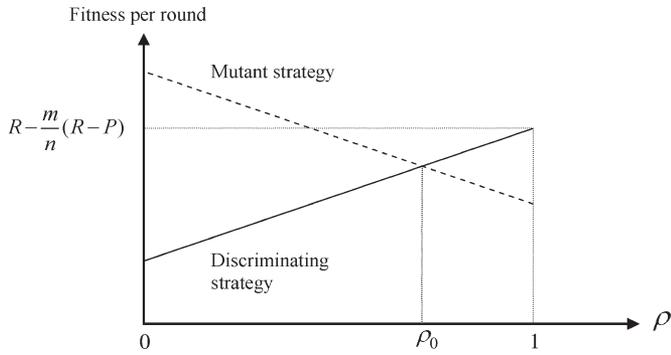


Fig. 2. DS receives higher fitness than any mutant strategies if its frequency  $\rho > \rho_0$  and the mutants can be identified in  $l + m < n - (T + S - R - P/2(R - P))$  rounds.

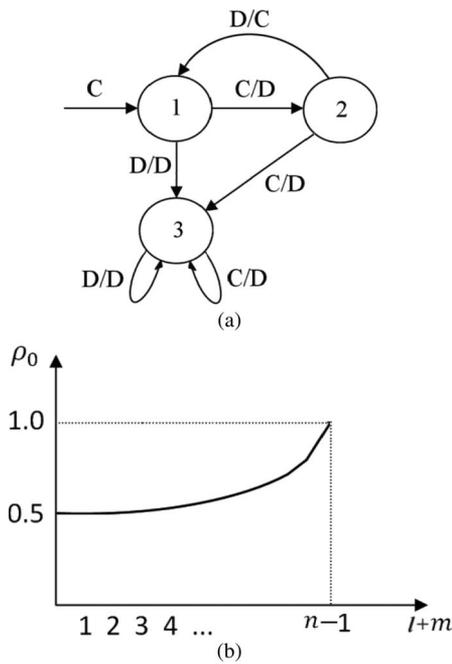


Fig. 3. (a) Finite-state machine of a DS. This strategy plays “C” in the first move. It alternatively plays “C” and “D” when the opponent is a kin member and plays always “D” otherwise. The opponent will be identified to be non-kin if state 3 is reached. (b) The minimum frequency of DS for a group of identified mutants to be expelled.

and its frequency in the population. As shown in Fig. 2, the fitness of DS is positively proportional to its frequency in most cases (the fitness of a DS could be negatively proportional to its frequency if the opponent adopts unconditional cooperative strategies like “always cooperate”). DS reaches the highest fitness,  $R - (m/n)(R - P)$ , when the population is 100% of the DS.

C. Example of DS

As an example, let’s consider a DS with the finite-state machine as shown in Fig. 3(a). This strategy alternatively plays C and D until the opponent is identified to be non-kin. The condition for the strategy to expel an identified mutant can be computed according to (4). When  $T=5, R=3, P=1, S=0, n=50$ , for example, the condition is that  $\rho > \rho_0$  and  $l+m < 50$ . The values of  $\rho_0$  with respect to  $l+m$  are shown in Fig. 3(b).

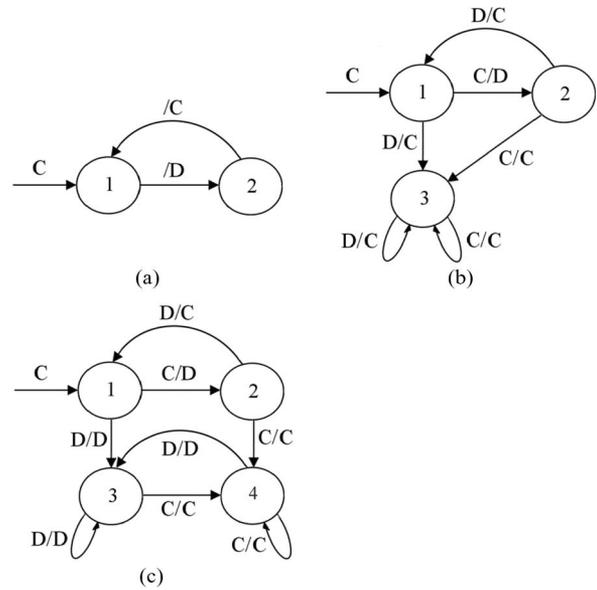


Fig. 4. (a) A deterministic strategy that alternatively plays C and D. (b) This strategy alternatively plays C and D if the opponent does the same. Otherwise, it behaves as “always cooperate.” (c) This strategy alternatively plays C and D if the opponent does the same. Otherwise, it behaves as tit-for-tat.

The situations that DSs cannot handle well is when the opponent cannot be identified within a finite number of rounds, or  $l + m \geq n$ . For example, the DS shown in Fig. 3 cannot correctly identify the strategies shown in Fig. 4. When interacting with the DS, these strategies play the same sequence of C and D as their opponent does. However, they may cooperate with other strategies. DSs cannot resist the invasion of these kin cheaters, and there is the opportunity for other strategies to indirectly invade if the quantity of kin cheaters is significant in the population.

Although the identification mechanisms of DSs fail in identifying kin cheaters, kin cheaters can be expelled by specific strategies in the process of evolution. In the environment where there are periodic invasions of these strategies, kin cheaters will be expelled or reduced to a small number [8]. For example, a mixed population of DS as shown in Fig. 3(a) and the strategies as shown in Fig. 4 tends to be a homogeneous population of DS when there are continuous invasions of AllD. Noise and mutation could also help a population expel kin cheaters. If there are occasional mistakes in the interactions between IPD players, kin cheaters could also be expelled [9]. Under these special conditions, a homogenous population of DSs could remain stable in evolution.

In the following section, we show that the competitions between groups of different DSs help the DSs to expel their kin cheaters, and a steady rate of discriminatory behaviors could be maintained in a heterogeneous population.

V. EVOLUTION OF DISCRIMINATING BEHAVIORS

Once a mechanism of kin recognition is adopted by a species, any mutant strategy that does not play the deterministic sequence of moves will be expelled. A homogenous population of a DS could resist the invasion of a small group of other strategies. With the presence of kin cheaters, the population of

TABLE I  
SIMULATION RESULTS

Identification mechanism	Mutation rate	Extinction rate of DS	Average frequency of DS	Average frequency of kin cheaters	Average payoff	Average rate of cooperation
$m=35$	0.002	0%	0.968	0.032	1.6	29.9%
	0.005	24%	0.451*	0.547*	1.58*	29.7%*
	0.01	86%	0.397*	0.584*	1.47*	26.2%*
$m=25$	0.002	0%	0.693	0.307	1.99	49.7%
	0.005	6%	0.368*	0.629*	1.98*	49.1%*
	0.01	32%	0.343*	0.654*	1.96*	48.2%*
$m=15$	0.002	0%	0.715	0.285	2.59	69.6%
	0.005	0%	0.433	0.566	2.58	69.4%
	0.01	0%	0.327	0.671	2.56	69.2%
$m=10$	0.002	0%	0.689	0.311	2.40	79.7%
	0.005	0%	0.372	0.627	2.38	79.4%
	0.01	0%	0.332	0.665	2.37	78.9%
$m=5$	0.002	0%	0.687	0.313	2.78	89.6%
	0.005	0%	0.367	0.632	2.77	89.4%
	0.01	0%	0.351	0.647	2.76	89.3%

The extinction rate of DS denotes the frequency of the results in that DS is distinct in 50 runs.

\* These values were computed by only taking into account the runs in which DS survived.

the DS is vulnerable to invasions of other strategies, particularly other DSs. The negative effect of kin cheaters is not necessarily the reduction of the cooperation rate or the fitness of the species. Instead, it may increase the fitness of invaders, which weakens the evolutionary stability of the DS.

We first show the negative effect of kin cheaters on the evolutionary stability of the DS in Section V-A. Five types of DSs with different identification mechanisms are chosen as representatives. The processes that a homogeneous population of DS is invaded by their kin cheaters are simulated. We then illustrate that competition between different types of DSs favors a low ratio of kin cheaters in Section V-B. Two or more types of DSs, as well as their kin cheaters, are involved in both evolutionary IPD and spatial IPD. We simulate the situations in which different types of DSs, and their kin cheaters, compete under a range of mutation rates (from 0.002 to 0.02).

#### A. Invasion of Kin Cheaters

Kin cheaters are those strategies with different genotypes but which cannot be identified as non-kin by the recognition mechanism of a species. With the presence of kin cheaters in the population, the evolutionary stability of the DS decreases, and other strategies have the opportunity to indirectly invade.

The simulation begins with a homogeneous population of 10 000 individuals. Three mutation rates, from low to high, 0.002, 0.005, and 0.01 are used in simulations. The mutant strategies are randomly chosen from a set of genotypes that includes most well-known strategies for IPD [39] and some kin cheaters of DS (strategies described in Fig. 4). In each generation, each agent plays each other agent in a 50-round IPD, and then stochastic universal sampling is used to select parents to produce offspring by cloning and mutation. Each

evolution is repeated for 50 runs, and the outcomes are averaged so as to minimize any randomness. We study five types of DSs with different  $m$  values. The  $m$  value denotes the number of defect choices in the sequence of identification mechanisms. For example, the DS shown in Fig. 3 has  $m = 25$ , which means that it chooses to defect 25 times in 50 rounds when interacting with an unknown strategy. The results are shown in Table I.

The frequencies of DS and kin cheaters converge to steady values under a specific mutation rate. As shown in Table I, the frequency of kin cheaters could be high when the mutation rate is high, which means that a population of DSs is vulnerable to invasion by kin cheaters and other strategies under a high mutation rate.

The DSs with high value of  $m$  receive lower average payoff than the DSs with a low value of  $m$ ; therefore, the possibility for them to be replaced by other strategies is high when there has been a significant percentage of kin cheaters in the population. In the case that  $m \geq 25$  and the mutation rate is 0.01, there shows an obvious probability that both the DS and their kin cheaters become extinct. On the other hand, the DSs with very low  $m$  value are more vulnerable to kin cheaters.

Note that the rates of cooperation and defection remain stable no matter what frequency of kin cheaters there are in the population. Fig. 5(a) shows that the DS with  $m = 10$  is dominant in the population when the mutation rate is low. In addition to DS, the rest of the population are all kin cheaters. When the mutation rate is high, the frequencies of kin cheaters could be significant (Fig.5 (b)). In both cases, the rates of cooperation in the population remain stable (about 80%).

The negative effect of kin cheaters on evolutionary stability lies in their cooperating with some mutant strategies, which increases the fitness of both the mutant strategies and kin cheaters. As a result, the frequency of DS decreases.

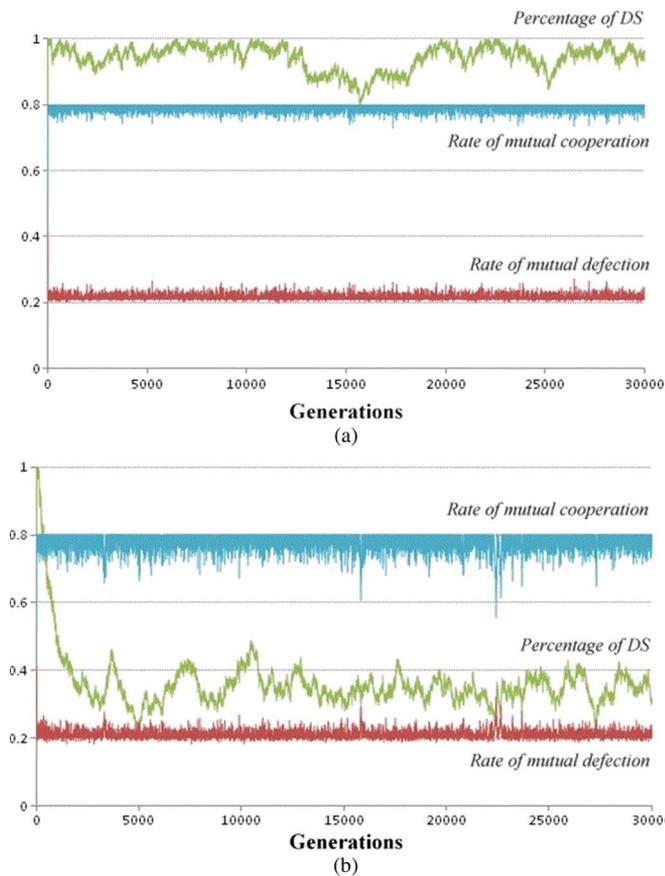


Fig. 5. (a) DS is dominant in the population (with  $m = 10$  and mutation rate 0.001). (b) There is significant percentage of kin cheaters (with  $m = 10$  and mutation rate 0.005).

**B. Competition Between Different DSs**

Consider the situation where there is more than one type of DS in the population. There is competition among different DSs and also competition between DSs and their kin cheaters. Our objective in this subsection is to analyze the effect of two types of competitions on the persistence of cooperation in evolution.

We first simulate the situation in which a homogeneous population of a DS is invaded by some other DSs. The evolution starts with a homogeneous population of 10 000 individuals. The mutation rate is set to be 0.005.

The competition between two DSs is mainly determined by their frequencies in the population. The species with a higher frequency will expel another species. Fig. 6 shows that one DS species expels another when there is a small-frequency difference between two species. The species with lower frequency becomes extinct.

When there are kin cheaters, the species with less kin cheaters will expel those with more kin cheaters. Fig. 7 shows that the DS with  $m = 15$  expels another DS with  $m = 5$  when they are originally equal in quantity but there are more kin cheaters for the latter.

We find that the competitions between different discriminating strategies help to expel kin cheaters. Consider that a population of DS is continuously being invaded by both kin cheaters and some other DSs. Compared with the situation that there is not an invasion of other DSs, the frequency of kin

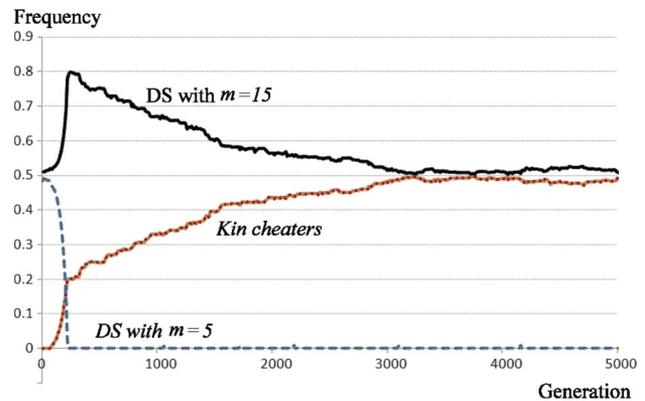


Fig. 6. The DS with higher quantity expels another DS. At the beginning, the frequency of the DS with  $m = 15$  is 0.51, and the frequency of another DS is 0.49. The mutation rate is set to 0.005.

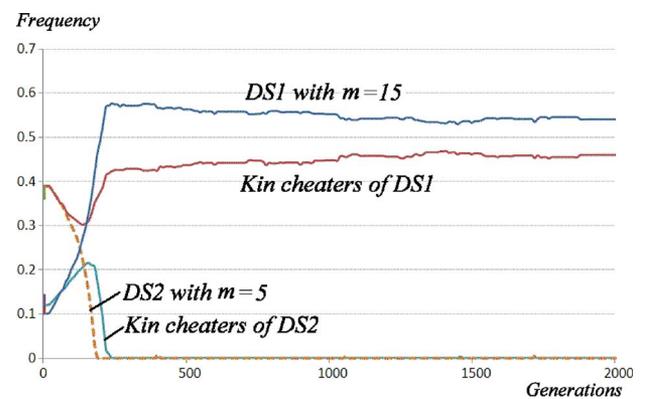


Fig. 7. The DS with less kin cheaters expels another DS with more kin cheaters. The simulation starts with two species. Species one contains DS1 with  $m = 15$  and kin cheaters, whose frequencies are 39% and 10%, respectively. In species two, there are DS2 with  $m = 5$  and kin cheaters, whose frequencies are 39% and 12%, respectively.

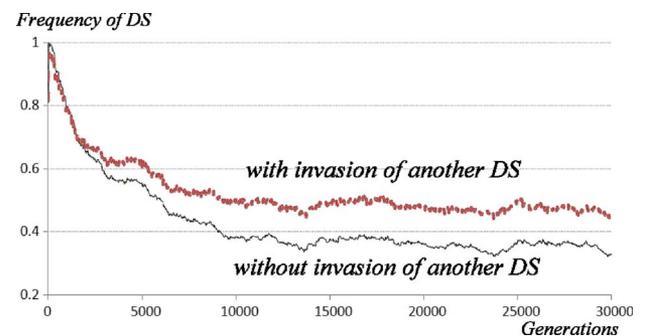


Fig. 8. Invasion of another DS decreases the frequency of kin cheaters. The simulation starts with a population of 80% DS with  $m = 15$  and 20% random chosen strategies. The invading DS is with  $m = 25$ . Mutation rate is set to 0.005.

cheaters is decreased (as shown in Fig. 8). It shows that a type of kin cheater can be expelled by a specific DS. For example, the kin cheaters shown in Fig. 4(a) and (b) can be expelled by the DS that plays  $D$  in the first move. Thus, the kin cheaters could be expelled in the situation where there are continuous invasions of a variety of DSs, as shown in Fig. 9.

It is well accepted that group selection assists the evolution of cooperation. A population is subdivided into groups and each individual only interacts with those in the same group. Individuals reproduce proportional to their payoff. If a group reaches a certain size, it can split into two. In this case, another

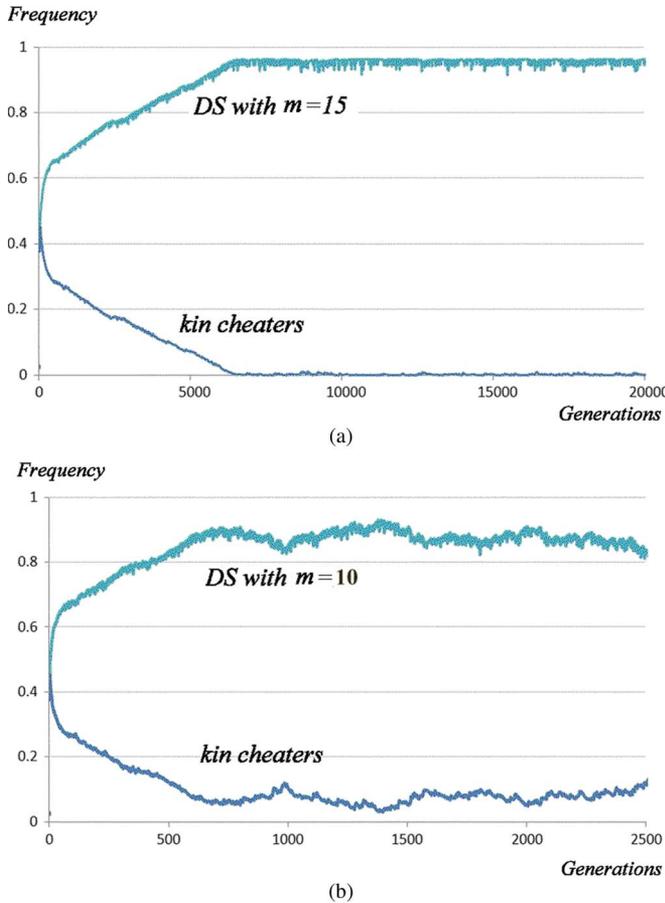


Fig. 9. The kin cheaters are expelled in the environments where there are continuously invasions of a variety of DSs. (a) DS is with  $m = 15$  and mutation rate is 0.005; (b) DS is with  $m = 10$  and mutation rate is 0.01; The simulation starts with a population of 40% DS, 40% kin cheaters, and 20% random chosen strategies.

group becomes extinct in order to constrain the total population size. There are two levels of competition in the population, inter-group competitions and intra-group competitions. On the one hand, cooperation is favored by inter-group competitions because the groups with more cooperators receive higher fitness than the groups with more defectors. On the other hand, defection is favored by intra-group competitions because defectors reproduce faster than cooperators.

The competition between different DSs resembles group selection. The discriminatory behaviors of DSs actually divide the population into groups although no boundary of groups is defined. There are both inter-group competitions between different DSs and intra-group competitions between a DS and its kin cheaters. Inter-group competition favors the group with high average payoff and less kin cheaters. Intra-group competition favors a mixed population of both DS and kin cheaters.

In order to simulate long-term interactions between DSs, a spatial IPD in which each strategy is located in a cell of a 2-D grid is adopted. In spatial IPD, each strategy has its position and only plays IPD with its neighbors. After interactions between neighbors, each site is occupied either by its original owner or by one of the neighbors, depending on who scores the highest total payoff in interacting with its neighbors [25], [40]. The framework of simulation is a  $200 \times 200$  square lattice. Each

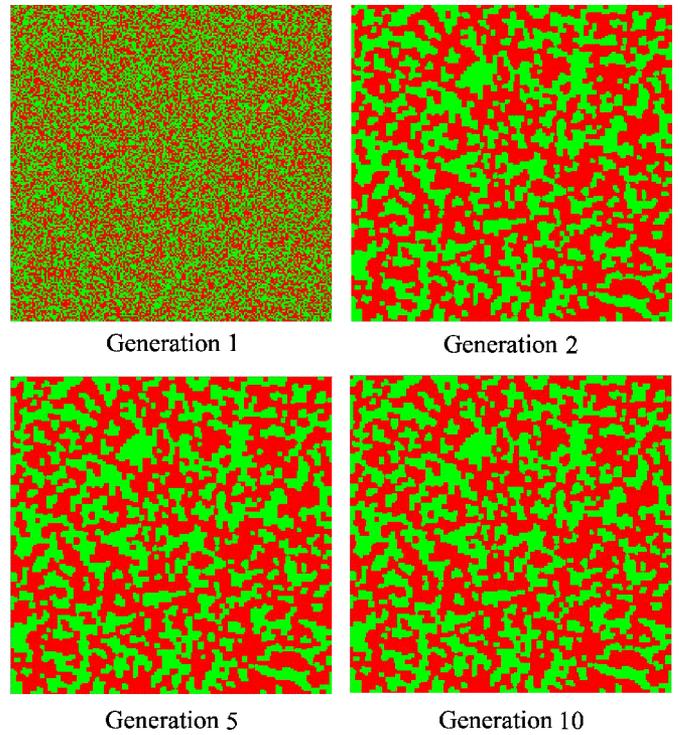


Fig. 10. Two DSs coexist in spatial IPD. Red and green represent DS1 and DS2, respectively. The game starts with a randomly mixed population of 50% DS1 and 50% DS2. No mutation.

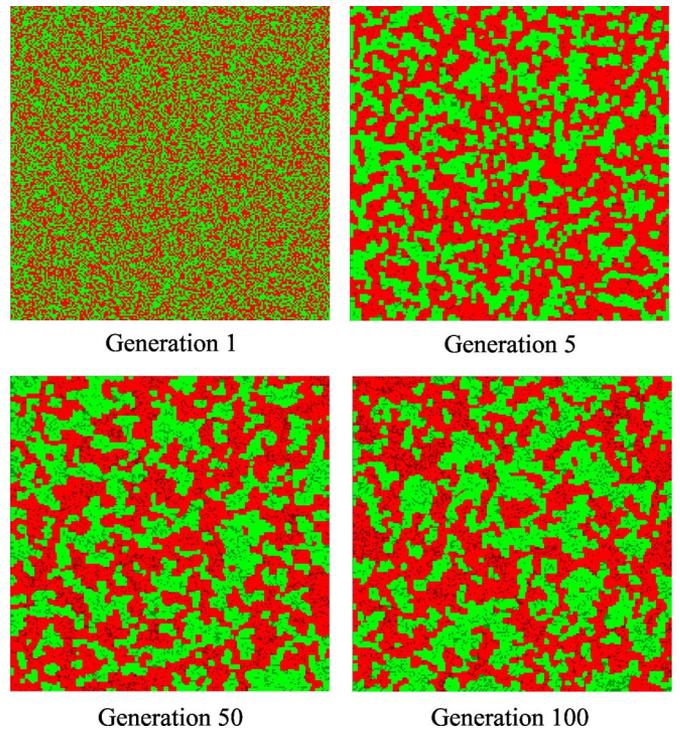


Fig. 11. Two DSs compete in spatial IPD where there are mutations of kin cheaters. Red and green represent DS1 and DS2, respectively. The dark dots represent kin cheaters. The game starts with a randomly mixed population of 50% DS1 and 50% DS2. Mutation rate is 0.02.

strategy occupies a cell and plays 50 rounds of PD with its eight immediate neighbors. In the next generation, an individual cell is occupied with the strategy that received the highest payoff.

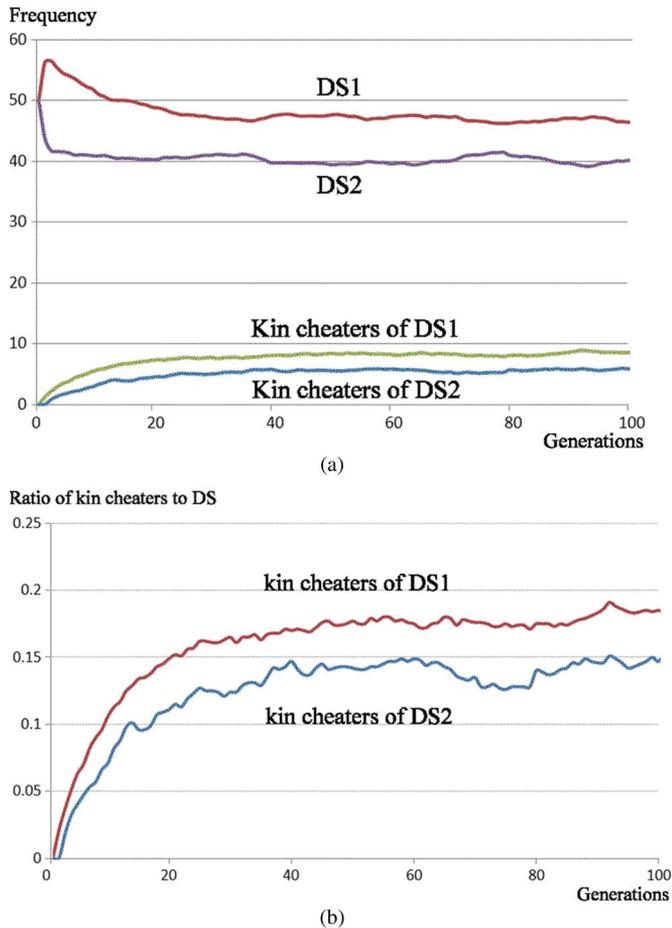


Fig. 12. (a) The frequencies of DSs and kin cheaters remain stable in spatial IPD. (b) The ratio of kin cheaters in DS1 species is higher than the ratio of kin cheaters in DS2 species.

There is also mutation in each generation. That is, the original owner of each cell is, with a small probability, replaced by a randomly chosen mutant strategy.

Fig. 10 shows the situation in which two DSs coexist in spatial IPD. DS1 is with  $m = 15$  and DS2 is with  $m = 10$ . The game starts with a randomly mixed population of 50% DS1 and 50% DS2. After ten generations, it reaches a stable state with 56.6% DS1 and 43.4% DS2.

In the situations where there are mutations of kin cheaters, the game converges to a dynamic equilibrium in which the frequencies of DSs and kin cheaters remain stable (as shown in Figs. 11 and 12). The game starts with 50% DS1 and 50% DS2, and the mutation rate is 0.02. In the equilibrium, the frequency of DS1 is higher than DS2 while the ratio of kin cheaters in DS1 species is higher than that of DS2 species.

With a very high mutation rate (0.2), the frequencies of DSs and kin cheaters still remain stable, as shown in Fig. 13. It shows that the larger group of DS incurs more kin cheaters, so that the smaller group has the chance to survive.

The original make up of the population has limited influence on the equilibrium state with which the game ends. We have tried different original distributions of DSs and find that the game always converges to an equilibrium state with similar frequencies of DSs and kin cheaters. For example, when the

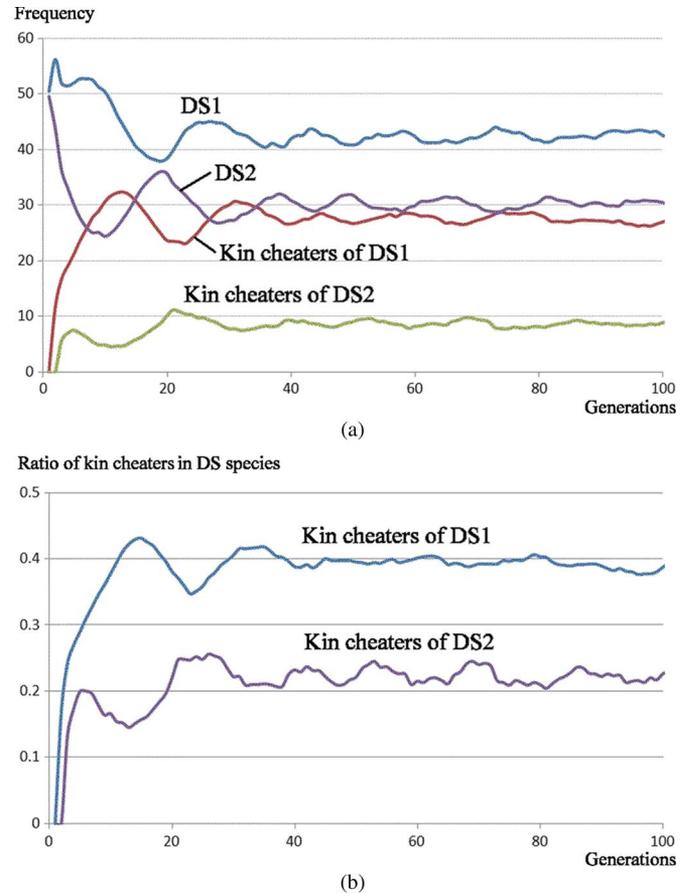


Fig. 13. Mutation rate is set to 0.2. (a) The frequencies of DSs and kin cheaters remain stable. (b) DS1 is with larger group and more kin cheaters than DS2.

original population constitutes 30% DS1 and 70% DS2 and the mutation rate is 0.2, the game converges to a similar state to that of Fig. 13 (as shown in Figs. 14 and 15). In this state, the frequency of every strategy in the population is almost steady, and the rates of cooperation and defection remain stable.

Simulations in this subsection show that kin cheaters could be restrained at a low ratio in the population when there are frequent invasions of various types of DSs, which means that a population of DS could be dynamically stable in specific environments even with the presence of kin cheaters. This conclusion is nontrivial in explaining how cooperation persists in evolution. Discriminating behavior (a specific sequence of cooperation and defection) is evolutionarily stronger than kin altruism because unconditional cooperation is hard to sustain with the presence of kin cheaters.

## VI. CONCLUSION

Discriminating strategies are particularly strong in maintaining a stable population in evolution. By means of an identification mechanism and discriminatory behaviors, a group of DS maximizes the average payoff of kin members and minimizes the payoffs of non-kin members. The payoff of DS is positively proportional to its frequency in the population. Once a discriminatory behavior has been adopted by the majority of the population, other strategies would be expelled, and the

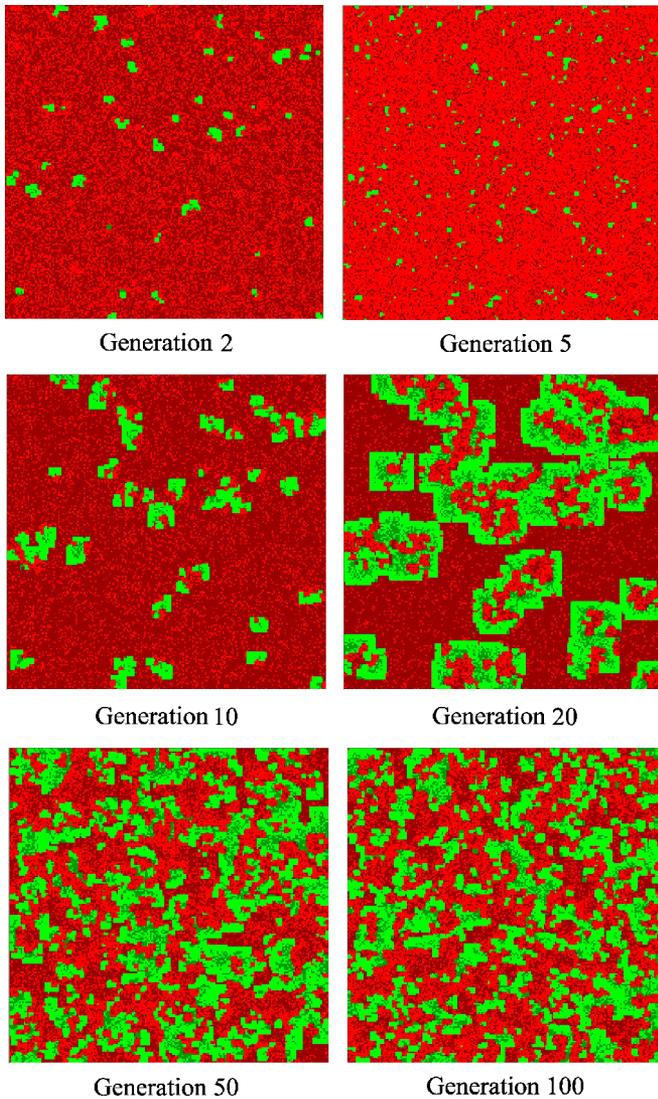


Fig. 14. Game converges to the equilibrium state with steady frequencies of DSs and kin cheaters. Red and green represent DS1 and DS2, respectively. The dark dots represent kin cheaters. The game starts with a randomly mixed population of 30% DS1 and 70% DS2. Mutation rate is 0.2.

rates of cooperation in the population could remain stable. The condition for a homogeneous population of DSs to be in evolutionarily stable state is deduced. It is proved that a group of invaders can be expelled if their strategies could be identified in a limited moves, and their quantity does not exceed a threshold.

Competition of different DSs favor low frequencies of kin cheaters, else DS can be invaded by its kin cheaters. There is the opportunity for other strategies to indirectly invade if the quantity of kin cheaters is significant in the population. We found that the frequencies of kin cheaters could be reduced to a very low level in the environment where there are invasions of a variety of DSs. This assists in explaining how the rate of cooperation could remain stable with the presence of kin cheaters.

There are two levels of competition in the evolution of discriminatory behaviors: competitions between DSs and their kin cheaters and competitions between different DSs. The former favors a steady percentage of kin cheaters in the species, while the latter favors the species with a larger size and less kin cheaters. We find that the joint effect of the competitions leads

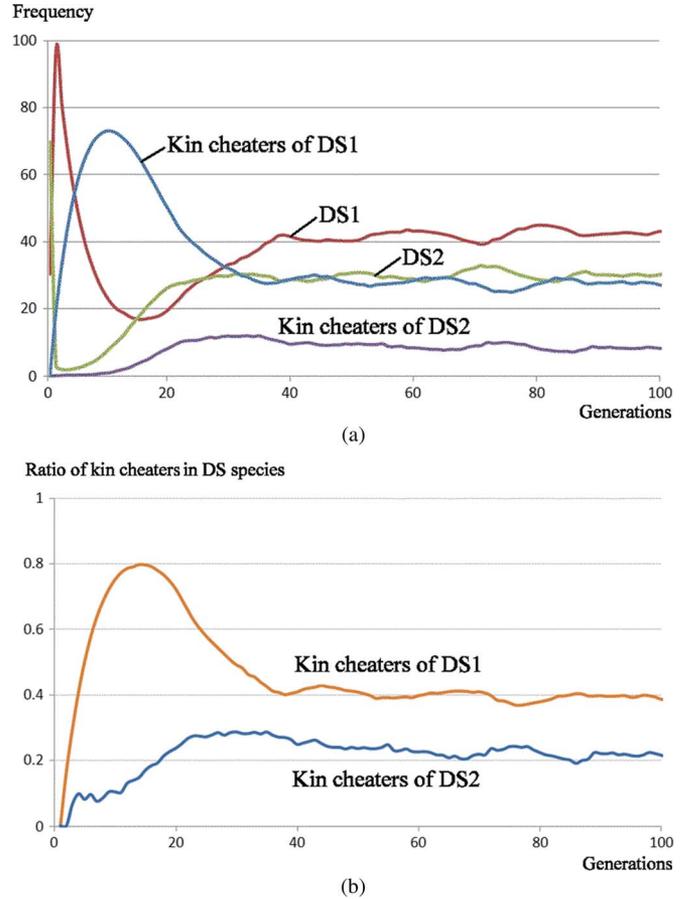


Fig. 15. (a) The frequencies of DSs and kin cheaters. (b) The ratio of kin cheaters. The game starts with a randomly mixed population of 30% DS1 and 70% DS2. Mutation rate is 0.2.

to either a nearly homogeneous population of DSs with small frequency of kin cheaters or a mixed population of different DSs. In both situations, the game converges to some dynamic stable states in which the frequencies of strategies as well as the rate of cooperation remain stable.

Future work can be performed to consider the effect of noise and learning in the evolution of discriminatory behaviors. In a noisy environment, the efficiency of kin identification decreases so that the fitness of DSs decreases. On the other hand, noise restrains kin cheaters from thriving. An investigation of the robustness of DSs in a noisy environment would be interesting. It will also be interesting to study more complex DSs that adopt the learning techniques such as heuristics and mimetic learning.

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