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Hawk-Dove Game with Relatedness

Some Aspects of Hawk-Dove Game with Relatedness

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Abstract

We reconsider the Hawk – Dove game which Maynard Smith and Price considered with the notion of inclusive fitness. We studied the relation between the relatedness and the stationary frequencies of two groups such that one group is more aggressive than the other group.

Key words
Hawk-Dove game, relatedness

1. Introduction

In the conflict among the individuals of the same species, they rarely go on fighting until each of them dies. In many cases, the conflict comes to end by the ceremonial threat and even if they begin to fight, they stop fighting at the point that they have known the ability of the rival each other. As the reason that the animals behaves like this, the ethologists explained that the instinct to keep the species restrains to fight with the individuals in the same species. But that explanation goes against the natural selection theory that the genotype with the higher reproductive success will spread within the population. Maynard Smith and Price succeeded in explaining such behavior of the animals along the natural selection context with the game theory (Maynard Smith and Price 1973). They applied the model of Hawk – Dove game.

In this paper, with the notion of inclusive fitness, we reconsider the Hawk-Dove game which Maynard Smith and Price considered. In the traditional Hawk–Dove game, two types of individual are assumed in the considered population: one takes Hawk strategy and another takes Dove strategy. Hawk strategy is such that the individual fights until it wins or is beaten. Dove strategy is the strategy that the individual does not want to fight and runs away if the rival challenges him to fight. Now, we assume that two individuals fight over the food with its value V, which means that the fitness of the individual who gets the food increases by V. There are three cases of fight, (1) Hawk vs Hawk; (2) Hawk vs Dove; (3) Dove vs Dove: In the case that Hawk vs Hawk, the fight goes on until one of them is beaten and runs away. Individual alternatively wins or is beaten with the probability 1/2. The fitness of the winner increases by V and that of the loser decreases by C due to the cost for the fight. Hence, the expected gain for the Hawk individual in this case is $(V - C)/2$. In the case that Hawk vs Dove, Hawk always defeats Dove. Therefore, the expected gain of Hawk is V, while that for Dove is 0 because he runs away before wounded. In the case that Dove vs Dove, they always share the food. Therefore, the expected gain for each of them is $V/2$. Table 1 shows the expected fitness gain based on these assumptions. The column denotes the strategy for the considered individual and the row does that for the rival.

Maynard Smith and Price considered two types of strategy (Maynard Smith and Price 1973). One is the pure strategy, and another is the mixed one. Pure strategy is such that every individual can take only one specific strategy, Hawk or Dove strategy. Mixed one is such that every individual takes Hawk strategy with probability P and Dove one with probability $1 - P$.

They also defined the evolutionary stable strategy (ESS) as follows: If almost all members take the strategy, no mutants who take the strategy different from it can have the higher fitness and increase within the population.

2. Assumption

In this paper, we consider the relatedness between individuals. We assume the followings: If a individual takes the same strategy as the rival takes, the relatedness between both of them is R $(0 \le R \le 1)$. If a individual takes the different strategy which the rival takes, the relatedness between both of them is and r $(0 \le r \le 1)$. The relatedness among individuals with the same strategy is assumed to be higher than that between individuals with different strategies:

$$r \le R. \tag{1}$$

3. Pure strategy

We assume that the frequency of Hawk individuals in the considered population is Q, and that of Dove is $1 - Q$. So, it is expected with probability Q that the encountered rival is with Hawk strategy, and with probability $1 - Q$ that it is with Dove one.

Let W_H and W_D respectively denote the expected fitness of Hawk individual and that of Dove one. There are four types of the result of fight and the expected fitness gain as shown in Table 1. Then W_H and W_D are given as follows:

$$W_H = W_0 + Q(1+R)(V-C)/2 + (1-Q)V \tag{2}$$
$$W_D = W_0 + QrV + (1-Q)(1+R)\,V/2, \tag{3}$$

where W_0 is the fitness of the individual before fight. Now we assume that the fitness before fight is common among any individuals. We define the difference ΔW between W_H and W_D as follows:

$$\Delta W = W_H - W_D. \tag{4}$$

From (2) and (3), ΔW is appears as follows:

$$\Delta W = \frac{Q\,\{\,2(R-r)V - (1+R)C\,\} + (1-R)V}{2}. \tag{5}$$

If ΔW is positive, the frequency of Hawk individuals is expected to increase in the subsequent generations. If ΔW is negative, the frequency of Dove individuals is expected to increase in the subsequent generations. If ΔW is zero, the frequency of Hawk individual would not change. When V and C are constant, the final frequency of Hawk individuals and Dove individuals depends on r and R. If one of the following two is satisfied, ESS is the Hawk strategy (see Fig. 1(a, b)).

$$V > C \quad \text{and} \quad 0 \le r < \frac{V-C}{V}\,,\ \max\left\{r\,,\ \frac{2V}{V-C}r - 1\right\} \le R \le 1; \tag{6}$$

$$V = C \quad \text{and} \quad r = 0\,,\ 0 \le R < 1. \tag{7}$$

If the following is satisfied, ESS is the Dove strategy (see Fig. 1).

$$\frac{V-C}{V} < r \le 1\ ,\ R=1. \tag{8}$$

If one of the following three is satisfied, Hawk and Dove groups coexist (see Fig. 1).

$$V \ge C \quad \text{and} \quad \frac{V-C}{V+C} < r < 1\ ,\ r \le R < \min\left\{\frac{2V}{V-C}r-1\ ,\ 1\right\}; \tag{9}$$

$$V \ge C \quad \text{and} \quad r = \frac{V-C}{V}\ ,\ R=1; \tag{10}$$

$$V < C \quad \text{and} \quad 0 < r < 1\ ,\ r \le R < 1. \tag{11}$$

If $V > C$ and $r = (V-C)/V\,,\ R=1$ or if $V=C$ and $r=0\,,\ R=1$, the population remains at the initial state; otherwise the frequency of Hawk individuals would asymptotically change to a certain positive value Q^* at a stationary state.

We consider the dependence of the stationary frequency of Hawk individuals on R. If $V \le C$ (Fig. 2(b, c)), the stationary frequency Q^* of Hawk individuals is monotonically decreasing function of R. If $V > C$ (see Fig. 2(a)), the (r, R) – dependence of Q^* is shown in the Table 2 (also see Fig. 2).

Next we consider dependence of Q^* on r (see Fig. 2). We find that Q^* is monotonically decreasing in terms of r.

From the above argument, we find the followings: Only when $R=1$, that is, when the individuals in the same group have the common gene, it is possible that ESS is Dove strategy. When $V < C$, it is impossible that ESS is Hawk strategy. Since the expected fitness gain of Hawk individual which fights with other Hawk individual is negative, the more the number that Hawk individual fights with another Hawk individual is, the less the fitness of Hawk individual is. When $V \le C$ or when $V > C$ and $r > (V-C)/V$, the stationary frequency Q^* of the Hawk individuals is decreasing in terms of both r and R. That is, the more r or R is, the less Q^* is. If r increases, the probability that the other individual in another group has the same gene become higher. Then the expected gain of Dove individual which fights with Hawk individual becomes larger (see Table 1). So it is expected that the frequency of Dove individuals increases. In contrast if R increases, the probability that the other individual in the same group has the same gene becomes higher. Then the increasing quantity of the expected fitness gain of Hawk individual which fights another Hawk individual is lower than the increasing expected fitness gain of Dove individual which fights with another Dove individual (see Table 1). Therefore, the frequency of Dove individuals increases. When $V > C$ and $(V-C)/(V+C) < r < (V-C)/V$, the frequency of Hawk individuals is increasing in terms of R.

4. Mix strategy

In this chapter, we consider the case when considered individual takes the mixed strategy of Hawk strategy and Dove strategy. We consider two groups, P_1 group and P_2 one. The individual of P_1 group takes Hawk strategy with probability P_1 and Dove with probability $1 - P_1$. The individual of P_2 group takes Hawk strategy with probability P_2 and Dove with probability $1 - P_2$. We assume that the individual of P_1 group is more aggressive than one of P_2, so that

$$0 \leq P_2 < P_1 \leq 1. \tag{12}$$

And we assume that the frequency of P_1 individuals in the considered population is Q, and thus that of P_2 individuals is $1-Q$. So, it is expected with probability Q that the rival is one of P_1 group, and with probability $1 - Q$ that the rival is one of P_2 group.

Let W_1 and W_2 respectively denote the expected fitness of the individual of P_1 group and that of one of P_2 group. There are eight types of the fight and the resulted expected fitness gain for each of them is shown in Table 3. Then the expected fitness of W_1 and W_2 are given as follows:

$$\begin{aligned} W_1 &= W_0 + P_1\Big[P_1 Q\frac{(V-C)(1+R)}{2} + P_2(1-Q)\frac{(V-C)(1+r)}{2} \\ &\quad + \big\{(1-P_1)Q + (1-P_2)(1-Q)\big\}V\Big] \\ &\quad + (1-P_1)\Big\{P_1 QRV + P_2(1-Q)rV \\ &\quad + (1-P_1)Q\frac{V(1+R)}{2} + (1-P_2)(1-Q)\frac{V(1+r)}{2}\Big\} \end{aligned} \tag{13}$$

$$\begin{aligned} W_2 &= W_0 + P_2\Big[P_1 Q\frac{(V-C)(1+r)}{2} + P_2(1-Q)\frac{(V-C)(1+R)}{2} \\ &\quad + \big\{(1-P_1)Q + (1-P_2)(1-Q)\big\}V\Big] \\ &\quad + (1-P_2)\Big\{P_1 QrV + P_2(1-Q)RV \\ &\quad + (1-P_1)Q\frac{V(1+r)}{2} + (1-P_2)(1-Q)\frac{V(1+R)}{2}\Big\}. \end{aligned} \tag{14}$$

We define the difference ΔW between W_1 and W_2 as follows:

$$\Delta W = W_1 - W_2. \tag{15}$$

From (13) and (14), ΔW appears as follows:

$$\begin{aligned} \Delta W &= \frac{1}{2}\Big[V(1-r)(P_1-P_2) + C(1+R)\big\{-QP_1^2 + (1-Q)P_2^2\big\} \\ &\quad +(1-2Q)\big\{V(r-R) + CP_1P_2(1-r)\big\}\Big] \end{aligned} \tag{16}$$

We could consider three final state of the population: i) P_1 group occupies the population; ii) P_1 and P_2 groups coexist; iii) P_2 group occupies the population. Table 4–6 show respectively the conditions that P_1 group occupies the population, that P_1 and P_2 groups coexist, and that P_2 group occupies the population. Q^* is such that $\Delta W(Q^*) = 0$, and Q' is the initial frequency of the P_1 individuals in the population.

Figs. 3 and 4 show the stable region and the unstable region. The stable region is such that the stationary frequency of the P_1 group is positive for any initial value Q'. The unstable region is such that the stationary frequency of P_1 depends on the initial value Q'.

Provided that P_1 group evolves from P_2 group, we can consider that the initial frequency Q' of P_1 group is sufficiently small, and that P_1 is a little larger than P_2. Then, we can regard the unstable region and the region such that $\Delta W < 0$ as the region that P_1 group can not spread within the population, and the stable region and the region that $\Delta W > 0$ as the region that P_1 group can spread within the population.

5. Conclusion

We found that whether the stationary frequencies of the Hawk and Dove groups depend on not only the benefit of foods and the cost of fight but also the relatedness. In the case that an individual takes only one of Hawk and Dove strategies, it is possible only when the individuals in the same group have the common gene that Hawk group occupy the population. In the case that an individual takes mixed strategy, it is hardly possible that the frequency of the mutants which are a little more aggressive than others increase. However, when $C > V$ it is possible that the mutants occupy the population.

References

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Appendix A The definitions of α, β, E_1, E_2, E_3 and ρ

$$\alpha = \frac{(2+R-r)(1-r)}{(R-r)(1+R)}(P_1+P_2) \tag{17}$$

$$\beta = \frac{(1-r)\sqrt{(2+R-r)(R+r)}}{(R-r)(1+R)} \tag{18}$$

$$E_1(\alpha,\beta) = \frac{(R-r)(1+R)^2}{4(1-r)^2)(2+R-r)}(\alpha^2+\beta^2) \tag{19}$$

$$E_2(\alpha,\beta) = \frac{(R-r)(1+R)^2\left\{\sqrt{(R+r)(2+R-r)}(\alpha^2+\beta^2)+2(1+R)\alpha\beta\right\}}{4(1-r)^2(2+R-r)\left\{\sqrt{(2+R-r)(R+r)}+(1+R)\beta\right\}} \tag{20}$$

$$E_3(\alpha,\beta) = \frac{(R-r)(1+R)^2\left\{\sqrt{(R+r)(2+R-r)}(\alpha^2+\beta^2)-2(1+R)\alpha\beta\right\}}{\sqrt{(2+R-r)(R+r)}-(1+R)\beta} \tag{21}$$

$$\rho = \frac{\sqrt{(2+R-r)(R+r)}}{1+R} \tag{22}$$

Figure and Table Captions

Table 1. The expected fitness gain for each fight in the case that an individual takes either Hawk strategy or Dove strategy.

Table 2. R –dependence of Q^* when $V > C$. If $R = 1$ and $r = (V - C)/V$, the frequency remains at the initial value.

Talbe 3. The expected fitness gain for each fight in the case that an individual takes Hawk strategy and Dove one.

Table 4. The condition that P_1 group occupies the population. The definitions of α, β, E_1, E_2, E_3, and ρ are given in Appendix A

Table 5. The condition that P_1 and P_2 groups coexist.

Table 6. The condition that P_2 group occupies the population.

Fig. 1. (r – R) - dependence of the stationary state. The region H is such taht Hawk strategy is ESS; D such that Dove strategy is ESS; C such that Hawk and Dove groups coexist.

Fig. 2. The stationary frequency Q^* of Hawk individuals. (a) is when $V > C$; (b) is when $V = C$; (c) is when $V < C$.

Fig. 3(a). The light grey regions is the unstable ones. The dark grey regions is the stable ones. The black regions is the one in which $\Delta W < 0$, that is, the frequency of the individuals of P_1 group would always decrease. $r = 0.3$, $R = 0.5$, $C = 11.0$ and $V = 1.0$.

Fig. 3(b). The region of stable and that of unstable. $r = 0.3$, $R = 0.5$, $C = 3.0$ and $V = 1.0$. The white region is the one in which $\Delta W > 0$. The black region is the one in which $\Delta W < 0$.

Fig. 4(a). The region of stable and that of unstable. $r = 0.3$, $R = 0.5$, $C = 1.0$ and $V = 1.0$. The white region is the one in which $\Delta W > 0$.

Fig. 4(b). The region of stable and that of unstable. $r = 0.3$, $R = 0.5$, $C = 1.0$ and $V = 5.0$. The white region is the one in which $\Delta W > 0$.

Fig. 4(c). The region of stable and that of unstable. $r = 0.3$, $R = 0.5$, $C = 1.0$ and $V = 15.0$. The white region is the one in which $\Delta W > 0$.

	strategy of rival	
	Hawk	Dove
onw strategy		
Hawk	$\frac{(1+R)(V-C)}{2}$	V
Dove	rV	$\frac{(1+R)V}{2}$

	$R < \frac{V-C}{V}$	$R \geq \frac{V-C}{V}$
$r < \frac{V-C}{V}$	constant ($Q^* = 1$) or monotonically increasing	constant ($Q^* = 1$) or monotonically increasing
$r = \frac{V-C}{V}$	–	constant $\left(Q^* = \frac{V}{2V-C}\right)$
$r > \frac{V-C}{V}$	–	monotonically decreasing

	strategy of rival			
	rival in the same group		rival in another group	
	Hawk	Dove	Hawk	Dove
own strategy				
Hawk	$\dfrac{(V-C)(1+R)}{2}$	V	$\dfrac{(V-C)(1+r)}{2}$	V
Dove	RV	$\dfrac{(1+R)V}{2}$	rV	$\dfrac{(1+r)V}{2}$

<table>
<tr><td>$r = R < 1$</td><td colspan="3">$r \leq \dfrac{V(P_1 - P_2) - CP_1(P_1 + P_2)}{(P_1 - P_2)(CP_1 + V)}$</td></tr>
<tr><td rowspan="6">$r < R$</td><td rowspan="2">$\beta \geq \rho$</td><td colspan="2">$E_1 \leq \dfrac{V}{C}$</td></tr>
<tr><td>$(\alpha - 1)^2 + \beta^2 > 1$</td><td>$E_2 < \dfrac{V}{C} < E_1$</td></tr>
<tr><td rowspan="4">$\beta < \rho$</td><td rowspan="2">$(\alpha - 1)^2 + \beta^2 > 1$</td><td>$E_2 < \dfrac{V}{C} \leq E_3$</td></tr>
<tr><td>$Q' > Q^*$</td></tr>
<tr><td>$(\alpha - 1)^2 + \beta^2 = 1$</td><td>$E_1 = E_2 = E_3 < \dfrac{V}{C},\ Q' > Q^*$</td></tr>
<tr><td>$(\alpha - 1)^2 + \beta^2 < 1$</td><td>$E_2 \leq \dfrac{V}{C},\ Q' > Q^*$</td></tr>
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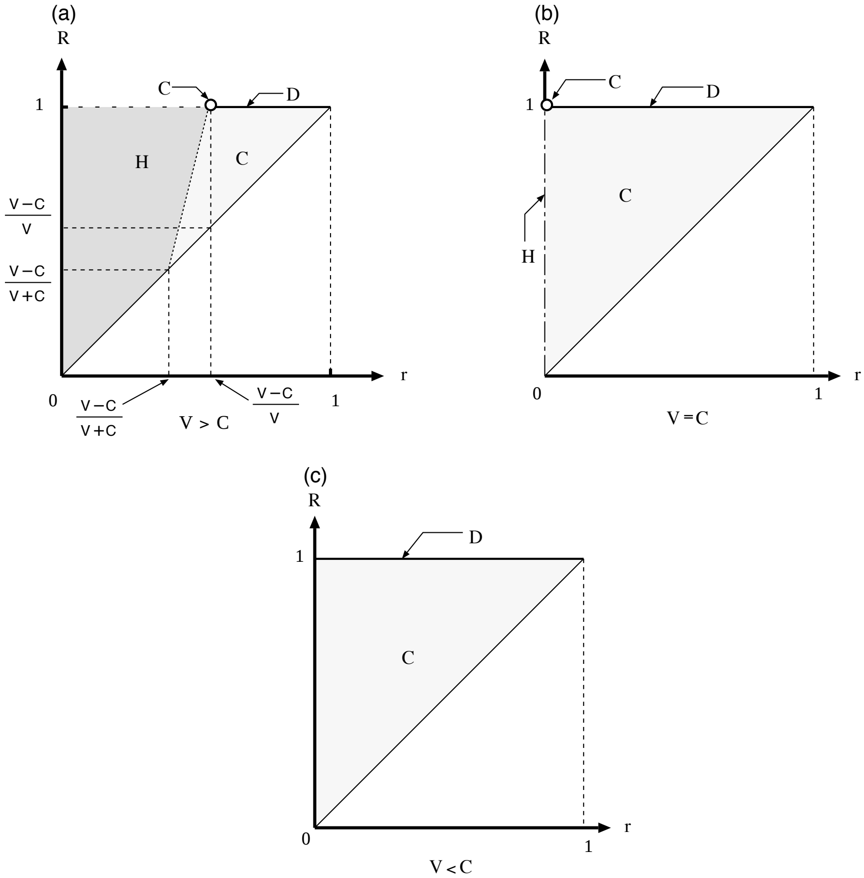
<tr><td>$E_2 \leq \dfrac{V}{C},\ Q' = Q^*$</td></tr>
</table>

$r < R$	$\beta < \rho$	$(\alpha - 1)^2 + \beta^2 > 1$	$\frac{V}{C} \leq E_2,\ Q' < Q^*$
			$E_3 < \frac{V}{C},\ Q' < Q^*$
		$(\alpha - 1)^2 + \beta^2 = 1$	$E_1 = E_2 = E_3 < \frac{V}{C}$
		$(\alpha - 1)^2 + \beta^2 < 1$	$E_3 \leq \frac{V}{C}$
			$Q' < Q^*$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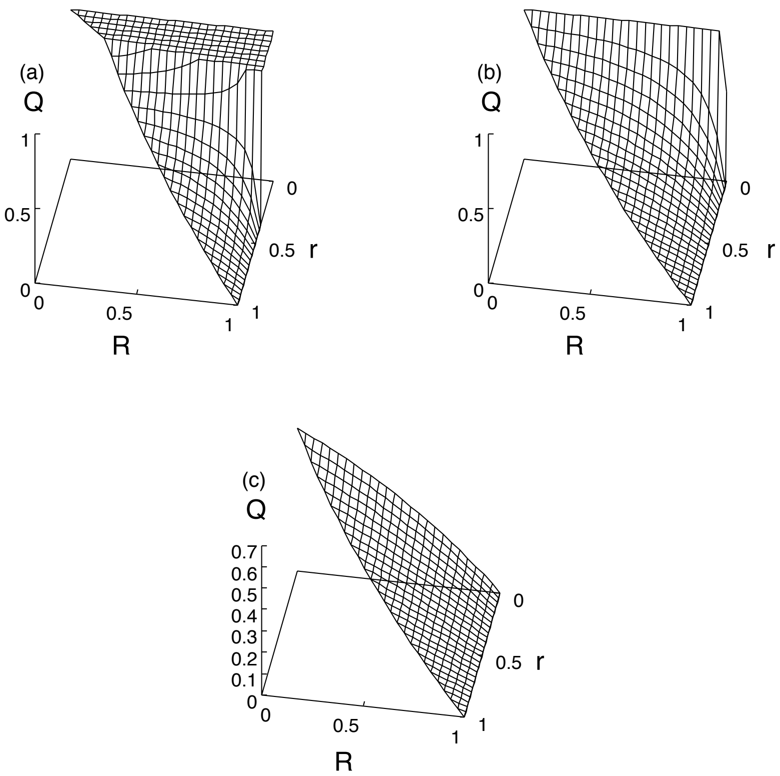
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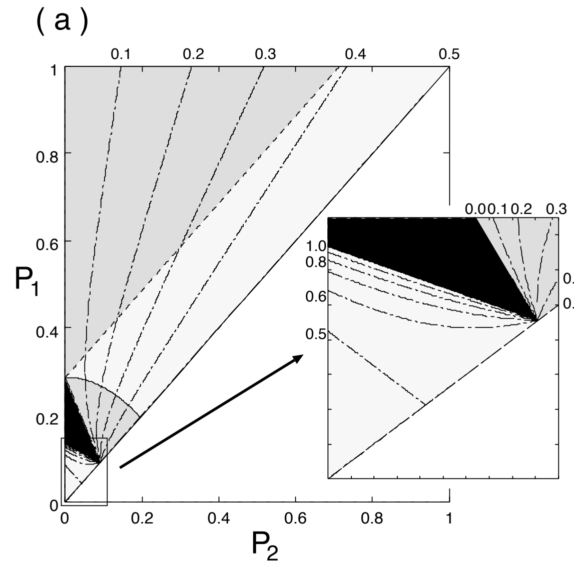
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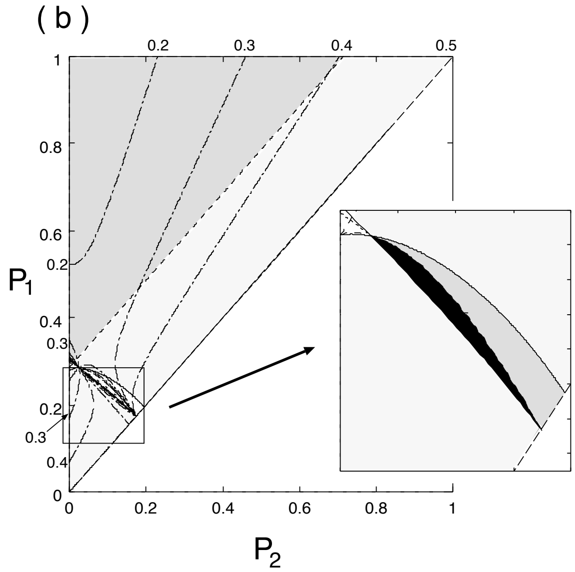
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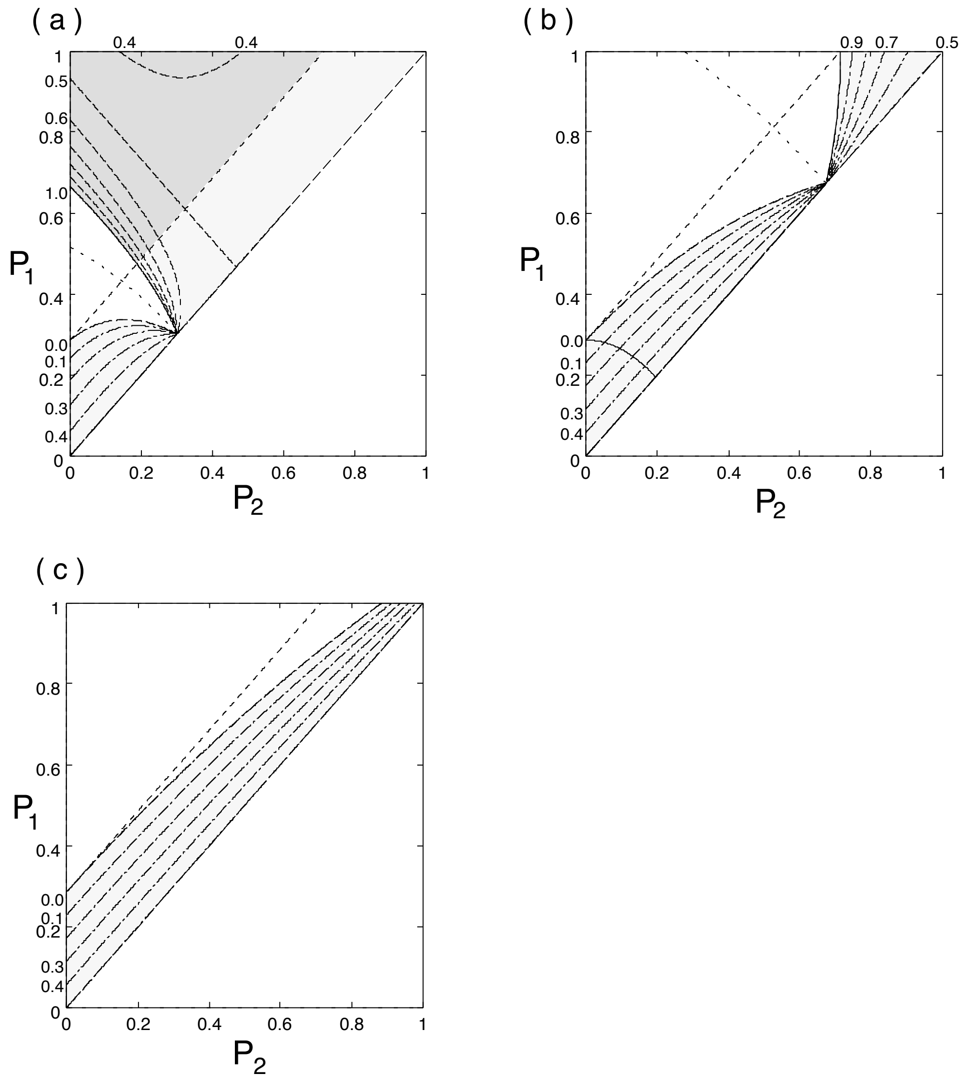
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