Memory-based snowdrift game on networks

Wen-Xu Wang,^{1,2} Jie Ren,² Guanrong Chen,^{1,*} and Bing-Hong Wang²

¹Department of Electronic Engineering, City University of Hong Kong, Hong Kong SAR, China

²Department of Modern Physics, University of Science and Technology of China, Hefei 230026, China

(Received 16 June 2006; revised manuscript received 4 September 2006; published 28 November 2006)

We present a memory-based snowdrift game (MBSG) taking place on networks. We found that, when a lattice is taken to be the underlying structure, the transition of spatial patterns at some critical values of the payoff parameter is observable for both four- and eight-neighbor lattices. The transition points as well as the styles of spatial patterns can be explained by local stability analysis. In sharp contrast to previously reported results, cooperation is promoted by the spatial structure in the MBSG. Interestingly, we found that the frequency of cooperation of the MBSG on a scale-free network peaks at a specific value of the payoff parameter. This phenomenon indicates that properly encouraging selfish behaviors can optimally enhance the cooperation. The memory effects of individuals are discussed in detail and some nonmonotonous phenomena are observed on both lattices and scale-free networks. Our work may shed some new light on the study of evolutionary games over networks.

DOI: 10.1103/PhysRevE.74.056113

PACS number(s): 89.75.Hc, 02.50.Le, 87.23.Ge

Among the previous work, the effects of individuals'

I. INTRODUCTION

Evolutionary game theory has been considered an important approach to characterizing and understanding the emergence of cooperative behavior in systems consisting of selfish individuals [1]. Such systems are ubiquitous in nature, ranging from biological to economic and social systems. Since the groundwork on repeated games by Axelrod [2], the evolutionary prisoner's dilemma game (PDG) as a general metaphor for studying the cooperative behavior has drawn much attention from scientific communities. Due to the difficulties in assessing proper payoffs, the PDG has some restriction in discussing the emergence of cooperative behavior. Thus, the proposal of the snowdrift game (SG) was generated to be an alternative to the PDG. The SG, equivalent to the hawk-dove game, is also of biological interest [3]. However, in these two games, the unstable cooperative behavior is contrary to the empirical evidence. This disagreement motivates a number of extensions of the original games to provide better explanations for the emergence of cooperation [2,4].

The spatial game, introduced by Nowak and May [5], is a typical extension, which can result in emergence and persistence of cooperation in the PDG. Motivated by the idea of the spatial game, many interests have been given to the effects of spatial structures, such as lattices [6] and networks [8], on cooperative behavior. In a recent paper [9], Hauert and Doebeli found that compared to the PDG, cooperation is inhibited by the spatial structure. The surprising finding is in sharp contrast to one's intuition, since in comparison with the PDG, the SG favors cooperation. More recently, Santos and Pacheco [10] discovered that scale-free networks provide a unified framework for the emergence of cooperation. In addition, Szabó et al. [11] presented a stochastic evolutionary rule to capture the bounded rationality of individuals for better characterizing the dynamics of games in real systems.

056113-1

memory have not received much attention in the study of evolutionary games on networks. We argue that individuals usually make decisions based on the knowledge of past records in nature and society, and the historical memory would play a key role in an evolutionary game. Therefore, in the present work, we propose a memory-based snowdrift game (MBSG), in which players update their strategies based on their past experience. Our work is partially inspired by Challet and Zhang [12], who presented a so-called "minority game," in which agents make decisions exclusively according to the common information stored in their memories. It is found that finite memories of agents have crucial effects on the dynamics of the minority game [13]. We focus on the evolutionary SG for its general representation of many social and biological scenarios. The MBSG on different network structures, including lattices and scale-free networks, is studied. Transitions of spatial patterns with relevant sudden decreases of the frequencies of cooperation are observed in lattices. Local stability analyses are provided for explaining such phenomena. In a scale-free network, cooperation level peaks at a specific value of payoff parameter, which is different from previously reported results. For both lattices and scale-free networks, we found that memory effects play different roles on the frequency of cooperation for distinct ranges of the payoff parameter.

II. THE MODEL

We first briefly describe the original SG model. Imagine that two cars are trapped on either side of a huge snowdrift. Both drivers can either get out of the car to shovel (cooperate: *C*) or stay in the car (defect *D*) in any one negotiation. If they both choose *C*, then they both gain benefit *b* of getting back home while sharing labor *c* of shovelling, i.e., both get payoff b-c/2. If both drivers choose *D*, they will still be trapped by the snowdrift and get nothing. If one shovels (*C*) while the other one stays in the car (*D*), then they both can get home but the defector pays no labor cost and gets a

^{*}Electronic address: gchen@ee.cityu.edu.hk

perfect payoff b, while the cooperator gets b-c. Without losing generality, b-c/2 is usually set to be 1 so that the evolutionary behavior of the SG can be investigated with a single parameter, r=c/2=c/(2b-c). Thus, one has a rescaled payoff matrix

$$\begin{array}{ccc} C & D \\ C & 1 & 1-r, \\ D & 1+r & 0 \end{array}$$

where $0 \le r \le 1$. Though, compared with the PDG, the payoff rank of the SG favors the emergence of cooperation, cooperation is still unstable, which results from the highest payoff of defectors.

Here, we introduce the rules of the evolutionary MBSG. Consider that N players are placed on the nodes of a certain network. In every round, all pairs of connected players play the game simultaneously. The total payoff of each player is the sum over all its encounters. After a round is over, each player will have the strategy information (C or D) of its neighbors. Subsequently, each player knows its best strategy in that round by means of self-questioning, i.e., each player adopts its antistrategy to play a virtual game with all its neighbors, and calculates the virtual total payoff. Comparing the virtual payoff with the actual payoff, each player can get its optimal strategy corresponding to the highest payoff and then record it into its memory. Taking into account the bounded rationality of players, we assume that players are quite limited in their analyzing power and can only retain the last M bits of the past strategy information. At the start of the next generation, the probability of making a decision (choosing C or D) for each player depends on the ratio of the numbers of C and D stored in its memory, i.e., $P_C = \frac{N_C}{N_C + N_D} = \frac{N_C}{M}$ and $P_D = 1 - P_C$, where N_C and N_D are the numbers of C and D, respectively. Then, all players update their memories simultaneously. Repeat the above process and the system evolves.

III. MBSG ON LATTICES

The key quantity for characterizing the cooperative behavior is the frequency of cooperation f_C , which is defined as the fraction of C in the whole population. f_C can be obtained by counting the number of cooperators in the whole population after the system reaches a steady state, at which the number of cooperators shows slight fluctuations around an average value. Hence, f_C is the ratio of the cooperator number and the total number of individuals N. One can easily see that f_C ranges from 0 to 1, where 0 and 1 correspond to cases of no cooperators and entire cooperator state. First, we investigate the MBSG on two-dimensional square lattices of four and eight neighbors with periodic boundary conditions. Simulations are carried out for a population of N=10000individuals located on nodes. Initially, the strategies of C and D are uniformly distributed among all players. The memory information of each player is randomly assigned, and we have checked that this assignment has no contributions to the stable behavior of the system. Each data point is obtained by averaging over 40 different initial states. Figures 1(a) and



FIG. 1. (Color online). The frequency of cooperation f_C as a function of the payoff parameter r for two-dimensional (a) fourneighbor and (b) eight-neighbor lattices, respectively. (\triangle), (\bigcirc), and (\square) are for M=2, 7, and 30, respectively. Each data point is obtained by averaging over 40 different initial states and f_C for each simulation is obtained by averaging from MC time step t=5000 to $t=10\ 000$, where the system has reached a steady state. The top inset of (a) is f_C as a function of memory length M for two different cooperation levels. The bottom inset of (a) is a time series of f_C for r=0.4 in the case of M=1. Since for M=1, f_C as a function of t displays a big oscillation, we do not compute the f_C over a period of MC time steps. The inset of (b) is f_C depending on M for four cooperation levels in the range of 0 < r < 0.5. The network size is $N=10\ 000$.

1(b) show f_C as a function of the parameter r on the lattices of four and eight neighbors, respectively. In these two figures, four common features should be noted: (i) f_C has a step structure, and the number of steps corresponds to the number of neighbors on the lattice, i.e., four steps for the fourneighbor lattice and eight steps for the eight-neighbor lattice; (ii) the two figures have 180°-rotational symmetry about the point (0.5, 0.5); (iii) the memory length M has no influences on the dividing point r_c between any two cooperation levels, but has strong effects on the value of f_C in each level; (iv) for a large payoff parameter r, the system still behaves in a high cooperation level, contrary to the results reported in Ref. [9]. It indicates that although selfish individuals make decisions based on the best choices stored in their memories to maximize their own benefits, the cooperative behavior can emerge in the population in spite of the highest payoff of D.

The effects of memory length M on f_C in the fourneighbor lattice are shown in the insets of Fig. 1. Since f_C is independent of r within each cooperation level, we simply choose a value of r in each level to investigate the influence of M on f_C . Moreover, due to the inverse symmetry of f_C about the point (0.5, 0.5), we concentrate on the range of 0 < r < 0.5. The top inset of Fig. 1(a) reports f_C as a function of M for the ranges of 0 < r < 0.25 and 0.25 < r < 0.5. One can find that f_C is a monotonous function of M for both levels and the decreasing velocity of f_C in the first level is faster than that in the second one. In contrast, in the eightneighbor lattice, f_C exhibits some nonmonotonous behaviors as M increases. As shown in the bottom inset of Fig. 1(b), there exists a minimum f_C in the first level corresponding to M=23, and f_C is an increasing function of M in the second



FIG. 2. Typical spatial patterns in two distinct payoff parameter ranges (a) 0 < r < 0.25, (b) 0.25 < r < 0.5. The *C* is in black and the *D* is in white. A 50×50 portion of the full 100×100 lattice with four neighbors is illustrated. (c) and (d) are the relevant stable local patterns of (a) and (b). W_C and W_D are the payoffs of the center individual A by choosing *C* and *D* with fixing strategies of neighbors for each local pattern. r=0.25 in (c) and 0.5 in (d).

level. A maximum value of f_C exists in the third and fourth levels when M is chosen to be 5, as shown in the top inset of Fig. 1(b). Thus, memory length M plays a very complex role in f_C reflected by the remarkably different behaviors in four cooperation levels. It is worth to point out that in case of M=1, the evolutionary behavior of the system sharply differs from that of M>1, since each individual will definitely adopt the exclusive strategy stored in its memory to play the game at the next time step. A typical example with M=1 for two types of lattices is shown in the bottom inset of Fig. 1(a). A big oscillation of f_C is observed. The unstable behavior will be explained in terms of the evolution of spatial patterns later.

We give a heuristic analysis of local stability for the dividing points r_c of different levels. At each critical point r_c between any two levels, the payoff of an individual with strategy C should equal that of the individual with D. We assume the number of C neighbors of a given node to be *m*, thus in the *K*-neighbor lattice, the quantity of defector neighbor is K-m. Accordingly, we get the local stability equation $m + (K-m)(1-r_c) = (1+r_c)m$, where the left side is the payoff of the given individual with C, and the right side is the payoff of the individual with D. This equation results in $r_c = (K - m)/K$. Considering all of the possible values of m in the four-neighbor lattice, the values of r_c are 0.25, 0.5 and 0.75, respectively. Similarly, the dividing points of the eightneighbor lattice are obtained as $1/8, 2/8, \ldots, 7/8$. As shown in Figs. 1(a) and 1(b), the simulation results are in good accordance with the analytical predictions. Moreover, it should be noted that there exists a sharp decrease of f_C at r_c , which implies the sudden transformation of the evolutionary pattern of the system.

To gain some intuitionistic insights into the evolution of the system, we investigate the spatial patterns for different ron lattices. Figure 2 illustrates typical patterns of two cooperation levels on the four-neighbor lattice. The patterns are



FIG. 3. Typical spatial patterns in two distinct payoff parameter ranges (a) 0.25 < r < 0.375; (b) 0.375 < r < 0.5. The color coding is the same as Fig. 2. A 50×50 portion of the full 100×100 lattice with eight neighbors is illustrated.

statistically static, independent of initial states. Figure 2(a), for 0 < r < 0.25, is a typical spatial pattern of "C lines" against a background of "chessboard" form, i.e., a site is surrounded by antistrategy neighbors. Figure 2(b) is for the range of 0.25 < r < 0.5. In contrast to Fig. 2(a), "C lines" are broken in some places by D sites, and some flowerlike local patterns are observed. The patterns in the ranges of 0.5 < r < 0.75 and 0.75 < r < 1 are the patterns of Figs. 2(b) and 2(a) with C and D site exchanged, respectively, which are not shown here. Therefore, there exist four kinds of spatial patterns with typical features corresponding to four levels of f_C . The pattern formation can be explained in terms of steady local patterns. In Fig. 2(c), we show the steady local patterns existing in the first cooperation level. From the payoff ratio by choosing C and D of individual A, i.e., $W_C: W_D$, the third local pattern is the most stable one with the highest payoff ratio. In parallel, the fourth local pattern is the counterpart of the third one, so that it is also very stable. Hence, the pattern in Fig. 2(a) has a chessboardlike background together with C lines composed of the first and second local patterns. Similarly, the chessboardlike background in Fig. 2(b) is also attributed to the strongest stability of the fourth and fifth local patterns, and the probability of the occurrence of other local patterns is correlated with their payoff ratios. Whereafter, we study the spatial patterns on the eightneighbor lattice. In Fig. 3, we figured out that each cooperation level exhibits a unique pattern and the difference between the patterns of r < 0.5 and r > 0.5 is the exchange of C and D sites. For the first and second levels, D sites take the minority and submerge into the ocean of C sites. While in the third and fourth levels, interesting patterns emerge. As shown in Fig. 3(a), D sites form zonary shapes, surrounded by C lines. Figure 3(b) is for the range of 0.375 < r < 0.5. The pattern shows a shape of labyrinth, and the fraction of C sites is slightly larger than that of D sites. The pattern style can also be explained by the stability of local patterns as that in the four-neighbor lattice.

We have discussed the static patterns on lattices, next we will provide a description of patterns in the case of M=1, where the patterns are unstable, reflected by a big oscillation in the inset of Fig. 1(a). Two typical patterns for M=1 on a four-neighbor lattice are displayed in Fig. 4. One can see that a large fraction of adjacent defectors [denoted by the white



FIG. 4. Typical patterns for the time step t=8001 and t=8002 in the case of memory length M=1, r=0.4. C is in black and D is in white. A 50×50 portion of the full 100×100 lattice with four neighbors is illustrated.

area in Fig. 4(a)] switch to cooperators together at the next time step [denoted by the large area in black in Fig. 4(b)], which contributes to the big oscillation of f_C . The strategyswitch behavior of large proportional individuals can be easily explained by noting the fact that individuals will update their strategies by adopting the exclusive strategy in their memories (M=1). Moreover, individuals record the strategy on the basis of their neighbors' strategy at the last time step. In the strategy-switch area, individuals have identical strategies at each time step. Therefore, at the next step, each individual should choose the antistrategy of its neighbors to gain more payoffs since each one only records its last step's history. Once the drastic strategy switch occurs, it will maintain forever.

In addition, we should briefly introduce a recent work of Sysi-Aho *et al.* [7], which is correlated with the present MBSG model. In Ref. [7], the authors proposed a spatial snowdrift game played by myopic agents. In such model, lattices are used and each individual can adopt its current anti-strategy at the next time according to its neighbors' strategies with a probability p. Similar spatial patterns are observed for eight-neighbor lattices, as well as the step structure of f_C depending on r. However, we note that p in this model nearly has no effect on the cooperative behavior, while in our model the memory length M plays different roles in each cooperation level. Furthermore, in the case of no memory length, i.e., M=1, our model doesn't recover the spatial snowdrift game with myopic agents, confirmed by the big oscillation of f_C in the inset of Fig. 1(a).

IV. MBSG ON SCALE-FREE NETWORKS

Going beyond two-dimensional lattices, we also investigate the MBSG on scale-free (SF) networks, since such structural property is ubiquitous in natural and social systems. Figure 5 shows the simulation results on the Barabási-Albert networks [14], which are constructed by the preferential attachment mechanism. Each data point is obtained by averaging over 30 different network realizations with 20 different initial states of each realization. Figures 5(a1) and 5(a2) display f_C depending on r on BA networks in the cases of average degree $\langle k \rangle = 4$ and $\langle k \rangle = 8$ for different memory



FIG. 5. (Color online) f_C as a function of r in BA networks with (a1) average degree $\langle k \rangle = 4$ and (a2) $\langle k \rangle = 8$ for different M. A time series of f_C for M = 1 is shown in the inset of (a2). (b1) and (b2) are f_C as a function of M in the case of $\langle k \rangle = 4$ and $\langle k \rangle = 8$ for a special range of r. (c1) and (c2) are average degrees $\langle k_s \rangle$ of C and D players depending on r in the case of M = 7 for $\langle k \rangle = 4$ and $\langle k \rangle = 8$, respectively. The network size is 10 000. Each data point is obtained by averaging over 30 different network realizations with 20 different initial state of each realization. f_C for each simulation is obtained by averaging from MC time step t = 5000 to $t = 10\,000$, where the system has reached a steady state.

lengths M. There are some common features in these two figures. (i) In sharp, contrast to the cases on lattices, f_C is a nonmonotonous function of r with a peak at a specific value of r. This interesting phenomenon indicates that properly encouraging selfish behaviors can optimally enhance the cooperation on SF networks. (ii) It is the same as the cases on lattices that the continuity of f_C is broken by some sudden decreases. The number of continuous sections corresponds to the average degree $\langle k \rangle$. (iii) Two figures have a 180° -rotational symmetry about the point (0.5, 0.5). (iv) The memory length M does not influence the values of r, at which sudden decreases occur, as well as the trend of f_C , but affects the values of f_C in each continuous section. Then, we investigate the effect of M on f_C in detail. Due to the inverse symmetry of f_C about point (0.5,0.5), our study focus on the range of 0 < r < 0.5. We found that in both SF networks, there exists a unique continuous section, in which M plays different roles in f_C . For the case of $\langle k \rangle = 4$, the special range is from r=0.34 to 0.49, as shown in Fig. 5(a1). In this region f_C as a function of M is displayed in Fig. 5(b1). One can find that for r=0.42, f_C is independent of M. For 0.34 < r < 0.42, f_C is a decreasing function of *M*; while for $0.42 \le r \le 0.49$, f_C becomes an increasing function of M. Similar phenomena are observed in the SF network with $\langle k \rangle = 8$, as exhibited in Fig. 5(b2). r = 0.45 is the dividing



FIG. 6. Distributions of strategies in BA networks. Cooperators and defectors are denoted by gray bars and black bars, respectively. Each bar adds up to a total fraction of 1 per degree, the gray and black fractions being directly proportional to the relative percentage of the respective strategy for each degree of connectivity k. (a) is for the case of $\langle k \rangle = 4$ with r=0.1 and (b) is for the case of $\langle k \rangle = 4$ with r=0.49, at which f_C peaks. (c) shows the case of $\langle k \rangle = 8$ with r=0.05 and (d) displays the case of $\langle k \rangle = 8$ with r=0.16, which corresponds to the maximum value of f_C . All the simulations are obtained for network size N=1000 in order to make figures clearly visible.

point, and for r < 0.45 and r > 0.45, f_C shows decreasing and increasing behaviors respectively as M increases. In the case of M=1, the system has big oscillations as shown in the inset of Fig. 5(a2). Similar to the cases on lattices, the behavior of large proportion of individuals' strategy switches that induces the big oscillation of f_C in the SF network.

In order to give an explanation for the nonmonotonous behaviors reported in Figs. 5(a1) and 5(a2), we study the average degree $\langle k_s \rangle$ of cooperators and defectors depending on r. In Figs. 5(c1) and 5(c2), $\langle k_s \rangle$ of D vs r shows almost the same trend as that of f_C in Figs. 5(a1) and 5(a2), also the same sudden decreasing points at specific values of r. When r is augmented from 0, large-degree nodes are gradually occupied by D, reflected by the enhancement of D's $\langle k_s \rangle$. The detailed description of the occupation of nodes with given degree can be seen in Fig. 6. One can clearly find that on the four-neighbor lattice, in the case of low value of f_C [Fig. 6(a)], almost all high degree nodes are occupied by cooperators and most low degree nodes are occupied by defectors; while at the peak value of f_C [Fig. 6(b)], cooperators on most high degree nodes are replaced by defectors and on low degree nodes cooperators take the majority. Similarly, as f_{c} increases in the eight-neighbor lattices, defectors gradually occupy those high degree nodes, together with most very low degree nodes taken by cooperators [Figs. 6(c) and 6(d)]. Moreover, note that in SF networks, large-degree nodes take the minority and most neighbors of small-degree nodes are those large-degree ones, so that when more and more largedegree nodes are taken by D, more and more small-degree nodes have to choose C to gain payoff 1-r from each D neighbor. Thus, it is the passive decision making of smalldegree nodes which take the majority in the whole populations that leads to the increase of f_C . However, for very large r, the poor benefit of C results in the reduction of f_C . Therefore, f_C peaks at a specific value of r on SF networks. In addition, it is worthwhile to note that in the case of high f_C , the occupation of large degree nodes in the MBSG on SF networks is different from the recently reported results in Ref. [15]. The authors found that all (few) high degree nodes are occupied by cooperators, whereas defectors only manage to survive on nodes of moderate degree. While in our work, defectors take over almost all high degree nodes, which induces a high level of cooperation.

V. CONCLUSION

In conclusion, we have studied the memory-based snowdrift game on networks, including lattices and scale-free networks. Transitions of spatial patterns are observed on lattices, together with the step structure of the frequency of cooperation versus the payoff parameter. The memory length of individuals plays different roles at each cooperation level. In particular, nonmonotonous behavior are found on SF networks, which can be explained by the study of the occupation of nodes with give degree. Interestingly, in contrast to previously reported results, in the memory-based snowdrift game, the fact of high degree nodes taken over by defectors leads to a high cooperation level on SF networks. Furthermore, similar to the cases on lattices, the average degrees of SF networks is still a significant structural property for determining cooperative behavior. The memory effect on cooperative behavior investigated in our work may draw some attention from scientific communities in the study of evolutionary games.

ACKNOWLEDGMENTS

This work is funded by the Hong Kong Research Grants Council under the CERG Grant CityU No. 1114/05E and by the National Natural Foundation of China under Grant Nos. 704710333, 10472116, 10532060, 70571074, 10547004, and 10635040.

 A. M. Colman, Game Theory and its Applications in the Social and Biological Sciences (Butterworth-Heinemann, Oxford, 1995). York, 1984).

- [3] R. Sugden, *The Economics of Rights, Co-operation and Wel-fare* (Blackwell, Oxford, UK, 1986).
- [2] R. Axelrod and W. D. Hamilton, Science 211, 1390 (1981); R. Axelrod, *The Evolution of Cooperation* (Basic Books, New Cooperation)
- [4] M. Nowak and K. Sigmund, Nature (London) 355, 250 (1992); 364, 1 (1993).

- [5] M. Nowak and R. M. May, Nature (London) **359**, 826 (1992);
 Int. J. Bifurcation Chaos Appl. Sci. Eng. **3**, 35 (1993).
- [6] M. Doebeli and N. Knowlton, Proc. Natl. Acad. Sci. U.S.A. 95, 8676 (1998); T. Killingback, M. Doebeli, and N. Knowlton, Proc. R. Soc. London, Ser. B 266, 1723 (1999); T. Killingback and M. Doebeli, J. Theor. Biol. 191 (3), 335 (1998); Li-Xin Zhong et al., e-print physics/0602039.
- [7] M. Sysi-Aho et al., Eur. Phys. J. B 44, 129 (2005).
- [8] G. Abramson and M. Kuperman, Phys. Rev. E 63, 030901(R) (2001); B. J. Kim *et al.*, *ibid.* 66, 021907 (2002); H. Ebel and S. Bornholdt, *ibid.* 66, 056118 (2002); Z.-X. Wu *et al.*, *ibid.* 71, 037103 (2005); 74, 021107 (2006).

- [9] C. Hauert and M. Doebeli, Nature (London) 428, 643 (2004).
- [10] F. C. Santos and J. M. Pacheco, Phys. Rev. Lett. 95, 098104 (2005).
- [11] G. Szabó and C. Töke, Phys. Rev. E 58, 69 (1998); G. Szabó and C. Hauert, Phys. Rev. Lett. 89, 118101 (2002); G. Szabó and J. Vukov, Phys. Rev. E 69, 036107 (2004).
- [12] D. Challet and Y.-C. Zhang, Physica A 246, 407 (1997); 256, 514 (1998).
- [13] D. Challet *et al.*, J. Stat. Mech.: Theory Exp. (2005) P03004;
 P. Jefferies *et al.*, Eur. Phys. J. B 20, 493 (2001).
- [14] A.-L. Barabási and R. Albert, Science 286, 509 (1999).
- [15] F. C. Santos and J. M. Pacheco, J. Evol. Biol. 19, 726 (2006).