Evolution of signal emission by non-infested plants growing near infested plants to avoid future risk

Yutaka Kobayashi*, Norio Yamamura

Center for Ecological Research, Kyoto University, Kamitanakami-Hiranocho, Otsu, Shiga 520-2113, Japan

Abstract

Several plant species indirectly defend themselves against herbivory by attracting natural enemies of herbivores by releasing signal chemicals when infested. Previous empirical research suggested that the chemical signals also reflexively induce signal emission by neighboring undamaged plants. We hypothesize that such a reflexively induced signal is a defensive strategy used by undamaged plants to avoid possible future risk. Using a mathematical model, we show that this defense against future risk can evolve if the following conditions are met: (1) the cost of the signal is small relative to the cost of damage by infestation, (2) the attractiveness of the signal to natural enemies is positively correlated with the local density of the signal chemical, (3) plants with infested neighbors are at greater risk than those without infested neighbors, and (4) the lifespan of plants is long compared with that of herbivores. We also discuss the relationship between our model and recent models of the evolution of cooperation.
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1. Introduction

There are two types of plant defense against herbivory: "direct defense" and "indirect defense". Direct defense, which may be described simply as "resistance", denotes defense by means of physical defensive structures, toxins, or induced chemical compounds that diminish herbivore activity, such as various proteinase inhibitors. In addition to direct means, some plants defend themselves in a more roundabout way (indirect defense), by emitting volatile chemicals, which attract natural enemies of the herbivores, when infested (e.g., see Dicke, 1988; Turlings et al., 1990; Farmer, 1997). Natural enemies, which may be predators or parasitoids, find the infested plants by tracing the source of the odor and exploit the herbivore, benefiting both the natural enemy and the plant. Such a signal odor has been called an "SOS signal" (Bruin et al., 1995), because the plants beg natural enemies of the herbivore for help. This may be interpreted as mutualism across trophic levels, in which the natural enemies act as bodyguards

for the plants. Several authors have shown that the SOS signal system can evolve, using mathematical models (Sabelis and De Jong, 1988; Godfray, 1995).

In relation to this indirect-defense strategy of plants, some plants "eavesdrop" on signals emitted by other plants; that is, the plants receive and utilize chemical signals that may have originally been released to attract natural enemies by nearby infested plants (Dicke and Bruin, 2001). For example, in some plant species, undamaged individuals or leaves increase their resistance to herbivory when exposed to volatile chemicals emitted by damaged individuals or leaves (Haukioja et al., 1985; Zeringue, 1987; Farmer and Ryan, 1990; Shulaev et al., 1997; Arimura et al., 2000; Dolch and Tscharntke, 2000). Interestingly, the eavesdropper and emitter can be different species (Karban et al., 2000; Karban, 2001; Karban and Maron, 2002). This phenomenon suggests that undamaged plants near damaged plants utilize volatile chemicals from damaged neighbors as cues to future attack by herbivores, and prepare to defend against herbivory in advance.

Therefore, chemical signals can affect the direct defense of plants. In addition, some research suggests that chemical signals emitted by infested individuals reflexively promote the emission of chemical signals by

*Corresponding author. Tel.: +81-77-549-8020; fax: +81-77-549-8201.

E-mail address: yutaka@ecology.kyoto-u.ac.jp (Y. Kobayashi).

nearby undamaged plants (Dicke et al., 1990; Bruin et al., 1992; Birkett et al., 2000; Chamberlain et al., 2001; Dicke and Dijkman, 2001). In other words, undamaged plants turn into signalers, after eavesdropping on the signal, although the signal released by the eavesdroppers is weaker than the original. We refer to a signal reflexively emitted by undamaged plants as a "cooperative signal" or more simply as a "co-signal", because the undamaged and infested individuals signal together as if they were cooperating to call bodyguards. Neither the physiological mechanism nor the underlying evolutionary meaning of cooperative signals is clear. When undamaged plants receive signals from neighboring plants that have been attacked, do they benefit from signaling together with the infested neighbors? Is such a trait adaptive, even if signal emission is costly? Our primary aim in this paper is to provide a theoretical answer to this question by constructing and analysing a mathematical model. In the next paragraph, we address the hypothesis underlying our model. We consider other interpretations of the evolution of the cooperative signal in Section 3.

We start with a plant population in which a SOS signal has already been established; that is, there exists a mutualistic relationship between plants and natural enemies, with natural enemies acting as bodyguards for the plants. We do not deal with the evolution of the SOS signal system, but focus on the evolution of the cooperative signal. One of the most significant assumptions of our hypothesis is that a non-infested plant near an infested plant is more likely to be attacked in the near future than one without infested neighbors. Of course, some natural enemies might exterminate herbivores infesting nearby plants fortuitously, since the attacked neighbor is calling bodyguards. Since the risk of infestation remains, the non-infested plant should do something to avoid future possible risk and to improve its potential fitness. What can the plant when faced with such danger?

Suppose that the effectiveness of the odor in attracting natural enemies is positively correlated with the local number of plants simultaneously emitting the odor. This is plausible, because the strength of an odor increases with the chemical concentration. If so, the cooperative signal improves the attractiveness of the signal, and leads to the effective extermination of the herbivores infesting the original signaler. Therefore, the co-signaler can reduce its potential future risk. In a sense, we may regard this behavior literally as cooperation between neighboring plants, since the co-signaler increases not only its own potential fitness, but also the fitness of nearby infested plants. From the viewpoint of the co-signaler, however, the purpose of the behavior is to improve its own fitness by removing the risk of future infestation, and this behavior is favored by natural selection if the fitness gain exceeds the cost of the signal.

Therefore, we postulate that the cooperative signal evolves to avoid possible future risk, improving the attraction of natural enemies and eliminating the herbivores in advance.

In this paper, we mathematically model this idea to confirm its preciseness. We investigate the conditions under which the cooperative strategy will evolve. We also discuss the relationship between our model and recent models of the evolution of cooperation. We have defined the many symbols used throughout this paper in Appendix A.

2. Model

2.1. Structure

Our model considers a plant population composed of an infinitely large number of patches, in which N individuals inhabit every patch. Individuals in the same patch are neighbors spatially. We assume that there is no genetic relationship between patch-mates and that they are random samples of the population as a whole. For convenience, we assign successive integers $(1, 2, 3, \ldots, N)$ to all individuals in each patch. Imagine that we rearrange them linearly in numerical order from left to right. Hereafter, we refer to the individual with the smallest number, i.e. 1, as the "leftmost" individual. Each plant is in one of two possible states: infested (state 1) or non-infested (state 0). We state that a patch is in state $L|Q$, when the leftmost individual is in state L and there are Q infested individuals other than the leftmost. By definition, L is either 0 (non-infested) or 1 (infested) and $0 \leqslant Q \leqslant N - 1$. Therefore, there are two possible values of L and N possible values of Q, so that there are $2N$ different patch states. Note that $L + Q$ gives the number of infested individuals in a patch in state $L|Q$.

We define two plant strategies or phenotypes: "cooperative" (strategy C) and "un-cooperative" (strategy U). Every plant in the population is one of these two phenotypes, and the phenotype of an individual never changes. Individuals of both phenotypes signal to attract natural enemies when infested, which implies that the SOS signal system is already established. In addition, C strategy individuals emit the signal when the number of infested individuals in that patch reaches a threshold n^* ($1 \leqslant n^* \leqslant N - 1$), regardless of their own state. This implies that the density of the signal chemical monotonically increases with the number of signaling individuals, and that the signal induces cooperative signal emission by C strategy individuals when the density reaches a threshold. We define type X/Y patches as patches in which the leftmost individual is phenotype X and *all* the others are type Y. Throughout this paper, we use the symbols X and Y to denote any one of C and U. Therefore, there are four types of

patches: C/C, C/U, U/C, and U/U. From the definition of patch type, many patches are not classified into any of these four types. For convenience, we refer to patches that do not belong to any type as type */− patches. Here, the asterisk to the left of the slash implies that the leftmost individual can be of any type, and the minus sign to the right implies that not all of the individuals other than the leftmost are of the same type.

We assume that generations are discrete and that one generation has T time steps (Fig. 1). Here, a time step means the lifespan of the herbivore, so that T means the relative length of the lifespan of the plants to that of the herbivores. No plant individual dies during a generation. After T time steps, the plants reproduce asexually and all the parents die. Offspring have the same phenotypes as their parents; they are randomly dispersed over the population, and then the next generation starts from the initial time step. We assume that none of the individuals are infested at the initial time step. Therefore, all patches are initially in state 0|0. Each time
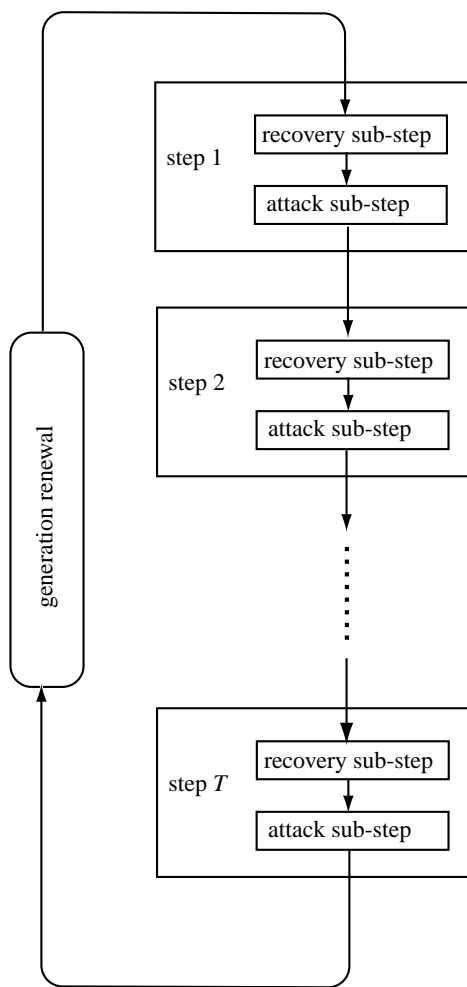

Fig. 1. Diagram describing the events in the life cycle of plants. Generations are discrete, and recovery steps and attack steps are alternately repeated T times in a generation. After T time steps, asexual reproduction occurs, and the next cycle begins.

step consists of two sub-steps in the order: "recovery step" and "attack step". In other words, recovery and attack sub-steps are repeated alternately T times per generation. The events that occur in those two steps are addressed in detail below.

First, in recovery sub-steps, infested plants can recover to become non-infested. Imagine infested plants emitting signal chemicals and attracting natural enemies. If the natural enemies find them, the infested plants are rescued and shift to the non-infested state (state 0). We assume that recovery occurs in an all-or-nothing manner; i.e. all the infested individuals in the patch recover when recovery occurs. Therefore, recovery is equivalent to transition to state 0|0. This assumption implies that the natural enemies find herbivores on individuals in the same patch simultaneously, because they are in close proximity. The probability of recovery of a patch depends on the number n_s of signaling individuals within the patch. We assume that the recovery probability of a patch with n_s signaling individuals is given by $V(n_s)$, which is an increasing function of n_s. That is, the signal is more effective when emitted simultaneously by multiple individuals than when emitted solely by a single individual. Note that we need not consider $n_s = 0$, because in such a patch, no plant is infested, so recovery does not occur (or in other words recovery occurs with probability 1). Therefore, we have $V(1) \leqslant V(n_s) \leqslant V(N)$. We also denote the minimum and maximum values of $V(n_s)$ by r and R, respectively, i.e. $r = V(1)$ and $R = V(N)$.

Second, in attack sub-steps, herbivores attack non-infested individuals. The probability that a non-infested individual is attacked is given by the function $Z(k)$, where k is the number of infested individuals in that patch. $Z(k)$ is an increasing function, which implies that individuals with many infested patch-mates are at greater risk than those with few infested patch-mates. Note that we need not consider $k = N$, because in such a patch, there are no non-infested individuals. Therefore, we have $Z(0) \leqslant Z(k) \leqslant Z(N - 1)$. We also denote the minimum and maximum values of $Z(k)$ by h and H, respectively; i.e., $h = Z(0)$ and $H = Z(N - 1)$. We assume that attacks of non-infested individuals in an attack step are independent. That is, the number of newly infested individuals is determined by a binary distribution: the probability that l individuals are newly attacked in a patch with k already-infested individuals is given by

$$\binom{N - k}{l} Z(k)^l \{1 - Z(k)\}^{N-k-l},$$

where

$$\binom{N - k}{l}$$

is the number of combinations of l individuals out of $N - k$ individuals.

One might wonder why each generation starts with a recovery step, not an attack step. We discuss this in detail in Section 3. Here, note only that the initial recovery step does not affect the result, because it makes the transition only from state 0|0 to state 0|0 in all patches (recall that all patches are initially in state 0|0).

We do not explicitly consider the population dynamics of herbivores and natural enemies. In addition, the size of the plant population is temporally constant. At the end of each time step (before the next recovery step), each signaling individual incurs the cost S of the signal. Furthermore, if the individual is infested, it incurs the additional cost d of damage by infestation. Since infested individuals always signal, they incur cost $S + d$ per time step. We assume that costs are additive for mathematical simplicity; that is, the total cost of a plant at the end of a generation is equivalent to the sum of all the costs that the plant incurs during its lifetime. We assume that the initial frequency of cooperative individuals is q and that individuals of both phenotypes are randomly distributed over the population. We derive the condition under which the cooperative strategy increases in frequency, i.e. it is selected for. However, we do not explicitly follow the change of frequency of each phenotype, but instead investigate which of the two phenotypes has a greater average fitness (smaller average cost) at the end of a single generation, i.e. after T time steps.

In the following sub-sections, we derive the conditions under which the cooperative strategy increases in frequency, and investigate the effect of various parameters on these conditions. In Section 2.2, we analyse the model for $N = 2$, because under this restriction, the model is analytically tractable and the result is relatively easy to understand. In Section 2.3, we consider all N. The result for $N = 2$ gives a basis for understanding the results for all N, which is contrasted with the result for $N = 2$.

2.2. Analysis for N=2

When $N = 2$, there are only four possible patterns of patch state: 0|0, 1|0, 0|1, and 1|1. For convenience, we assign scalars 1, 2, 3, and 4 to the coupled states 0|0, 1|0, 0|1, and 1|1, respectively. Note that all the patches are classified into one of four types C/C, C/U, U/C, and U/U under $N = 2$; i.e. there are no type $*/-$ patches. We can also use the terms "left" and "right" to indicate the two individuals in a patch. Note that $V(n_s)$ and $Z(k)$ can take only their maximum or minimum values, because $V(1) \leqslant V(n_s) \leqslant V(2)$ and $Z(0) \leqslant Z(k) \leqslant Z(1)$. Consequently, we need only four values $r = V(1)$, $R = V(2)$, $h = Z(0)$, and $H = Z(1)$ to completely describe functions $V(n_s)$ and $Z(k)$. Since $1 \leqslant n^* \leqslant N - 1$, we have

$n^* = 1$ under $N = 2$; therefore, cooperative individuals always signal when their partners are infested.

From this, the state transition diagram of a recovery step is as shown in Fig. 2a. In the diagram, circles denote the state of the patch and each arrow represents a transition between the two states. The values beside the arrows are the probabilities of the transitions. Note that recovery is equivalent to transition to state 1 (state 0|0). In state 1, nobody is infested, so patches in state 1 do not change state in a recovery step. Therefore, the transition probability from state 1 to state 1 is unity. In state 4, both individuals are infested and are also signaling; therefore, the recovery probability is $V(2) = R$. In state 2 (state 1|0), the probability of recovery $r_{X/Y,2}$ depends on the strategy Y of the non-infested individual on the right. If the individual on the right is cooperative ($Y \equiv C$), it signals because the left individual is infested. Therefore, $r_{X/C,2} = V(2) = R$, and both individuals signal. Conversely, if the individual on the right is not cooperative ($Y \equiv U$), only the left individual signals, so

(a)

(b)
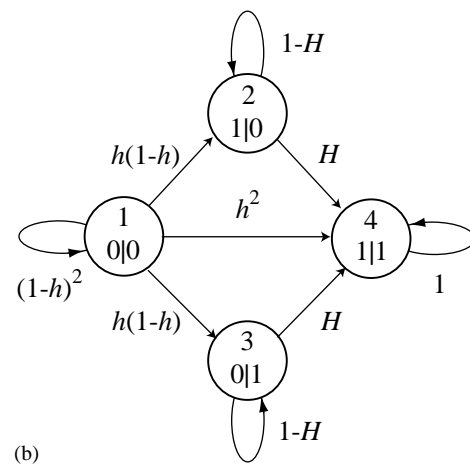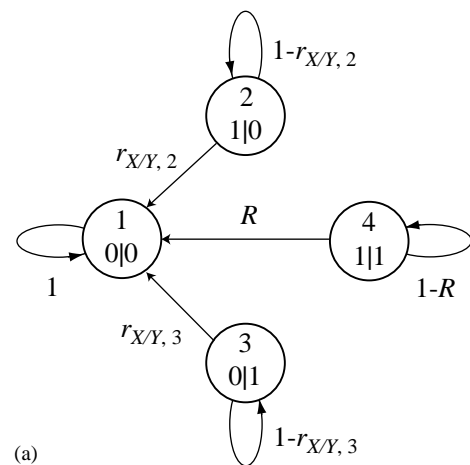
Fig. 2. State transition diagrams for (a) recovery steps and for (b) attack steps under $N = 2$. Circles represent possible states of patches. Arrows represent the state transitions. Numbers beside the arrows are the transition probabilities.

that $r_{X/U,2} = V(1) = r$. Similarly, for state 3 (state 0|1), $r_{C/Y,3} = V(2) = R$ and $r_{U/Y,3} = V(1) = r$ for any Y. Therefore, the state transition probabilities depend on the type of patch.

The state transition diagram for an attack step is shown in Fig. 2b. The notation is the same as in Fig. 2a. We can easily calculate the transition probabilities in the diagram of the attack step, noting that the number of attacks on individuals follows a binary distribution, as mentioned above. For example, nobody is infested in state 1, so that the probability of attack per individual is h. Therefore, the probability that the individual on the left is attacked and that on the right is not is $h(1 - h)$, which is equivalent to the probability of the transition from state 1 to state 2.

Comparing the average per-step cost to cooperative individuals with that to un-cooperative individuals, we can assess the relative cost per generation and examine whether the cooperative strategy increases in frequency under selection. Since the calculation is complicated, we present it in Appendix B. As shown in the appendix, the cooperative strategy increases in frequency when

$$\frac{S}{d} < \Theta(q, T), \tag{1}$$

where $\Theta(q, T)$ is calculated from the initial frequencies of all patch states and the values of $r, R, h, H, q,$ and T. Note that arguments of Θ, i.e. q and T, are shown for simplicity, and many other parameters actually affect the value of Θ. We represent the values of Θ for specific values of q or T using expressions such as $\Theta(1, T)$, $\Theta(q, 1000)$, or $\Theta(0.5, 20)$. We may omit the arguments for Θ when there is no confusion.

Θ is independent of S and d (see Appendix B). Therefore, Eq. (1) implies that the cooperative strategy increases in frequency if the signal cost S is small relative to the damage cost d; otherwise it decreases. Therefore, Θ represents the upper threshold of S/d under which the cooperative phenotype increases. As Θ increases, the condition becomes moderate; consequently, Θ reflects the advantage of the cooperative strategy over the un-cooperative strategy.

As shown in Appendix B, we cannot obtain an analytical expression of Θ for general T. However, we can calculate $\Theta(q, \infty)$, i.e. Θ for infinite T:

where

$$\zeta = \{1 - (1 - h)^2(1 - R)\} \{1 - (1 - H)(1 - r)\}. \tag{2b}$$

Note that the un-cooperative strategy cannot invade a population composed entirely of cooperative individuals if Eq. (1) is satisfied for $q = 1$. Namely, an "evolutionarily stable" (Maynard Smith, 1982) cooperative strategy arises when $S/d < \Theta(1, T)$. Substituting $q = 1$ for Eq. (2), we obtain $\Theta(1, T)$ for infinite T, i.e. $\Theta(1, \infty)$:

$$\Theta(1, \infty) = \frac{(R - r)(H - h)}{\{1 - (1 - H)(1 - R)\}\{1 - (1 - h)^2(1 - r)\}}. \tag{3}$$

Eq. (3) shows that $\Theta(1, \infty) = 0$ for $R = r$ or $H = h$. This means that the cooperative strategy can never be evolutionarily stable under those conditions. This is intuitively correct. That is, if the cooperative signal has no effect, i.e. $R = r$, cooperative individuals obviously cannot obtain any benefit. Likewise, the cooperative signal is nothing more than a waste of energy when $H = h$, because there is no additional future risk to avoid.

If Eq. (1) is satisfied for $q = 0$, the cooperative strategy can invade a population of un-cooperative individuals. Therefore, invasion occurs when $S/d < \Theta(0, T)$. From Eq. (2), we can calculate $\Theta(0, \infty)$:

$$\Theta(0, \infty) = \frac{(R - r)[\{1 - (1 - H)(1 - r)\}(H - h) - (1 - H)(R - r)h(1 - h)]}{\{1 - (1 - H)(1 - R)\}[\{1 - (1 - H)(1 - r)\}\{1 - (1 - h)^2(1 - r)\} + (R - r)h(1 - h)]}. \tag{4}$$

Note that the condition for invasion, $S/d < \Theta(0, T)$, becomes the condition under which the un-cooperative strategy is evolutionarily stable, by reversing the direction of the inequality sign. $\Theta(0, \infty)$ becomes 0 for $R = r$, as well as $\Theta(1, \infty)$. Conversely, $\Theta(0, \infty)$ is strictly negative for $H = h$, as long as $R > r$ and $0 < h < 1$. This implies $\Theta(0, \infty) < \Theta(1, \infty)$, that is, the condition for invasion is more severe than that for evolutionary stability. We confirm this below.

Eq. (2) shows that $\Theta(q, \infty)$ is a function of $R, r, H, h,$ and q. In the following, we graphically investigate the relationship between $\Theta(q, \infty)$ and those parameters. First, $\Theta(q, \infty)$ is an increasing function of q (Fig. 3). This implies that Eq. (1) never fails during selection, once satisfied. That is, if $\Theta(q, \infty) > S/d$, selection increases q, and this leads to an even larger Θ. Therefore, the cooperative phenotype continues to increase in frequency until it is fixed in the population (see Fig. 3). The same argument is also applicable to the

$$\Theta(q, \infty) = \frac{(R - r)[\{\zeta + 2q(R - r)h(1 - h)\}(H - h) - (1 - q)(1 - H)(R - r)h(1 - h)\{1 - (1 - h)^2(1 - R)\}]}{\{1 - (1 - H)(1 - R)\}[\{\zeta + 2q(R - r)h(1 - h)\}\{1 - (1 - h)^2(1 - r)\} + (1 - q)(R - r)h(1 - h)\{1 - (1 - h)^2(1 - R)\}]}, \tag{2a}$$
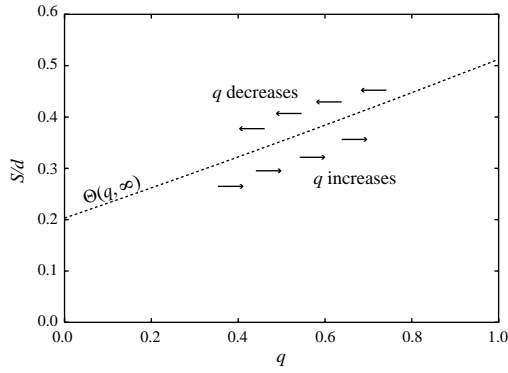
Fig. 3. This figure shows where q increases or decreases in $q - S/d$ plane. The dotted line shows the value of $\Theta(q, \infty)$ against q. In the upper and lower regions of the line, q decreases and increases, respectively.

un-cooperative strategy. Therefore, these two phenotypes never stably coexist.

The effects of H and h are quite simple (Figs. 4a and b). $\Theta(q, \infty)$ increases with increasing H and decreasing h. This effect is easy to understand, because the advantage Θ of avoiding future risk should be positively correlated with the relative risk H of plants with infested neighbors to the risk h of plants with non-infested neighbors.

Figs. 4c–f show the effects of R and r on Θ. Since the advantage of calling bodyguards is positively correlated with the efficacy of the signal, i.e. the relative magnitude of R to r, we expect the advantage Θ of the cooperative strategy to increase with increasing R and decreasing r. This is consistent with the result of the model when H is
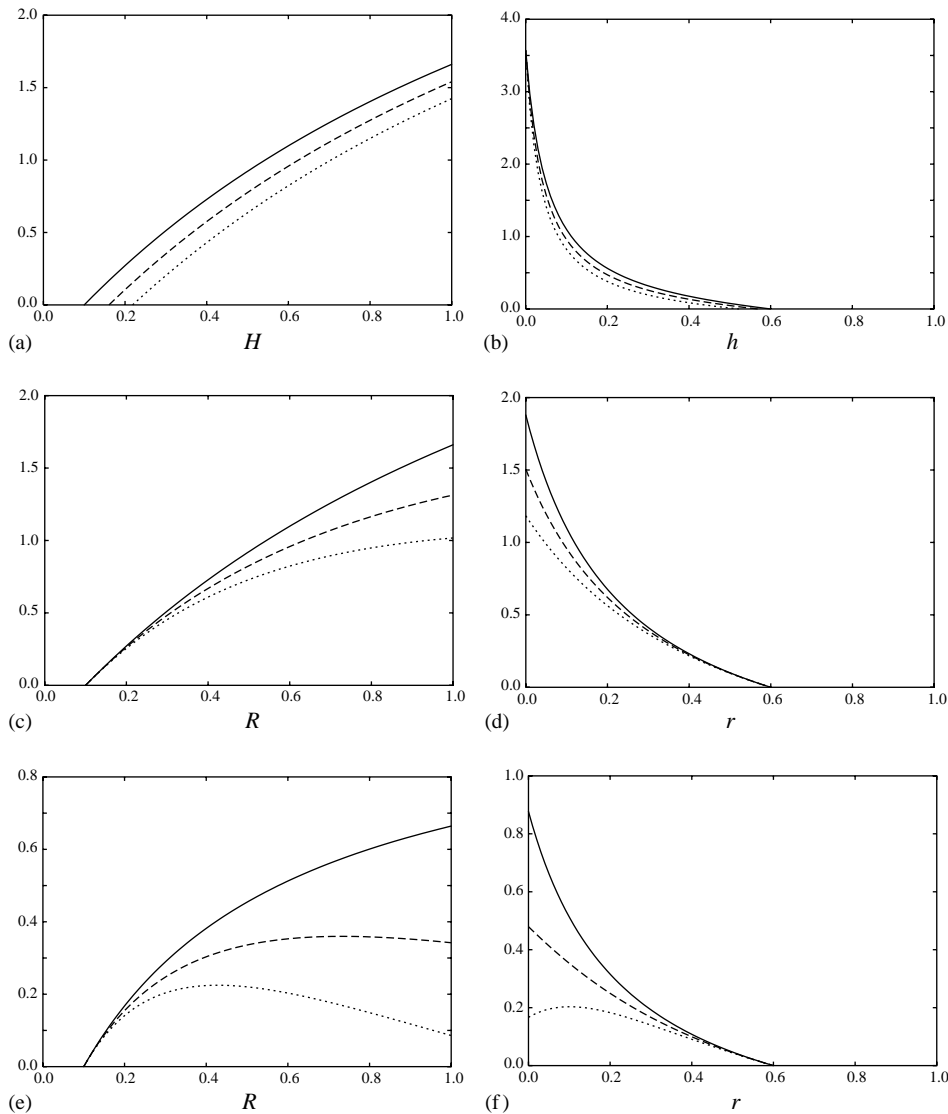

Fig. 4. Effect on $\Theta(q, \infty)$ of (a) H under $h = 0.1$, $R = 0.6$ and $r = 0.1$, (b) h under $H = 0.6$, $R = 0.6$, and $r = 0.1$, (c) R under $H = 0.6$, $h = 0.1$, and $r = 0.1$, (d) r under $H = 0.6$, $h = 0.1$, $R = 0.6$, (e) R under $H = 0.3$, $h = 0.1$, and $r = 0.1$, and (d) r under $H = 0.3$, $h = 0.1$, and $R = 0.6$. The dotted lines, broken lines, and solid lines in the figures correspond to $q = 0.0$, $q = 0.5$, and $q = 1.0$, respectively.

somewhat larger than h (Figs. 4c and d). However, a counterintuitive relationship appears when H is close to h; that is, in this case, $\Theta(q, \infty)$ can take a maximum value given medium values of R or r (Figs. 4e and f). This is probably because of a hidden negative effect of increasing R, which is explained below. Note that the future risk of plants is almost independent of whether their partners are infested under $H \approx h$. Now, which is better for plants, having an infested or a non-infested partner? Imagine that an individual has just been attacked. If it has an infested partner, it can recover with probability R. Conversely, if it has a non-infested partner, it might only recover with probability r, because the partner might be an un-cooperative individual. Following this logic, plants can decrease their risk by having infested neighbors. That is, plants should positively ignore their neighbors' unhappiness. We may call such intentional un-cooperation "heartlessness". The negative effect of heartlessness obviously increases with increasing relative magnitude of R to r, and may reverse the effect of increasing R or decreasing r. Figs. 4e and f show this effect.

So far, we have assumed that T is infinitely large for analytical tractability. To check the validity of this approximation, we calculated values of Θ for finite T. Fig. 5 shows that the approximations overestimate the real values, but they are fairly good for large T. The real values are about 90% of the approximated values for $T = 10$. The advantage Θ of the cooperative strategy decreases with decreasing T. This is reasonable, because plants with a short lifespan need not consider their short future. For example, when $T = 1$, the cooperative strategy is foolish, because plants have no future in which to recover the signal cost.
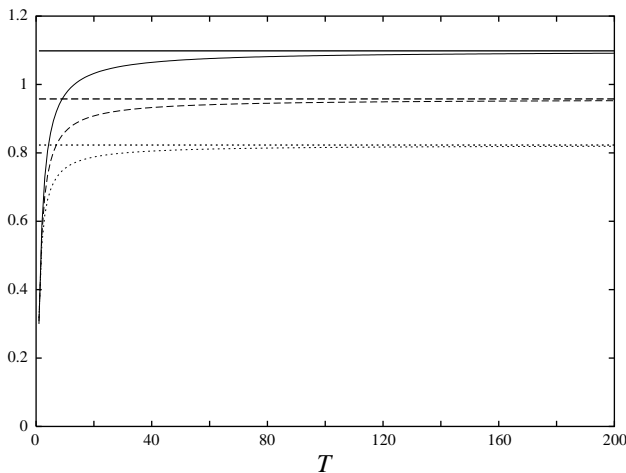
2.3. Analysis for all N

Now we consider all N. Unlike the special case of $N = 2$, we need explicit functions in the form $V(n_s)$ and $Z(k)$. Therefore, we assume the following simple functions:

$$V(n_s) = (R - r)\frac{n_s - 1}{N - 1} + r, \tag{5a}$$

$$Z(k) = (H - h)\frac{k}{N - 1} + h. \tag{5b}$$

We derived these equations by assuming that $V(n_s)$ and $Z(k)$ increase linearly with n_s and k, respectively. Note that these functions reduce to those treated in the previous subsection by substituting $N = 2$. For mathematical simplicity, we investigate only the conditions producing evolutionary stability and invasion, and we do not treat all q. As shown in Appendix C, we can obtain the following conditions for evolutionary stability and invasion:

$$\frac{S}{d} < \Psi_1(N, T), \tag{6a}$$

$$\frac{S}{d} < \Psi_0(N, T), \tag{6b}$$

where we can numerically obtain Ψ_0 and Ψ_1. The subscripts imply the values of q. The arguments N and T are shown for convenience (recall Eq. (1)) and imply that Ψ_0 and Ψ_1 depend on those parameters. Note that $\Psi_0(2, T)$ and $\Psi_1(2, T)$ should have values equivalent to $\Theta(0, T)$ and $\Theta(1, T)$ from the definitions of those symbols.

The effects of $R, r, h,$ and H on Ψ_0 and Ψ_1 are similar to those under $N = 2$ (Fig. 6). Therefore, the main results of the previous subsection are preserved. Fig. 7 shows the effect of n^* on Ψ for different values of N. From the figure, as N increases, both Ψ_0 and Ψ_1 decrease. This is explained as follows. Suppose there are rare cooperative mutants in an un-cooperative population. From Eq. (5a), increasing N decreases the contribution of one individual signaler to the recovery probability of the patch; that is, when N is large, an additional signal by a cooperative mutant improves the recovery probability only slightly. Therefore, as N increases, cooperative mutants become less likely to invade. Likewise, when N is large, un-cooperative mutants in a cooperative population decrease the recovery probability of the patch only slightly. Therefore, as N increases, the un-cooperative mutants become more likely to invade. Therefore, whether the cooperative phenotypes are rare or dominant, increasing N makes the cooperative strategy disadvantageous, as shown in Fig. 7. At the limit $N \to \infty$, the relative contribution of an individual disappears. Therefore, each individual signaler can never affect the recovery

Fig. 5. Effect of T on $\Theta(q, T)$ under $H = 0.6$, $h = 0.1$, $R = 0.6$, and $r = 0.1$. The dotted lines, broken lines, and solid lines in the figures correspond to $q = 0.0$, $q = 0.5$, and $q = 1.0$, respectively. The thinner curved lines represent $\Theta(q, T)$, and the bold horizontal lines represent $\Theta(q, \infty)$.
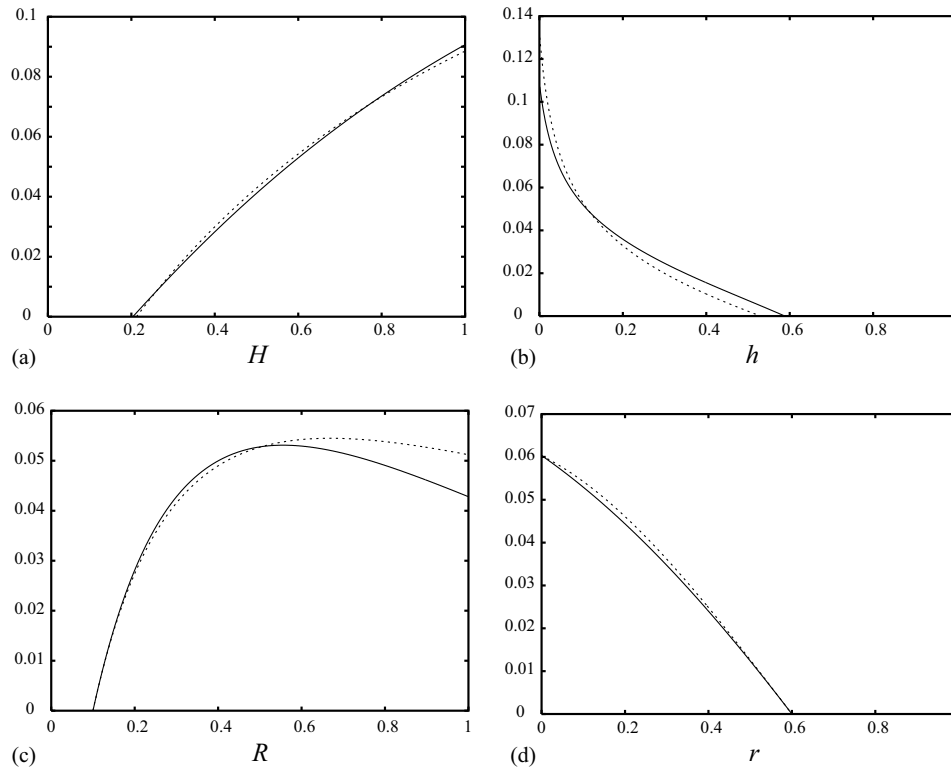
Fig. 6. Effect on $\Psi_0(N,T)$ (dotted lines) and $\Psi_1(N,T)$ (solid lines) of (a) H under $h = 0.1$, $R = 0.6$ and $r = 0.1$, (b) h under $H = 0.6$, $R = 0.6$, and $r = 0.1$, (c) R under $H = 0.6$, $h = 0.1$, and $r = 0.1$, and (d) r under $H = 0.6$, $h = 0.1$, $R = 0.6$. In every figure, $N = 6$, $n^* = 3$, $T = 100$.

probability of the patch by itself, and the cooperative signal is always disadvantageous.

Fig. 7 also shows that Ψ increases with n^* for each N. Therefore, the cooperative strategy is advantageous when cooperative individuals do not signal until many patch-mates become infested. This is probably because the advantage of the cooperative signal increases with the increasing certainty of the risk. That is, as the number of infested patch-mates increases, the risk increases, and the cooperative signal becomes more necessary.

Note that Ψ_1 is not always larger than Ψ_0, while $\Theta(1,T)$ was always larger than $\Theta(0,T)$ (compare Figs. 4 and 6). The two strategies coexist stably when $\Psi_1 < S/d < \Psi_0$, that is, when the cooperative strategy can invade, but is not evolutionarily stable. Therefore, the two strategies can coexist under $N > 2$, unlike when $N = 2$.

Fig. 8 shows the boundary line that splits the $h - n^*$ plane into two regions, according to the sign of $\Psi_0 - \Psi_1$. Different lines correspond to different values of N. In the region above the boundary, $\Psi_0 - \Psi_1$ is negative, i.e. the two strategies cannot coexist. Conversely, in the lower region, $\Psi_0 - \Psi_1$ is positive, so they can coexist if S/d is between Ψ_1 and Ψ_0. Note that the lines in Fig. 8 intersect the n^* axis at points where $n^* = N - 1$, which means that the two strategies never coexist under $n^* = N - 1$. This suggests why the two strategies
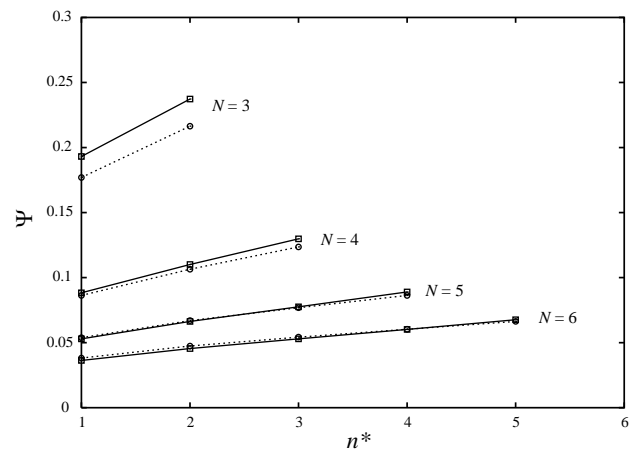

Fig. 7. Effect of n^* on $\Psi_0(N,T)$ (dotted lines) and $\Psi_1(N,T)$ (solid lines) for several N's (3, 4, 5, and 6) under $H = 0.6$, $h = 0.1$, $R = 0.6$, $r = 0.1$, and $T = 100$.

can coexist under $N > 2$. Note that even when the un-cooperative strategy is not evolutionarily stable, un-cooperative mutants can invade a population of co-operative individuals as "sneakers". That is, in a cooperative population, un-cooperative mutants can benefit from cooperative signals emitted by cooperative residents, without signaling themselves. Under $n^* = N - 1$, however, a cooperative signal by a non-infested resident never occurs, as long as the mutant is not
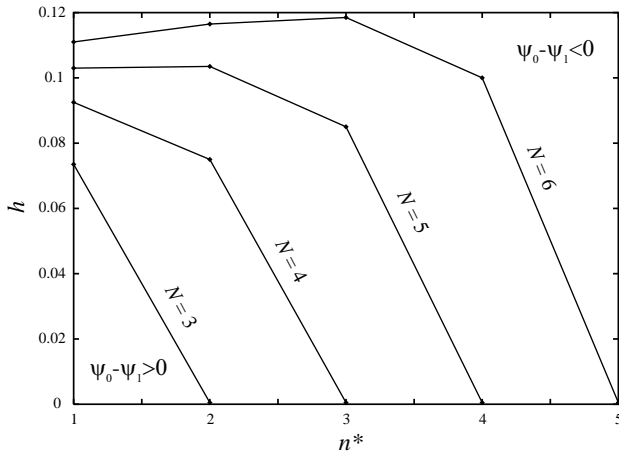
Fig. 8. This figure shows where $\Psi_0 - \Psi_1$ is positive or negative in $h - n^*$ plane for several N's (3, 4, 5, and 6) under $H = 0.6$, $R = 0.6$, $r = 0.1$, and $T = 100$. In the region upper than the line, $\Psi_0 - \Psi_1$ is negative, and in the region lower than the line, $\Psi_0 - \Psi_1$ is positive.

infested. Therefore, an un-cooperative mutant cannot steal benefits without paying the cost of signal and damage, so that sneakers cannot invade. Therefore, the two strategies cannot coexist under $n^* = N - 1$. In the previous subsection, we already showed that the two strategies cannot coexist under $N = 2$, for which $n^* = N - 1 = 1$. Here, we explained an understandable aspect of the mechanism of coexistence. Many factors, which are no longer intuitive, may affect the possibility of coexistence.

3. Discussion

There is much evidence that chemicals convey information between plants. Water-soluble or volatile chemicals are transferred from wounded or infested plants to undamaged plants via the soil or air (see articles in *Biochem. Sys. Ecol.* 29, 2001). For example, undamaged plants or plant leaves exposed to chemicals emitted by damaged plants can increase their resistance to herbivory. In addition, several papers have suggested that plants reflexively release info-chemicals when exposed to info-chemicals from other plants. We call such a secondarily released signal a "cooperative signal" or "co-signal" in this paper.

We theoretically investigated how a cooperative signal can evolve. We hypothesized that a cooperative signal evolves to reduce possible future risk and analysed a mathematical model. As a result, we confirmed that our hypothesis functions generally, as we expected. The model showed that the cooperative signal is adaptive, especially in the following situations: (1) the cost of the signal is small compared with the cost of damage by infestation, (2) the efficacy of the signal is significantly correlated with the local density of the chemical ($R \gg r$),

(3) plants with infested neighbors are at greater risk than those without infested neighbors ($H \gg h$), and (4) the lifespan of the plants is long relative to that of herbivores ($T \gg 1$). However, too efficacious a cooperative signal ($R \approx 1$) may decrease its advantage via the effect of heartlessness (see Section 2.2).

We know of two systems in which the cooperative strategy might exist. One involves herbivorous mites and beans (Dicke et al., 1990; Bruin et al., 1992; Dicke and Dijkman, 2001), and the other involves aphids and their host plants (Birkett et al., 2000; Chamberlain et al., 2001). These systems satisfy condition (4) well. That is, mites and aphids generally have very short life cycles and increase explosively, overexploiting their hosts (Bruin et al., 1992; Dixon, 1985), which means that T is quite large. Moreover, mites spread by passive aerial dispersal, and the distribution of their dispersal distance shows a slope that declines with distance from the release point (Jung and Croft, 2001). Therefore, in the mite system, condition (3) should be satisfied ($H \gg h$).

We also showed that the cooperative strategy is more likely to evolve when N is small. In our model, a "patch" is the region where the efficacy of the signal is correlated with the number of signalers. Therefore, small N implies that signal emission by an individual does not contribute to the recovery of individuals far from the signaler. The cooperative strategy also becomes advantageous with increasing n^*. That is, the cooperative signal is advantageous if the co-signalers emit the cooperative signal only under situations of great risk. From this result, one might think that a larger n^* would evolve if it were an evolutionary trait. However, we compared only the costs of the cooperative and un-cooperative strategies here, and not the costs of strategies with different n^* values. If there is selection on n^*, an intermediate n^* might be favored. This problem is beyond the scope of this paper and remains to be solved.

The model shows that the cooperative and un-cooperative strategies can coexist stably under specific conditions. For the two strategies to coexist stably, they must be able to invade each other. Our model suggests how mutual invasion is realized. First, the cooperative mutants can increase in frequency via a mechanism similar to "group selection". That is, under specific conditions, patches with many cooperative individuals have greater fitness than those with few cooperative individuals, because those patches can prevent the spread of herbivores in advance. This group-level or patch-level selection favors patches with many cooperative individuals and prevents fixation of the un-cooperative strategy. Conversely, un-cooperative mutants can invade a population using the cooperative strategy, because they can benefit from the cooperative signal emitted by residents, i.e. cooperative individuals, without paying the cost of signaling. Therefore, both

strategies can invade each other. Of course, this balance is kept only when the parameters are within narrow limits.

In some aspects, our model is interestingly similar to models of the evolution of altruism or cooperation; that is, the cooperative and un-cooperative strategies are analogous to altruism and selfishness, respectively. First, the cooperative strategy is favored by group-level selection. In several models of the evolution of altruism, altruism evolves by group selection. For example, subpopulations or groups with many altruistic individuals have greater fitness than those with few altruistic individuals, so that the altruistic individuals increase in frequency (e.g. see Wilson, 1990; Wilson and Dugatkin, 1997). Second, iteration, i.e. the repeated recovery and attack steps, is essential to our model, as in the *iterated prisoner's dilemma game* (Axelrod, 1984), which is a model of the evolution of cooperation. In the iterated prisoner's dilemma game, it is obvious that altruistic or cooperative strategies are never evolutionarily stable without iteration, because altruistic players can neither revenge the treachery of selfish players nor get any repayment for altruistic behavior. Similarly, in our model, cooperative signalers need iteration to obtain repayment of the signal cost.

Group-level selection favoring the cooperative strategy has an interesting feature. In most models of the evolution of cooperation by group selection, all individuals in a group obtain an equivalent benefit by cooperation. In our model, however, there are two kinds of benefit: future safety and present recovery. Non-infested individuals obtain future safety, while infested individuals obtain both future safety and present recovery. This asymmetry between non-infested and infested individuals might complicate the model.

In this paper, we assumed that recovery steps precede attack steps. One might think that attack should precede recovery. Actually, the order of the sub-steps is not important, but the timing of evaluation of the costs is important. Suppose that we evaluate the costs of plants just before attack steps instead of recovery steps. Note that there is an attack step and a recovery step in this order between two successive evaluations in this case. Therefore, some of the individuals attacked after an evaluation recover before the next evaluation, and their costs are not evaluated. To evaluate their costs, we must evaluate the costs just before recovery steps, as we did here. We assumed that costs are evaluated at the end of each time step for mathematical simplicity. From this assumption, it follows that the recovery step precedes the attack step in each time step. This also leads to the initial step in each generation being a recovery step, not an attack step, which seems somewhat strange. However, this is not problematic because the initial recovery step does not affect the result, as mentioned before.

Indirect defense seems unrealistic at a glance, in spite of much evidence for it. Furthermore, the hypothesis for a cooperative strategy proposed here is more complicated. One might think that the theory is too complicated and that there might be simpler interpretations of the phenomenon. We consider two alternative hypotheses below.

First, the cooperative strategy might have evolved via "kin selection" (Hamilton, 1964; Grafen, 1985; Taylor and Frank, 1996; Frank, 1998). That is, if neighboring plants are genetically related, the cooperative signal literally evolves to help neighboring relatives, not to reduce own future risk. In order for this hypothesis to be applicable, the following two conditions must be met: (1) relatives must tend to clump through the history of natural selection and (2) the signal efficacy is positively correlated with the local density of the chemicals, as assumed here.

Second, the co-signalers might intend to make natural enemies stay nearby, as combatants to protect against possible future risk. If bodyguards remain near the secondary signalers, at least for a while, in spite of the absence of prey, such a strategy would be effective in preventing herbivore attack.

We doubt the effects of these two hypotheses in several cases. For example, plants may not have been near relatives during past selection, invalidating the kin-selection hypothesis. We also feel that predators are not so patient that they will wait for the arrival of herbivores in the proximity of the plants. However, these mechanisms might combine with our mechanism to cause evolution of a cooperative signal.

Finally, we criticize our own theory. The primary criticism is that there is scant evidence or few studies in this area. Several studies have shown, directly or indirectly, that undamaged plants or leaves exposed to air gathered from near infested plants or leaves can also release signal chemicals, which attract natural enemies. However, the secondarily released signal is weaker and less effective than that released directly from damaged leaves (Bruin and Sabelis, 2001). The secondary signal might not be actively released. That is, the signal chemical emitted by infested plants might be absorbed into the surface of the leaves of neighboring undamaged plants, and the absorbed chemicals may then re-diffuse into the air (Bruin et al., 1992, 1995); in such a case, the secondary signal would not be a strategy, but merely a trivial physical phenomenon. Nevertheless, information chemicals released from the roots of an infested plant and transferred to the roots of a non-infested individual via water or soil can promote emission of the signal chemical from the leaves of the receiver plant (Chamberlain et al., 2001; Dicke and Dijkman, 2001). Therefore, our hypothesis is applicable underground. That is, plants can receive information through the soil.

Almost nothing is known about indirect defense against future enemies. More importantly, the significance and role of plant–plant communication or plant–predator communication are poorly understood. Many previous investigations of these topics were conducted under somewhat artificial situations. Moreover, the plants studied were often cultivated plants or closely related species. Therefore, from past experimental investigations we can estimate the significance of info-chemical communication throughout an ecosystem only abstractly. Field investigations under more natural conditions are desired.

Acknowledgements

Appendix A

Notation

N — the number of individuals per patch

$L|Q$ — the state of a patch, in which the leftmost individual is in state L and there are Q infested individuals other than the leftmost

X/Y — the type of patch, in which the leftmost individual is phenotype X and all the other patch-mates are phenotype Y

$*/-$ — patch that does not belong to any type

C — cooperative strategy

U — un-cooperative strategy

n^* — the cooperative signal occurs when the number of infested individuals is $\geqslant n^*$

n_s — the number of signaling individuals in a patch

T — the number of time steps per generation

$V(n_s)$ — recovery probability of patches in which n_s individuals are signaling

$Z(k)$ — probability of individuals with k infested patch-mates being attacked

R — maximum value of $V(n_s)$. i.e. $R = V(N)$

r — minimum value of $V(n_s)$. i.e. $r = V(1)$

H — maximum value of $Z(k)$, i.e. $H = Z(N-1)$

h — minimum value of $Z(k)$, i.e. $h = Z(0)$

S — cost of signal per time step

d — cost of damage per time step

q — frequency of cooperative individuals

$r_{X/Y,i}$ — recovery probability of a patch of type X/Y in state i under $N = 2$

Θ — the cooperative strategy increase in frequency when $S/d < \Theta$ under $N = 2$

$\mathbf{R}_{X/Y}$ — state transition matrix for type X/Y patches in a recovery step under $N = 2$

$\mathbf{H}$ — state transition matrix in an attack step under $N = 2$

$\gamma_{X/Y,i,t}$ — frequency of patches in state i at time step t within the group of type X/Y patches under $N = 2$

$\gamma_{X/Y,t}$ — vector whose i-th element is $\gamma_{X/Y,i,t}$

$\bar{\gamma}_{X/Y,i}$ — temporal average of $\gamma_{X/Y,i,t}$, i.e. $(1/T)\sum_{t=1}^{T}\gamma_{X/Y,i,t}$

$\tilde{\gamma}_{X/Y,i}$ — stationary value of $\gamma_{X/Y,i,t}$, i.e. $\lim_{t\to\infty}\gamma_{X/Y,i,t}$

$\bar{c}_{X/Y}$ — per-step average cost of leftmost individuals in type X/Y patches

x_X — cost of leftmost individuals of phenotype X in patches in state $0|m$ ($n^* \leqslant m \leqslant N - 1$)

Ψ_0 — cooperative mutants can invade the un-cooperative population when $S/d < \Psi_0$

Ψ_1 — the cooperative strategy is evolutionarily stable when $S/d < \Psi_1$

$\gamma_{X/Y,i|m,t}$ — frequency of patches in state $i|m$ just before the $(t+1)$-th recovery step within the group of type X/Y patches under general N

$\bar{\gamma}_{X/Y,i|m}$ — temporal average of $\gamma_{X/Y,i|m,t}$, i.e. $(1/T)\sum_{t=1}^{T}\gamma_{X/Y,i|m,t}$

$\eta_{X/Y,i|m,t}$ — frequency of patches in state $i|m$ just before the $(t+1)$-th attack step within the group of type X/Y patches under general N

$r_{X/Y,i|m}$ — recovery probability of type X/Y patches from state $i|m$

Appendix B. Condition causing the cooperative strategy to increase in frequency under $N = 2$

In this appendix, we derive Eqs. (1) and (2). Let $\mathbf{R}_{X/Y}$ and $\mathbf{H}$ denote the transition matrices for the recovery and attack steps, respectively. The subscript of $\mathbf{R}_{X/Y}$ implies that the matrix depends on the type X/Y of the patch. From the transition diagrams (Fig. 2), the matrices are as follows:

$$\mathbf{R}_{X/Y} = \begin{bmatrix} 1 & r_{X/Y,2} & r_{X/Y,3} & R \\ 0 & 1 - r_{X/Y,2} & 0 & 0 \\ 0 & 0 & 1 - r_{X/Y,3} & 0 \\ 0 & 0 & 0 & 1 - R \end{bmatrix}, \quad \text{(B.1a)}$$

$$\mathbf{H} = \begin{bmatrix} (1-h)^2 & 0 & 0 & 0 \\ h(1-h) & 1 - H & 0 & 0 \\ h(1-h) & 0 & 1 - H & 0 \\ h^2 & H & H & 1 \end{bmatrix}. \quad \text{(B.1b)}$$

As mentioned in Section 2.2, $r_{X/C,2} = r_{C/Y,3} = R$ and $r_{X/U,2} = r_{U/Y,3} = r$ for any X and Y. The transition matrix of a unit time step is given by the product $\mathbf{HR}_{X/Y}$ of these matrices. Note that the (i,j) element of matrix $\mathbf{R}_{X/Y}$ ($\mathbf{H}$) is the transition probability from state j to state i in a recovery (attack) step. Therefore, the (i,j) element of $\mathbf{HR}_{X/Y}$ gives the probability of the transition from state j to state i per time step.

Note that under $N = 2$, all patches are classified into any of the four types: C/C, C/U, U/C, and U/U. Therefore, we can split the population into the four corresponding groups according to the types of patches. We let $\gamma_{X/Y,i,t}$ denote the frequency of patches in state i just before the $(t+1)$-th recovery step within the group of type X/Y patches. We also let $\gamma_{X/Y,t}$ denote a vector whose i-th element is $\gamma_{X/Y,i,t}$. Note that this vector represents the frequency distribution of patch states *within group X/Y*; therefore, the absolute frequency of type X/Y patches in state i at time t is obtained by (the frequency of type X/Y patches)$\times \gamma_{X/Y,i,t}$. The distribution at the next time step is obtained as the product of the transition matrix and the distribution vector in the present time step:

$$\gamma_{X/Y,t+1} = \mathbf{HR}_{X/Y}\gamma_{X/Y,t}. \tag{B.2}$$

Iteration of Eq. (B.2) yields

$$\gamma_{X/Y,t} = (\mathbf{HR}_{X/Y})^t \gamma_{X/Y,0}, \tag{B.3}$$

where $\gamma_{X/Y,0}$ is the initial frequency distribution vector.

We denote the average per-step cost of left individuals in type X/Y patches by $\bar{c}_{X/Y}$. Left individuals incur no cost in state 1 (state 0|0). In states 2 (state 1|0) and 4 (state 1|1), they are infested and signal; therefore, their costs in states 2 and 4 are both $S + d$. Let x_X denote the per-step cost of left individuals of phenotype X in state 3 (state 0|1). x_X depends on phenotype X. If the left individual is phenotype C, it signals in state 3 (state 0|1), because its partner is infested; therefore, x_C equals the cost of signal S. By contrast, un-cooperative individuals do not signal, as they are safe; so x_U is 0. As mentioned before, we assume that costs are additive. Therefore, $\bar{c}_{X/Y}$ is given as

$$\begin{aligned}\bar{c}_{X/Y} &= \frac{1}{T}\sum_{t=1}^{T}[0 \times \gamma_{X/Y,1,t} + (S+d) \\ &\quad \times \{\gamma_{X/Y,2,t} + \gamma_{X/Y,4,t}\} + x_X\gamma_{X/Y,3,t}] \\ &= (S+d)\{\bar{\gamma}_{X/Y,2} + \bar{\gamma}_{X/Y,4}\} + x_X\bar{\gamma}_{X/Y,3},\end{aligned} \tag{B.4a}$$

where

$$\bar{\gamma}_{X/Y,i} = \frac{1}{T}\sum_{t=1}^{T}\gamma_{X/Y,i,t}. \tag{B.4b}$$

The overall per-step cost of phenotype X is equivalent to that of *left* individuals of phenotype X, because of the symmetry between left and right. A left individual of phenotype X appears in the left positions of type X/C and X/U patches with probabilities q and $(1 - q)$, respectively, because of the random distribution of individuals. Therefore, the per-step cost of left individuals of phenotype X is given by $q\bar{c}_{X/C} + (1 - q)\bar{c}_{X/U}$, and this equals the overall per-step cost of phenotype X. If the overall cost of phenotype C is smaller than that of phenotype U, phenotype C increases in frequency. Therefore, the condition causing the cooperative phenotype to increase in frequency is given by the following inequality:

$$q\bar{c}_{C/C} + (1 - q)\bar{c}_{C/U} < q\bar{c}_{U/C} + (1 - q)\bar{c}_{U/U}. \tag{B.5}$$

Substituting Eq. (B.4) for Eq. (B.5) and rearranging the resulting equation, we have

$$\frac{S}{d} < \Theta(q, T), \tag{B.6a}$$

where

$$\Theta(q, T) = \frac{q\bar{\gamma}_{C/C,3} + (1 - q)\bar{\gamma}_{C/U,3}}{q(1 - \bar{\gamma}_{C/C,1} - \bar{\gamma}_{U/C,2} - \bar{\gamma}_{U/C,4}) + (1 - q)(1 - \bar{\gamma}_{C/U,1} - \bar{\gamma}_{U/U,2} - \bar{\gamma}_{U/U,4})} - 1, \tag{B.6b}$$

where $\sum_{i=1}^{4}\bar{\gamma}_{X/Y,i} = 1$. Eq. (B.6) equals Eq. (1). Therefore, we have derived the condition causing the cooperative strategy to increase in frequency under $N = 2$. Since we can numerically calculate $\bar{\gamma}_{X/Y,i}$ for any X/Y and i from Eqs. (B.2) and (B.4b), we can also obtain the value of $\Theta(q, T)$ from Eq. (B.6b).

Since our system is a non-cyclical Markovian process, it has a stationary distribution $\tilde{\gamma}_{X/Y,i}$, and $\bar{\gamma}_{X/Y,i}$ approaches $\tilde{\gamma}_{X/Y,i}$, as T infinitely increases. One can easily obtain $\tilde{\gamma}_{X/Y,i}$ as the i-th element of the leading eigenvector of matrix $\mathbf{HR}_{X/Y}$ as

$$\tilde{\gamma}_{X/Y,1} = \frac{1 - h}{h\Omega}, \tag{B.7a}$$

$$\tilde{\gamma}_{X/Y,2} = \frac{1}{w_2\Omega}, \tag{B.7b}$$

$$\tilde{\gamma}_{X/Y,3} = \frac{1}{w_3\Omega}, \tag{B.7c}$$

$$\tilde{\gamma}_{X/Y,4} = \left\{\frac{2 - h}{R(1 - h)} - \frac{r_{X/Y,2}}{Rw_2} - \frac{r_{X/Y,3}}{Rw_3}\right\}\Omega^{-1}, \tag{B.7d}$$

where

$$\Omega = \frac{2 - h}{R(1 - h)} + \frac{1 - h}{h} + \frac{R - r_{X/Y,2}}{Rw_2} + \frac{R - r_{X/Y,3}}{Rw_3}, \tag{B.7e}$$

$$w_2 = 1 - (1 - r_{X/Y,2})(1 - H), \qquad (B.7f)$$

$$w_3 = 1 - (1 - r_{X/Y,3})(1 - H), \qquad (B.7g)$$

Then, substituting $\tilde{\gamma}_{X/Y,i}$ for $\bar{\gamma}_{X/Y,i}$ in Eq. (B.6b), we obtain the analytical expression of $\Theta(q, \infty)$, which is given in Eq. (2).

Appendix C. Conditions of evolutionary stability and invasion under general N

In this appendix, we derive the condition producing evolutionary stability and the condition resulting in invasion for the cooperative strategy for general N. First, as we did in Appendix B, we split the population according to the types of patches, and obtain five groups: i.e. groups of type C/C, C/U, U/C, U/U, and $*/-$. We let $\gamma_{X/Y,i|m,t}$ denote the frequency of the patches in state $i|m$ just before the $(t + 1)$-th recovery step within the group of type X/Y patches. We let $\eta_{X/Y,i|m,t}$ denote the corresponding frequency just before the $(t + 1)$-th attack step. Since recovery is equivalent to the transition to state $0|0$, the state transition in a recovery step is described by the following equations:

$$\eta_{X/Y,0|0,t} = \sum_{i,m} r_{X/Y,i|m}\gamma_{X/Y,i|m,t}, \qquad (C.1a)$$

$$\eta_{X/Y,i|m,t} = (1 - r_{X/Y,i|m})\gamma_{X/Y,i|m,t} (i|m \neq 0|0), \qquad (C.1b)$$

where $r_{X/Y,i|m}$ is the recovery probability of type X/Y patches from state $i|m$. Note that Eq. (C.1) corresponds to matrix $\mathbf{R}_{X/Y}$ under $N = 2$.

In an attack step, a state $0|m$ patch arises from a state $0|k$ patch before the sub-step, where k is any number smaller than or equal to m. The state $0|k$ patch shifts to state $0|m$, if the leftmost individual is not attacked and $m - k$ other individuals are attacked. The probability of the former is $1 - Z(k)$, and that of the latter is

$$\binom{N - 1 - k}{m - k} Z(k)^{m-k}\{1 - Z(k)\}^{N-m-1},$$

where

$$\binom{N - 1 - k}{m - k}$$

is the number of combinations of $m - k$ individuals out of $N - 1 - k$ individuals. The product of these two probabilities gives the probability that a patch in state $0|k$ shifts to state $0|m$ in an attack step. Therefore, we have

$$\gamma_{X/Y,0|m,t+1} = \sum_{k=0}^{m} \binom{N - 1 - k}{m - k} Z(k)^{m-k}$$
$$\times \{1 - Z(k)\}^{N-m}\eta_{X/Y,0|k,t}. \qquad (C.2)$$

A state $1|m$ patch arises from one of the patches in state $0|k$ or state $1|k$ before the attack step, where $m \geqslant k$. A patch in state $0|k$ shifts to state $1|m$ if the leftmost individual and $m - k$ other individuals are attacked. The probability of the former condition is $Z(k)$, and that of the latter is

$$\binom{N - 1 - k}{m - k} Z(k)^{m-k}\{1 - Z(k)\}^{N-m-1}.$$

A patch in state $1|k$ shifts to state $1|m$ if $m - k$ individuals other than the leftmost are attacked anew. Since there are $k + 1$ infested individuals in a state $1|k$ patch, the condition is satisfied with probability

$$\binom{N - 1 - k}{m - k} Z(k+1)^{m-k}\{1 - Z(k+1)\}^{N-m-1}.$$

Therefore, we have

$$\gamma_{X/Y,1|m,t+1} = \sum_{k=0}^{m} \binom{N - 1 - k}{m - k} Z(k)^{m-k+1}$$
$$\times \{1 - Z(k)\}^{N-m-1}\eta_{X/Y,0|k,t}$$
$$+ \sum_{k=0}^{m} \binom{N - 1 - k}{m - k} Z(k+1)^{m-k}$$
$$\times \{1 - Z(k+1)\}^{N-m-1}\eta_{X/Y,1|k,t}. \qquad (C.3)$$

Together, Eqs. (C.2) and (C.3) represent the state transition in attack steps. Note that these equations correspond to matrix $\mathbf{H}$ defined in Appendix B. To iteratively calculate $\gamma_{X/Y,i|m,t}$ for each time step, we need the value of $r_{X/Y,i|m}$ in Eq. (C.1). $r_{X/Y,i|m}$ is a recovery probability, so it depends on the number of signaling individuals, n_s, according to Eq. (5a), and n_s depends on the type (X/Y) and state $(i|m)$ of the patch. In a patch in state $i|m$, the cooperative individuals signal if $i + m \geqslant n^*$ and any infested individuals signal. Therefore, we can calculate n_s for any set of patch type and state (see Table 1). Consequently, we can obtain the values of $r_{X/Y,i|m}$ from Eq. (5a) and Table 1. Then, applying Eqs. (C.1), (C.2) and (C.3) iteratively, we can calculate the values of $\gamma_{X/Y,i|m,t}$ for each time step.

We denote the average per-step cost of the leftmost individuals of phenotype X in type X/Y patches as $\bar{c}_{X/Y}$. Noting that an infested individual incurs cost $S + d$ and that costs are additive, we have

$$\bar{c}_{X/Y} = \frac{1}{T}\sum_{t=1}^{T}\left\{(S + d)\sum_{m=0}^{N-1}\gamma_{X/Y,1|m,t}\right.$$
$$\left. + x_X \sum_{m=n^*}^{N-1}\gamma_{X/Y,0|m,t}\right\}, \qquad (C.4)$$

where x_X depends on the phenotype X of the leftmost individual. If the leftmost individual is cooperative, it signals if there are at least n^* infested individuals; therefore, $x_C = S$ (note that the second sum in the

Table 1
Values of n_s for possible combinations of patch types and states

	STATE	
	$0\|m$	$1\|m$
TYPE		
C/C	m if $m < n^*$	$1+m$ if $1+m < n^*$
	N if $m \geqslant n^*$	N if $1+m \geqslant n^*$
C/U	m if $m < n^*$	$1+m$
	$1+m$ if $m \geqslant n^*$	
U/C	m if $m < n^*$	$1+m$ if $1+m < n^*$
	$N-1$ if $m \geqslant n^*$	N if $1+m \geqslant n^*$
U/U	m	$1+m$

n_s depends not only on types and states, but also on whether the number of infested individuals is larger than n^* or not. Therefore, n_s values are given with conditions in the table.

middle bracket in Eq. (C.4) is the sum for $n^* \leqslant m \leqslant N-1$). Conversely, if the individual is not cooperative, it does not signal so long as it is not infested; thus, $x_U = 0$.

If the cost of the wild type is smaller than the cost of rare mutants, the wild type is evolutionarily stable. If not, the mutant strategy can invade. Therefore, the respective conditions for evolutionary stability and invasion for the cooperative strategy are

$$\bar{c}_{C/C} < \bar{c}_{U/C}, \tag{C.5a}$$

$$\bar{c}_{C/U} < \bar{c}_{U/U}. \tag{C.5b}$$

Substituting Eq. (C.4) for Eq. (C.5), and rearranging the resulting equations, we have

$$\frac{S}{d} < \Psi_1 = \frac{\sum_{m=0}^{N-1} \bar{\gamma}_{U/C,1|m} - \sum_{m=0}^{N-1} \bar{\gamma}_{C/C,1|m}}{\sum_{m=0}^{N-1} \bar{\gamma}_{C/C,1|m} + \sum_{m=n^*}^{N-1} \bar{\gamma}_{C/C,0|m} - \sum_{m=0}^{N-1} \bar{\gamma}_{U/C,1|m}}, \tag{C.6a}$$

$$\frac{S}{d} < \Psi_0 = \frac{\sum_{m=0}^{N-1} \bar{\gamma}_{U/U,1|m} - \sum_{m=0}^{N-1} \bar{\gamma}_{C/U,1|m}}{\sum_{m=0}^{N-1} \bar{\gamma}_{C/U,1|m} + \sum_{m=n^*}^{N-1} \bar{\gamma}_{C/U,0|m} - \sum_{m=0}^{N-1} \bar{\gamma}_{U/U,1|m}}, \tag{C.6b}$$

where

$$\bar{\gamma}_{X/Y,i|m} = \frac{1}{T} \sum_{t=1}^{T} \gamma_{X/Y,i|m,t}. \tag{C.6c}$$

Eqs. (C.6) is equivalent to Eq. (6). We can calculate $\gamma_{X/Y,i|m,t}$ for any time step iteratively by applying Eqs. (C.1)–(C.3). Therefore, we can also obtain the values of Ψ_0 and Ψ_1 from Eqs. (C.6).

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