Article

Chinese Science Bulletin

SPECIAL ISSUE
Adaptive Evolution and Conservation Ecology of Wild Animals

June 2013 Vol.58 No.18: 2248–2254
doi: 10.1007/s11434-013-5810-6

Spatial games and the maintenance of cooperation in an asymmetric Hawk-Dove game

HE JunZhou[1,2], ZHAO Yue[3], CAI HengJin[3*] & WANG RuiWu[2*]

[1] *Statistics and Mathematics School, Yunnan University of Finance and Economics, Kunming 650221, China;*
[2] *Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming 650223, China;*
[3] *International School of Software, Wuhan University, Wuhan 430079, China*

Received October 22, 2012; accepted February 20, 2013; published online May 3, 2013

Classical theories explaining the evolution of cooperation often rely on the assumption that the involved players are symmetrically interacted. However, in reality almost all well-documented cooperation systems show that cooperative players are in fact asymmetrically interacted and that this dynamic may greatly affect the cooperative behavior of the involved players. Here, we developed several models based on the most well known spatial game of the Hawk-Dove game, while also considering the effects of asymmetric interaction. Such asymmetric games possess four kinds of strategies: cooperation or defection of strong player and cooperation or defection of weak player. Computer simulations showed that the probability of defection of the strong player decreases with decreasing the benefit to cost ratio, and that all kinds of strategy will be substituted by cooperation on behalf of the strong player if the benefit to cost ratio is sufficiently small. Moreover, weak players find it difficult to survive and the surviving weak players are mostly defectors, similar to the Boxed Pigs game. Interestingly, the patterns of kinds of strategies are chaotic or oscillate in some conditions with the related factors.

asymmetric interaction, cooperation, spatial games, Hawk-Dove game

Citation: He J Z, Zhao Y, Cai H J, et al. Spatial games and the maintenance of cooperation in an asymmetric Hawk-Dove game. Chin Sci Bull, 2013, 58: 2248–2254, doi: 10.1007/s11434-013-5810-6

Explaining how different individuals or units could be coherent to a functional unit (i.e. how an individual organism or group fit in within a cooperation system) remains one of the most elusive questions in biology. In genetics, if genes do not cooperate but over-exploit the resource of other genes by over-copying itself, the healthy tissue or organism becomes a tumor or cancer [1]. Similarly, if individuals within a group, team or society do not cooperate and over-exploit the common resources at the expense of others, the group, team or society will be disrupted [2]. This problem is equally true for species within an eco-system, since other studies have shown that almost all the species cooperate with at least one other species [3]. The eco-systems could not have evolved in to a functional unit if without cooperation [4,5].

*Corresponding authors (email: wangrw@mail.kiz.ac.cn; hjcai@whu.edu.cn)

Although cooperation interactions are one of the basic existence in both biological and social systems, the fundamental conundrum is why selfish individuals, or any other unit for that matter, do not over-exploit common resources at the expense of others, thereby disrupting the cooperation systems, especially when the common resource utilization are saturated, even when the interacted individuals are highly genetically or reciprocally related [6,7]. Classical explanatory theories including kin selection (i.e. Hamilton's rule), reciprocity selection (i.e. Iterated Prisoners' Dilemma) or group selection, argued, with the idea of the "contract", that spatial heterogeneity of the common resources or self-restraint will maintain the cooperation interaction when the conflict for the common resource exist among cooperative partners [5,8–11]. These theories suggested maintaining mechanisms, however, encounter an unsolvable problem: why do both mutants that could overcome the spatial heterogeneity or abandon the self-restraint do not reproduce and pass their behaviors down to their offspring or continue their actions? Logically, such a mutant or more selfish individuals lacking self-restraint should be able to utilize the common resources at the expense of others, receiving a benefit advantage after the saturation of the common resource utilization [2,5,12].

However, recent findings—especially in the experimental evidence of one of the most famous inter-specific cooperation between fig and its obligate pollinators—that spatial heterogeneity and self-restraint are not credible mechanisms to maintaining a cooperation system [5,13,14]. The empirical data in fig-fig wasp systems suggested that the asymmetric interaction between cooperative actors and the recipient might be a critical mechanism in maintaining the cooperation, but such an asymmetric interaction may potentially lead to indeterminate interaction (e.g., chaotic interaction) between the cooperative actors and the recipient. Such asymmetric interactions that may maintain the cooperation have also been implied to exist in other inter-specific cooperation [15,16], and intra-specific cooperation systems including ants, bees and a society of mammals [17–19]. Here, we modified this understanding of how asymmetric interaction maintains the cooperative interaction between the cooperative actors and recipients, based on one of the most well-known models, the Hawk-Dove game. Likewise, we explain how the cooperative interaction between cooperative actors and recipient chaotically vary or oscillate based on the change of related factors.

1 Background of the Hawk-Dove model

The Iterated Prisoners' Dilemma (IPD) is widely used to explain the evolution of cooperation [8,11]. In IPD, when they receive cooperation behavior from donors, cooperating and not defecting with counter partners becomes the predominant strategy for any involved players via Tit-for-Tat in a repeated game. This unique cooperating strategy for any players in IPD model does not, in fact, conform to real cooperation systems. In almost all real cooperation systems, ranging from the eusocial-society of insects to inter-specific cooperation systems, almost all cooperative partners take a mixed strategy of either cooperating or competing with their counter-partners [13,18,20–23]; as the same is true in the genetic expression of a coherent cell [24].

An alternate but equally famous model describing the evolution of cooperation is the Hawk-Dove game (HDG). In HDG, the payoff of different strategies satisfy $T>R>S>P$, differing from IPD in which the payoff satisfies $T>R>P>S$ and $2R>T+S$, where T and S are the respective payoffs of the defector and cooperator in the circumstance of unilateral cooperation, while R (P) are the payoff of cooperators (defector) during mutual cooperation (defection) [8,11,24]. The reverse between the payoffs P and S in the Hawk-Dove model fundamentally changes situation of the evolution of cooperation. In IPD, the recipient will predominantly reward the original donor because of the reciprocal exchange and Tit-for-Tat in the indefinitely iterated game between the recipient and donors. Taking a cooperative strategy will the predominant strategies for the involved partner of the cooperation systems in such a game. However, in HDG, the involved partners take a mixed strategy of either cooperation or defection, but not a pure strategy of cooperation, greatly differing from IPD. Assumptions that players in cooperation strategies will opt for mixed strategies is likewise more reasonable when examining real cooperation systems. Based on HDG, we would like to exploit how asymmetric interactions between the recipient and cooperative donor affect the cooperative behavior.

2 Model assumption and simulation

The Hawk-Dove model imagines that two players (e.g., gene of chromosome, individuals of animals, different species, etc.) are contesting a resource of value (v). Each player simultaneously decides whether to "Hawk" (i.e., defect, marked H) or "Dove" (i.e., cooperate, marked D). The game has four strategy profiles: (H, H), (H, D), (D, H), (D, D). The payoff of each player depends on both its own actions and those of its counter-partner. In the classical model based on pairwise and symmetric interaction between the players, there are four possible values for this payoff. The two cooperators thus get a *reward* ($R=v/2$) while two defectors receive a *punishment* ($P=(v-c)/2$) because mutual defection involves a cost (c) to both players. The trade between a cooperator and a defector gives *temptation* ($T=v$) for the latter, while the former receives the s*ucker's payoff* ($S=0$) [14,24].

In classic HDG, the co-players' strength is equal; however, most actual contests are asymmetric interactions. The interacting players may be different in size or strength, influencing the outcome of the game [21,24]. In asymmetric cooperation systems, the payoff for the players may depend on their strength and the strength ratio of the two players, k:(1−k) therefore describes the degree of asymmetry between the interacting players, here k and 1−k can be the percentage of resources dominated by each player, the probability of winning the fight with others, or any other parameters similarly characterized by an interaction between a dominate and sub-ordinates. We likewise assume that the cost (c) of defecting is greater than the benefit (v) of cooperation. If both then cooperate, their payoff depends on their strength, that is, $R_S=kv$, $R_W=(1-k)v$. If both defect, the injury level of players is inversely proportional to their strength, namely, $P_S=(v-c)/4k$, $P_W=(v-c)/4(1-k)$. Here, the indices "S" and "W" represent "the strong players" and "the weak players", respectively. In this payoff assumption, the payoff of each strategy will transform to the payoff of the classic Hawk-Dove game if k=0.5. With unilateral cooperation, the player's payoff is the same with that in the classic HDG model. According to the above assumptions, the payoff matrix is as shown in Table 1 [14].

Here, we analyzed the effects of asymmetric interaction and the benefit to cost ratio in spatial games via the asymmetric Hawk-Dove game. Classical spatial game theory does not include the effects of asymmetric interaction of individuals [24–28]. Considering these effects, we propose four simple kinds of strategies: defection of the strong player, cooperation of the strong player, defection of the weak player and cooperation of the weak player. These four strategies can be denoted by vectors as S^H=(1,0,0,0), S^D=(0,1,0,0), W^H=(0,0,1,0), W^D=(0,0,0,1), respectively. Using the method of Nowak and May [26], we explored the spatial array in the asymmetric Hawk-Dove game: in each round, every individual "plays the game" with its immediate neighbors. Afterward, each site is occupied either by its original owner or by one of the neighbors, depending on who scores the highest total in that round, and so on through the next round of the game [26]. This rule is named win-stay and lose-shift [27]. In order to calculate the scores of each player, we used the transformation of Harsnyi [29], based on Table 1, and created a new payoff matrices of the spatial game (Table 2).

Table 2 can be denoted by matrix as

$$A=\begin{bmatrix} (v-c)/2 & v & (v-c)/4k & v \\ 0 & v/2 & 0 & kv \\ (v-c)/4(1-k) & v & (v-c)/2 & kv \\ 0 & (1-k)v & 0 & v/2 \end{bmatrix}.$$

Then the total score of player i is

$$f_i=\sum_{j\in\Pi_i} x_i A x_j^T .$$

Here x_i is the vector of the kind of player i and x_j^T is transposition vector of strategy of player j, it can be S^H=(1,0,0,0) or S^D=(0,1,0,0) or W^H=(0,0,1,0) or W^D=(0,0,0,1); and Π_i is the neighbor set of player i.

For convenience, the degree of asymmetry can be mathematically defined by $h=k/(1-k)$, where k and $1-k$ are the respective strengths of dominates and sub-ordinates [14]. In HDG, the benefit to cost ratio (m) can also greatly affect the cooperation probability [14,30], where the $m=v/c$, and v and c are respectively the benefit of the resource and the cost of defect. In this model, it is interesting to explore how asymmetric interactions and the benefit to cost ratio intrinsically affect individual behavior in a cooperation systems under the fundamental mechanism of win-stay, lose-shift; wherein the win-stay and lose-shift is widespread rule in spatial evolution of cooperation [27,31].

3 Results and discussion

Considering the asymmetric payoff between the cooperative partners in HDG, our developed model shows that involved partners will change their strategies in different situations (e.g., difference in the benefit to cost ratio and the degree of asymmetry between strong and weak players). The simulations we illustrated showed that the cooperation of strong player, the defection of weak player, the defection of strong player could coexist if the benefit to cost ratio is lower than 1/2, but it should not be too small (e.g., m=1/2, 1/4, 1/7 in Figure 1 *Lower*); whereas, if the benefit to cost ratio is sufficient small (e.g., m=1/8 in Figure 1 *Lower* and Figure 2(a)), all kinds of strategy will be substituted by the cooperation of strong player. However, most of the involved partners will be substituted by the defection of strong player if the benefit to cost ratio is great (e.g. b/c is equal to 0.99 in Figure 1). The benefit to cost ratio can be seen as an important factor for limited dispersal or exit cost of cooperation systems. The less limited dispersal or more exit cost for the involved individuals, the more difficult it would be for the involved individuals to disperse to other colonies or groups [14,32]. More precisely, decreasing the limited dispersal or increasing exit cost for players in a system (i.e., decreasing the benefit to cost ratio, Figure 1), the cooperative participants may accordingly tend to cooperate in such a system.

We went further and simulated how the degree of asymmetry and the benefit to cost ratio affect the frequency of each kind of strategy in this model. Given the degree of asymmetry, the probability of cooperation of strong player will increase with the increasing benefit to cost ratio, but the other three strategies will subsequently decrease (Figure 3). Moreover, if the benefit to cost ratio is given, the probability of defection by the strong player reduces with increasing the degree of asymmetry, while the probability of defection of weak player increases; however, the probability of cooperation of strong and weak players are almost invariable under the variation of degree of asymmetry (Figure 4). Here,

Table 1 Payoff matrices for the asymmetric Hawk-Dove game

		Weak player	
		Hawk (*H*)	Dove (*D*)
Strong player	Hawk (*H*)	(($v-c$)/4k, ($v-c$)/4(1$-k$))	(v, 0)
	Dove (*D*)	(0, v)	(kv, (1$-k$)v)

Table 2 Payoff matrices for the symmetric after transformation of asymmetric Hawk-Dove game[a)]

		Player B			
		S^H	S^D	W^H	W^D
Player A	S^H	($v-c$)/2	v	($v-c$)/4k	v
	S^D	0	v/2	0	kv
	W^H	($v-c$)/4(1$-k$)	v	($v-c$)/2	v
	W^D	0	(1$-k$)v	0	v/2

a) Payoff is same to the classic HDG model when strong counter strong players or weak counter weak players, viz. the payoff of both players is symmetric. Additionally, parameters satisfy k>0.5 and v<c.

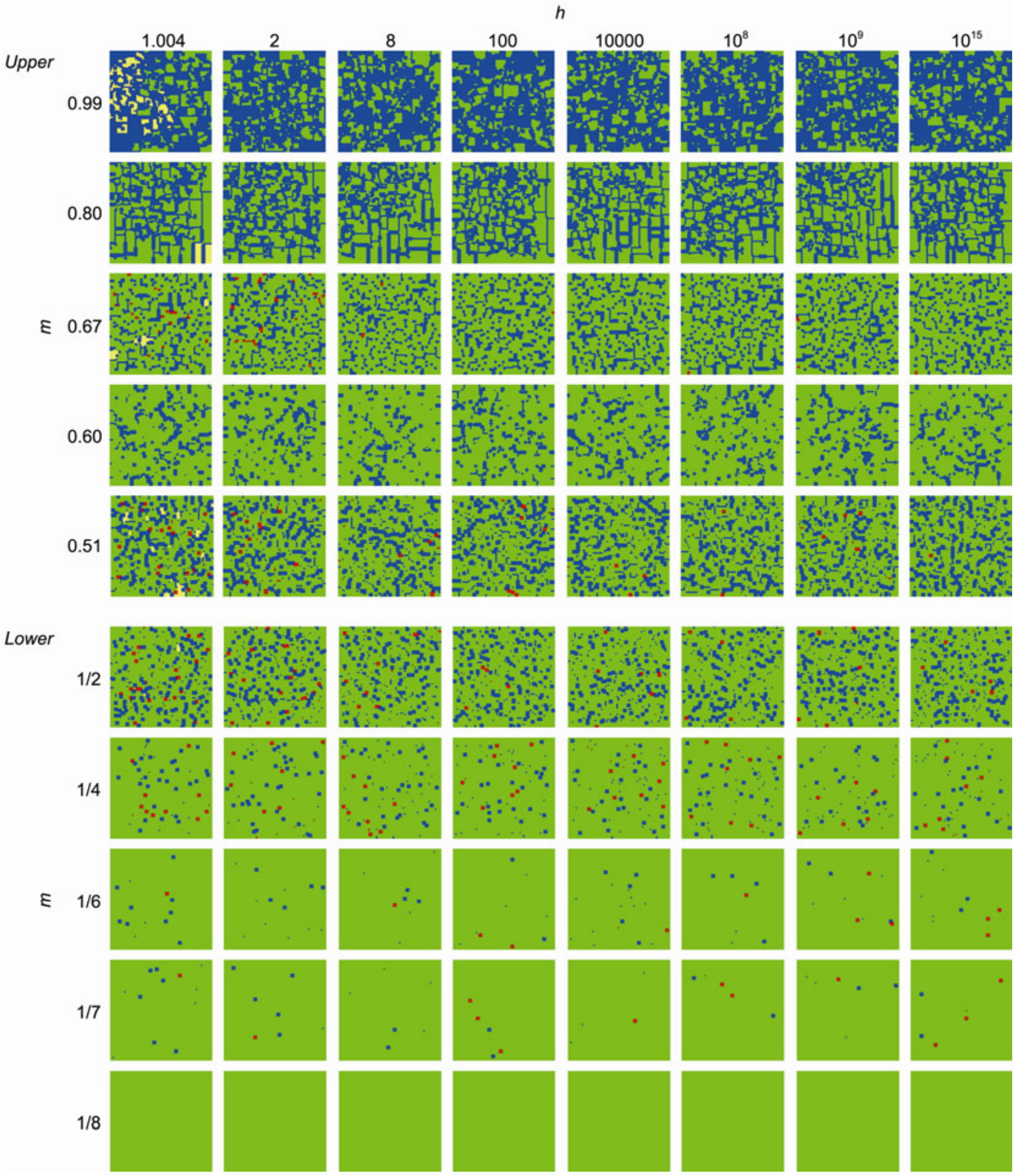

Figure 1 Spatial dynamics of four strategy players for discrete time simulations in the asymmetric spatial Hawk-Dove game. Simulations were performed on an 200×200 square lattice with periodic boundaries. Interaction occurs between the eight nearest neighbors and also includes self-interaction. Each picture shows the spatial distribution after 100 generations. The parameter *m* denotes the benefit to cost ratio (*b*/*c*) and *h* denotes the degree of asymmetry (*k*/(1−*k*), here *k*>0.5). Color codes are as follows: blue, defection of strong player (S^H); green, cooperation of strong player (S^D); red, defection of weak player (W^H); yellow, cooperation of weak player (W^D). The benefit of cooperation (*v*) is fixed at 1 and the initial value of the four strategies for all simulation is fixed at 0.25.

it is necessary to point out that the initial values for each of the four strategies are equal to 0.25 while the ratio of benefit to cost is lower than 1/2 in the above simulations.

Interestingly, when the benefit to cost ratio is greater than 1/2, the changing spatial patterns of each strategy present chaotic (Figure 1 *Upper*). In many situations with the condition that the cost ratio is greater than 1/2, both cooperation and defection of strong player could overtake the whole lattices, and the frequency of defection by the strong player will increase with increasing the benefit to cost ratio (Figure 1 *Upper* and Figure 3). There are a variety of kinds of strategies if the benefit to cost ratio is adjacent to 1/2, especially when the asymmetric interaction approaches symmetry (i.e., the degree of asymmetry equal to 1∶1) (Figure 1). This reality implies that cooperation systems may exists as the most appropriate condition for coexistence despite players employing a variety of different strategies.

Relative to the simulations of the symmetric model [26,27,30,33], the presence of asymmetric interaction increases the diverse forms of cooperation in the model we developed (Figures 1 and 2). If the benefit to cost ratio is small (e.g. *b/c* is less than 1/2 in Figure 1 *Lower*), the

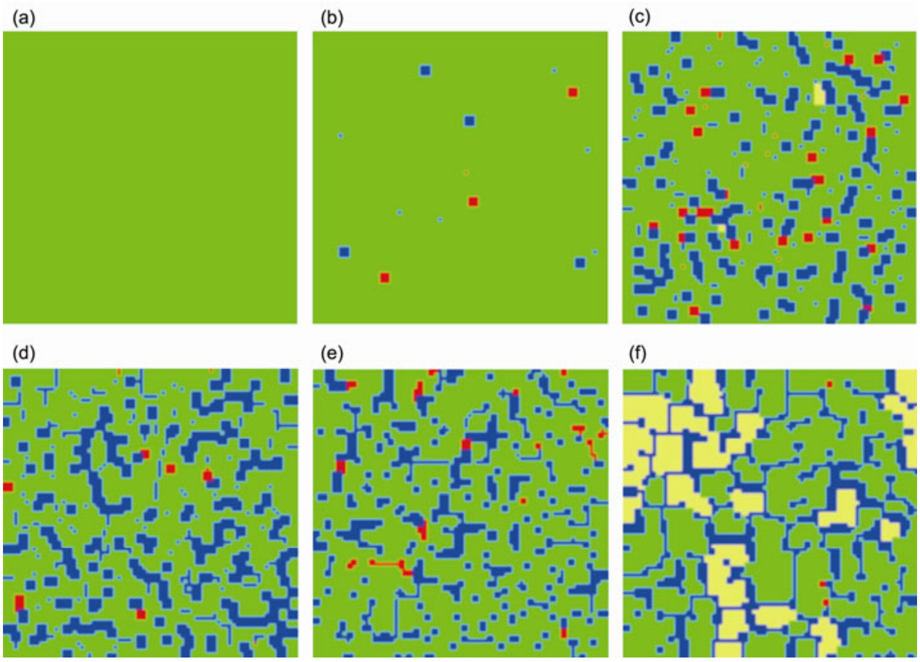

Figure 2 Scatter of four strategy players for different the benefit to cost ratio (a–c) and the degree of asymmetry (d–f) in the asymmetric spatial Hawk-Dove game. Vectors of the benefit to cost ratio and degree of asymmetry are (1/8, 8), (1/6, 2), (1/2, 1.004), (0.51, 8), (0.67, 2), (0.77, 1.004) in (a), (b), (c), (d), (e), (f), respectively.

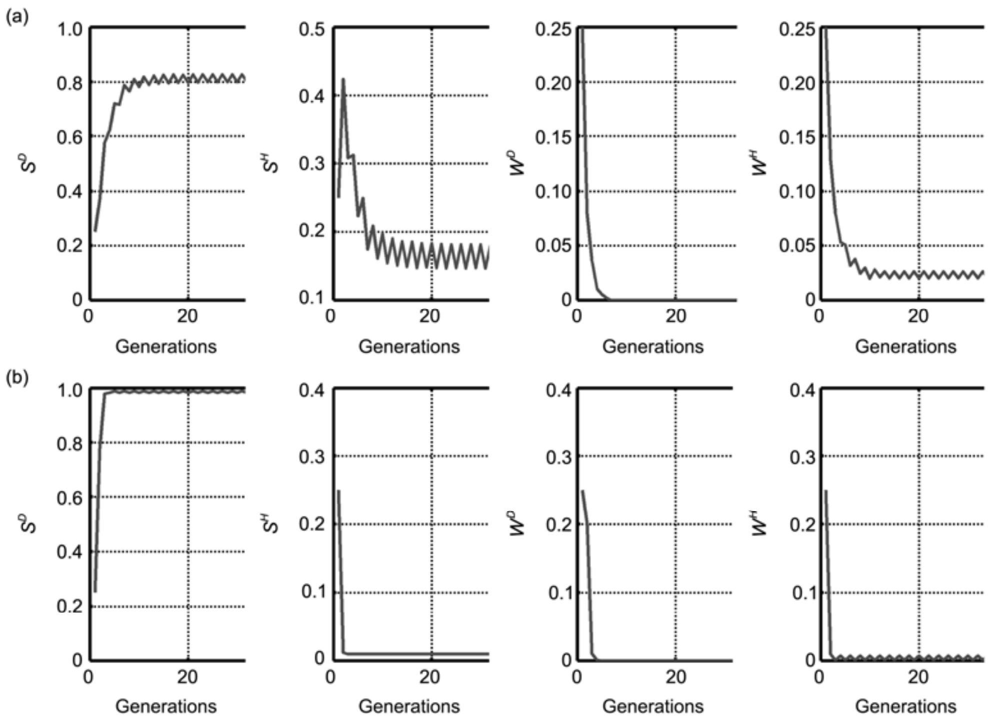

Figure 3 Probability of four strategies for different the benefit to cost ratio. The benefit to cost ratio are 1/2 and 1/6 in (a) and (b), respectively. The degree of asymmetry is fixed at 2. Note: The notations of W^H/W^D and S^H/S^D represent the probability of defection/cooperation of weak player and the probability of defection/cooperation of strong player (respectively).

weak players are all defector ("red"), and the probability of defection of strong player ("blue") will decrease with the concurrent decrease in the benefit to cost ratio (Figure 1 *Lower*). In essence, the strong players tend to cooperate while weak players defect, similar to the results of Boxed Pigs game [34]. However, if the benefit to cost ratio is great

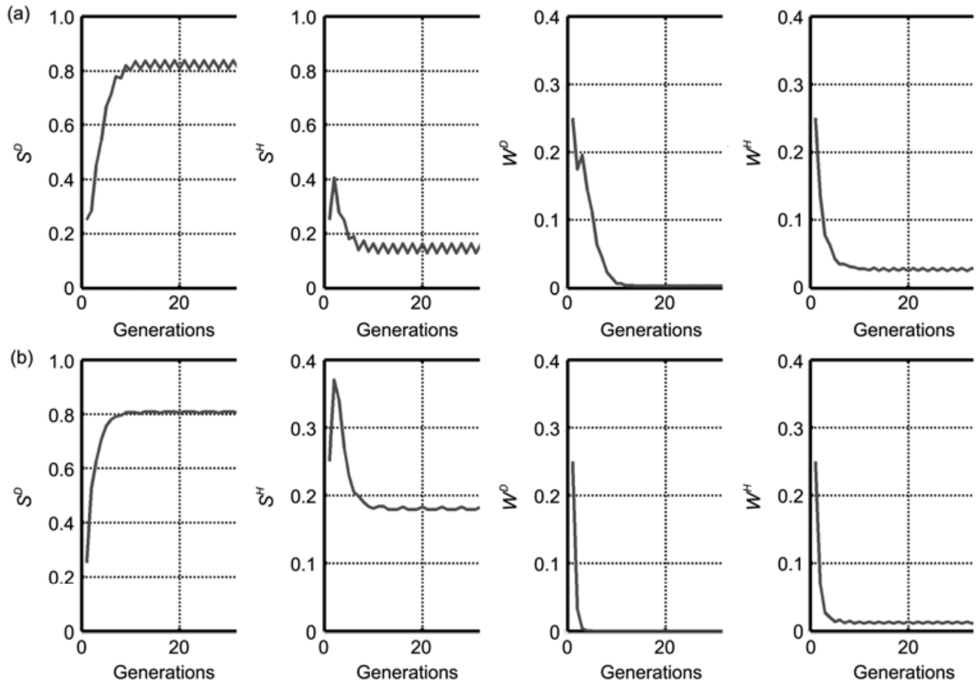

Figure 4 Probability of four strategies for different degrees of asymmetry. The degrees of asymmetry are 1.2 and 100 in (a) and (b), respectively. The benefit to cost ratio is fixed at 0.5.

(e.g. *b/c* is more than 1/2 in Figure 1 *Upper*), uncertainty in the cooperation systems will increase (Figure 1 *Upper*). In this situation, the weak players find it difficult to survive if the asymmetric interaction is great enough (e.g. *h* is more than 2 in Figure 1 *Upper*).

4 Conclusion

The Hawk-Dove game has often been given attention as a metaphor for understanding and analyzing the problems surrounding how cooperative behavior evolved. HDG has been considered useful in these endeavors because of the assumption in both biology and the social sciences that partners interact symmetrically [14,24,32,35,36]. This study has illustrated the effect of both the benefit to cost ratio and the degree of asymmetry on a spatial game of HDG. Our analysis demonstrates that these two factors greatly affect cooperative behavior of participants in cooperation systems.

Our simulations showed that the probability of cooperation of the system will increase with increasing the benefit to cost ratio; likewise, the probability of defection of the strong player will decrease while the probability of defection by the weak players will increase with increasing the degree of asymmetry. The variations between the other strategies were not as obvious. Moreover, the surviving weak players are mostly defectors, and the other kinds of strategy will be substituted by cooperation of strong player if the benefit to cost ratio is sufficiently small. These simulations also showed that there are a variety of viable strategies if the benefit to cost ratio is adjacent to 1/2, and the patterns this variety are chaotic or oscillate based on the change of related factors if the benefit to cost ratio is greater than 1/2. These findings have several implications that may help us more fully understand the dynamic of meta-populations [37]. Furthermore, the results potentially implicate that the dynamics of spatially extended systems possesses a wide variety of forms in both biological and social systems.

We would like to thank Li YaoTang, Wang Bo, Wang YaQiang, Li ChaoQian, Liu QiLong, and Gao Lei for their discussion and comments during the preparation and revision of this manuscript. This work was supported by the National Basic Research Program of China (2007CB411600), the National Natural Science Foundation of China (30670272, 30770500, 10961027, 31270433 and 10761010), the Yunnan Natural Science Foundation (2009CD104), the State Key Laboratory of Genetic Resources and Evolution, Kunming Institute of Zoology, Chinese Academy of Sciences (GREKF09-02), the West Light Foundation of the Chinese Academy of Sciences and Special Fund for the Excellent Youth of the Chinese Academy of Sciences (KSCX2-EW-Q-9).

1 Hanahan D, Weinberg R A. The hallmarks of cancer. Cell, 2000, 100: 57–70
2 Henrich J. Cooperation, punishment, and the evolution of human institutions. Science, 2006, 311: 60–61
3 Bronstein J L. The exploitation of mutualisms. Ecol Lett, 2001, 4: 277–287
4 Frank S A. Foundations of Social Evolution. Princeton, New Jersey: Princeton University Press, 1998
5 Wang R W, Sun B F, Zheng Q, et al. Asymmetric interaction and indeterminate fitness correlation between cooperative partners in the fig-fig wasp mutualism. J R Soc Interface, 2011, 8: 1487–1496
6 Hardin G. The tragedy of the commons. Science, 1968, 162: 1243–1248

7 West S A, Pen I, Griffin A S. Cooperation and competition between relatives. Science, 2002, 296: 72–75
8 Axelrod R. The Evolution of Cooperation. New York: Basic Books, 1984
9 Doebeli M, Knowlton N. The evolution of interspecific mutualisms. Proc Natl Acad Sci USA, 1998, 95: 8676–8680
10 Wang R W, Shi L, Ai S M, et al. Trade-off between reciprocal mutualists: Local resource availability-oriented interaction in fig/fig wasp mutualism. J Anim Ecol, 2008, 77: 616–623
11 Axelrod R, Hamilton W D. The evolution of cooperation. Science, 1981, 211: 1390–1396
12 Wang R W, Shi L. The evolution of cooperation in asymmetric systems. Sci China Life Sci, 2010, 53: 139–149
13 Wang R W, Ridley J, Sun B F, et al. Interference competition and high temperatures reduce the virulence of fig wasps and stabilize a fig-wasp mutualism. PLoS One, 2009, 4: e7802
14 Wang R W, Sun B F, Zheng Q. Diffusive coevolution and mutualism maintenance mechanisms in a fig-fig wasp system. Ecology, 2010, 91: 1308–1316
15 Pellmyr O, Huth C J. Evolutionary stability of mutualism between yuccas and yucca moths. Nature, 1994, 372: 257–260
16 Kiers E T, Rousseau R A, West S A, et al. Host sanctions and the legume-rhizobium mutualism. Nature, 2003, 425: 78–81
17 Reeve H K. Queen activation of lazy workers in colonies of the eusocial naked mole-rat. Nature, 1992, 358: 147–149
18 Clutton-Brock T H, Parker G A. Punishment in animal societies. Nature, 1995, 373: 209–216
19 Ratnieks F L W, Wenseleers T. Altruism in insect societies and beyond: Voluntary or enforced? Trends Ecol Evol, 2008, 23: 45–52
20 Ratnieks F L W, Wenseleers T. Policing insect societies. Science, 2005, 307: 54–56
21 He J Z, Wang R W, Christopher X J J, et al. Cooperation in an asymmetric volunteer's dilemma game with relatedness. Chin Sci Bull, 2012, 57: 1972–1981
22 Pellmyr O, Leebens-Mack J. Reversal of mutualism as a mechanism for adaptive radiation in yucca moths. Am Nat, 2000, 156: S62–S76
23 Clutton-Brock T. Breeding together: Kin selection and mutualism in cooperative vertebrates. Science, 2002, 296: 69–72
24 Maynard Smith J. Evolution and the Theory of Games. Cambridge: Cambridge University Press, 1982
25 Wang R W, He J Z, Wang Y Q, et al. Asymmetric interaction will facilitate the evolution of cooperation. Sci China Life Sci, 2010, 53: 1041–1046
26 Nowak M A, May R M. Evolutionary games and spatial chaos. Nature, 1992, 359: 826–829
27 Nowak M, Sigmund K. A strategy of win-stay, lose-shift that outperforms tit-for-tat in the prisoner's dilemma game. Nature, 1993, 364: 56–58
28 Nowak M A, Bonhoeffer S, May R M. More spatial games. Int J Bifurcation Chaos, 1994, 4: 33–56
29 Harsanyi J, Selten R. A general Theory of Equilibrium Selection in Gamesmit Press. Cambridge Massachussets: MIT Press, 1988
30 Hauert C, Doebeli M. Spatial structure often inhibits the evolution of cooperation in the snowdrift game. Nature, 2004, 428: 643–646
31 Domjan M, Grau J W. The Principles of Learning and Behavior. Belmont: Thomson Brooks/Cole Publishing Co, 1998
32 MacLeod W B. Equity, efficiency, and incentives in cooperative teams. Adv Econom Anal Participatory Labor Managed Firms, 1988, 3: 5–23
33 Wakano J Y. Evolution of cooperation in spatial public goods games with common resource dynamics. J Theor Biol, 2007, 247: 616–622
34 Eric R. Games and Information: An Introduction to Game Theory. Oxford: Basil Blackwell, 2001
35 Mesterton-Gibbons M. Ecotypic variation in the asymmetric hawk-dove game: When is bourgeois an evolutionarily stable strategy? Evol Ecol, 1992, 6: 198–222
36 Neugebauer T, Poulsen A, Schram A. Fairness and reciprocity in the hawk-dove game. J Econ Behav Organ, 2008, 66: 243–250
37 Huia C, McGeoch M. Spatial patterns of prisoner's dilemma game in metapopulations. Bull Math Biol, 2007, 69: 659–676