

# Evolution of talking plants in a tritrophic context: Conditions for uninfested plants to attract predators prior to herbivore attack

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Received 2 February 2006; received in revised form 14 May 2006; accepted 30 May 2006

Available online 13 June 2006

## Abstract

Herbivory induces plants to emit volatile chemicals that attract enemies of the herbivores (bodyguards of plants). In this way, the plant acquires protection and the bodyguards gain food. These plant signals cause neighboring plants, not under attack, to release signals as well. We hypothesize that such “secondary” signals help to reduce damage from future herbivore attacks by the protection received from the bodyguards. By modeling we explore the conditions for such secondary signals to evolve. Three kinds of strategies are considered: plants of the first strategy always emit a signal, those of the second strategy emit a signal only when infested, and those of the third strategy emit a signal not only when infested, but also when a certain number of neighbors are infested (i.e. secondary signaling). When signaling is much less (much more) costly than damage from herbivory, the first (second) strategy will be favored by selection, whereas for intermediate costs the third strategy, i.e. secondary signaling, will evolve. However, secondary signaling will not evolve when the primary signals lure the bodyguards too effectively. This is because the undamaged plant gains associational defense when the infested individual is defending very well; therefore, the need for secondary signaling decreases.

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**Keywords:** Plant–plant communication; Induced defense; Plant volatile; Herbivore; Natural enemy

## 1. Introduction

Plants increase the emission of volatile chemicals or emit new volatile chemicals at the onset of herbivory (Dicke and Vet, 1999). These herbivore-induced plant volatiles (HIPV) betray the location of herbivores to their enemies (Takabayashi and Dicke, 1996; Dicke and Vet, 1999; Sabelis et al., 1999b, 2002). Therefore, by tracking HIPV to their source, the enemies gain by finding food, whereas plants gain protection against herbivores. In fact, there is experimental evidence that emission of HIPV promotes plant protection and seed set as a measure of fitness (Van Loon et al., 2000; Fritzsche-Hoballah and Turlings, 2001). The emission of HIPV as an SOS signal has been shown to be evolutionarily stable in models of plant protection by

bodyguards (i.e. herbivores’ enemies) (Sabelis and De Jong, 1988; Godfray, 1995).

Plant volatiles may affect neighboring plants by adsorption to the plant cuticle and/or by triggering a physiological response. There is abundant empirical evidence for the latter, and even where the evidence pointed at a role of the adsorption, there was also solid evidence for physiological response (Choh et al., 2004). Plant volatiles can affect the defense strategies of neighboring plants (Baldwin and Schultz, 1983; Rhoades, 1983, 1985; for reviews, see e.g. Dicke and Bruin, 2001; Dicke et al., 2003). For example, exposure of a plant to HIPV subsequently increases the plant’s resistance to herbivores (Haukioja et al., 1985; Dolch and Tschardt, 2000; Karban et al., 2000; Karban, 2001; Karban and Maron, 2002; Karban et al., 2003; Ninkovic et al., 2003), induces avoidance of that plant by herbivores (Ninkovic et al., 2002; Glinwood et al., 2003, 2004), promotes the plant’s production of defense-related plant compounds or expression of resistance genes (Zeringue, 1987; Farmer and Ryan, 1990; Shulaev et al.,

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Nomenclature	
$N$	number of individuals in a patch
$T$	number of time steps per generation
$n$	threshold of signaling
$P$	probability that a signaling individual is visited by bodyguards
$H(N_{inf})$	probability that an individual is attacked in a patch having $N_{inf}$ infested individuals
$H_{min}$	minimum value of $H$ , i.e. $H(0)$
$H_{max}$	maximum value of $H$ , i.e. $H(N-1)$
$c_{sig}$	cost of a signal
$c_{dam}$	cost of damage
$\Theta_N(n n^*)$	threshold of $c_{sig}/c_{dam}$ that determines the invasion success of mutant strategy $n$ in the population of strategy $n^*$
$\tilde{\Theta}_N$	$\lim_{T \rightarrow \infty} \Theta_N$
$\gamma_{x,y}(t)$	probability that a type- $x$ patch is in state $y$ just before the $(t+1)$ th defense step
$\bar{\gamma}_{x,y}$	$(1/(T+1))\sum_{t=0}^T \gamma_{x,y}(t)$
$\tilde{\gamma}_{x,y}$	$\lim_{t \rightarrow \infty} \gamma_{x,y}(t)$
$\gamma_x$	column vector whose $i$ th element is $\gamma_{x,i}(t)$
$\tilde{\gamma}_x$	$\lim_{t \rightarrow \infty} \gamma_x(t)$
$C_{n/n^*}$	per-step average payoff for a marked individual of mutant strategy $n$ in the population of strategy $n^*$
$F_{n/n^*}$	$\sum_{j < n} \bar{\gamma}_{n/n^*,0 j}$ ; i.e. the per-step average of the probability that a marked individual of strategy $n$ is not signaling in the population of strategy $n^*$
$V_x$	transition probability matrix for a type- $x$ patch
$n/n^*$	type of patch in which the marked individual is strategy $n$ and the others are strategy $n^*$
$ij$	state of a patch in which the marked individual is in state $i$ and there are $j$ infested unmarked individuals
$Q_n(N_{inf})$	probability that an uninfested individual of strategy $n$ with $N_{inf}$ infested patch mates is visited by bodyguards in a defense step
$i.0$	state of an individual that is in state $i$ and is not protected
$i.1$	state of an individual that is in state $i$ and is protected
$i.j m.l$	state of a patch in which the marked individual is in state $i,j$ , $m$ unmarked individuals are infested, and $l$ unmarked individuals are protected
$\eta_{x,y}(t)$	probability that a type- $x$ patch is in state $y$ just before the $(t+1)$ th attack step

1997; Arimura et al., 2000, 2001, 2002), and also prime the plant's defenses to future attack (Choh et al., 2004; Engelberth et al., 2004). Those physiological responses may be manipulation by the emitter of volatiles or the strategy of the exposed plants. If the latter is the case, it means that neighbor plants exchange information on the potential for future herbivore attacks, and adjust their resistance level accordingly.

Not only resistance but also attractiveness of an uninfested plant to the bodyguards increases after exposure to chemicals released from infested plants (Dicke et al., 1990; Bruin et al., 1992; Birkett et al., 2000). Such secondary induction of signal emission can even occur underground and cause emission of volatiles from above-ground parts (Chamberlain et al., 2001; Dicke and Dijkman, 2001; Guerrieri et al., 2002). These phenomena require not only more empirical but also theoretical investigation to answer when "secondary signaling" evolves.

In an earlier paper (Kobayashi and Yamamura, 2003) on an iterated, frequency-dependent game prompted by a one-shot matrix game model described by Järemo et al. (1999), we proposed a hypothesis to address this question. The model was based on two crucial assumptions. First, plants with infested, as opposed to herbivore-free, neighbors are assumed to incur greater risk of receiving damage due to mobility of the herbivore. Second, the uninfested plant is assumed to promote arrival of bodyguards on the infested

plant, thereby indirectly reducing its own risk of incurring damage from herbivores currently infesting their neighbor. This second assumption is plausible because the uninfested plant increases the overall concentration of the volatile and act as guideposts leading bodyguards to targets (e.g. Bruin et al., 1995). Using evolutionary game theory, we showed that this hypothesis holds. Here, we refer to this as the "pre-attack extermination hypothesis" (PEH), to distinguish it from the new hypothesis presented below.

In this article, we maintain the first assumption of the PEH model, but alter the second in that even uninfested plants can obtain protection by signaling in advance of the actual attack. This requires that the uninfested plant not only attracts bodyguards but also make them stay for the time they need to discover that there are no herbivores to prey on. Thus, we hypothesize that prior to actual attack by herbivores, plants have evolved signaling in order to gain protection by bodyguards. We call this hypothesis the "pre-attack protection hypothesis" (PPH).

PEH and PPH have in common that the purpose of signaling is to avoid future infestation prior to an attack. However, they differ in how this purpose is realized. Under PEH, plants avoid the risk of future infestation by allowing predators to eliminate herbivores in their proximity, whereas under PPH plants reduce their risk by obtaining protection from bodyguards. In this article, we develop a game-theoretical model to assess the conditions under which PPH is valid.

## 2. Model

To test PPH, we use a model structure similar to that in Kobayashi and Yamamura (2003) who tested PEH (see Nomenclature for a summary of the symbols). Imagine a plant population composed of an infinitely large number of patches, each of which is occupied by  $N$  individuals. Patch mates are neighbors in space, but they are not genetically related because the population is assumed to be well mixed in every generation. The plants reproduce asexually. Each plant can be in one of two states: infested or uninfested. We assume that no individuals are infested at the start of each generation. Generations do not overlap. Each generation is composed of  $T$  time steps, and each time step further consists of two sub-steps: a “defense sub-step” and an “attack sub-step” (see Fig. 1 in Kobayashi and Yamamura (2003)). These sub-steps are explained in detail below. Each time step implies one reproduction cycle of herbivores relative to the lifespan of the plants.

Between any two succeeding steps (not sub-steps) infested individuals emit signals to attract bodyguards. Thus we assume from the start that SOS signaling has already established itself by evolution. Furthermore, plants also signal if the number of infested patch mates is larger than or equal to a threshold  $n$  ( $0 \leq n \leq N$ ). This threshold is an evolutionary trait that may differ among individuals. We refer to individuals whose threshold is  $n$  as “strategy- $n$ ” individuals. Note that strategy-0 individuals always signal, regardless of the number of infested patch mates. In contrast, strategy- $N$  individuals signal if and only if they are infested, because the number of infested patch mates never exceeds  $N-1$ . We are particularly interested in the conditions under which strategies with intermediate  $n$  ( $1 \leq n \leq N-1$ ) are favored by selection, because they emit a signal in response to the infestation of their neighbors (i.e. secondary signaling). We ignored alternative strategies (such as non-signalers) in the results presented in this paper, because including them leaves the main results essentially the same and makes them less transparent (see Appendix D for an example with respect to the case including non-signalers). In this paper, we assume that the patch size is larger than or equal to 2 ( $N \geq 2$ ), because there are no intermediate strategies under  $N = 1$ . We assume that signaling can occur even before the initial step and also after the last step. Therefore, there are  $T$  (the number of steps) + 1 opportunities to signal in one generation. We assumed this to simplify invasion analyses (Appendix A). It does not affect results whether there are  $T+1$  or  $T$  signaling opportunities, when  $T$  is large enough. At each of  $T+1$  signaling opportunities, any signaling individual gains a payoff  $-c_{sig}$ . That is,  $c_{sig}$  is the cost of the signal.

In each defense step, a signaling individual is successfully visited by bodyguards with probability  $P$ , which is a constant and does not depend on the states of other individuals; thus, we do not consider competition among plants for bodyguards for simplicity. When a plant is visited by bodyguards, the plant becomes uninfested, if it

was initially infested. Once bodyguards visit a plant, they continue to protect the plant until the end of the subsequent attack step, whether prey are present or not. Note that the model of PEH is different from the present model in two respects relating to the setting of the defense step (Kobayashi and Yamamura, 2003). First, the PEH model assumed that the probability of recruiting bodyguards is positively correlated with the number of signalers in the patch, whereas in the present model, it is constant. Second, the PEH model assumed that bodyguards do not remain on the plant to the end of the subsequent attack step but immediately disperse after feeding.

In the subsequent attack step, plants protected by bodyguards remain uninfested, while plants without protection are attacked by herbivores with probability  $H$ .  $H = H(N_{inf})$  is an increasing function of the number  $N_{inf}$  of infested patch mates; that is, plants surrounded by many infested patch mates are in greater danger than those surrounded by only a few. Note that we need not consider  $N_{inf} = N$  (patch size) because, in this case, there are no uninfested individuals around, i.e. no potential targets of attack in the patch. We denote the minimum and maximum of  $H$  by  $H_{min}$  and  $H_{max}$ , respectively; i.e.  $H(0) = H_{min}$  and  $H(N-1) = H_{max}$ , where  $H_{max} > H_{min}$ . We assume that attacks on different individuals are independent. At the end of the attack step, each individual gains a payoff  $-c_{dam}$  if it is infested. That is,  $c_{dam}$  is the cost of damage. After the attack step, bodyguards disperse and plants become vulnerable to herbivore attack. This process is then repeated in the following time steps.

After  $T$  time steps, the plants reproduce and the seeds enter a common pool of dispersers. Then, all parents die before the onset of the next generation. The fitness, i.e. the number of seeds, of a plant is positively correlated with the total payoff to the plant. For simplicity, we assume that the eventual payoff to a plant is given by the sum of the payoffs that the plant gained during its life, i.e. during the  $T$  time steps. Under those assumptions, the strategy with a payoff—averaged over individuals and time steps—larger than the average payoff to the population should increase in frequency in the next generation. In particular, if a rare mutant type has a larger payoff than the wild type, it successfully spreads in the population; otherwise, the wild type resists the invasion by the mutant. In Appendix A, we first derive the condition for which a given strategy can invade another strategy, and then we specify the condition for the evolutionarily stable strategy (ESS; Maynard Smith, 1982). We apply this analysis of Appendix A to case where the patch size is 2 ( $N = 2$ ) in Appendix B and to the general case for any value of  $N$  in Appendix C. We treated case  $N = 2$  separately, because the solution can be obtained analytically in that case, whereas  $N > 2$  requires numerical calculations. As shown in Appendix A, the relative size of the signal cost to the damage cost  $c_{sig}/c_{dam}$  is a crucial parameter for invasion success rather than absolute values of  $c_{sig}$  and  $c_{dam}$ . This is because the two kinds of costs  $c_{sig}$  and  $c_{dam}$  are assumed to be additive each

other and those costs are additive also with respect to time. Hence, we show how the ESS is determined from values of  $c_{sig}/c_{dam}$  and other parameters below. We found that the effect of the number of time steps  $T$  is more or less the same as in the PEH model; that is, as  $T$  increases, intermediate strategies (secondary signaling) become likely to evolve (Kobayashi and Yamamura, 2003). Hence, we omit the results for the effect of  $T$ , and confine the arguments to the case of very large  $T$ .

When the patch size is larger than 2 ( $N > 2$ ), we need an explicit function form of the attack probability  $H(N_{inf})$ , because  $H$  takes not only the maximum value  $H_{max}$  and the minimum value  $H_{min}$  but also intermediate values. In this study, we assumed that  $H(N_{inf})$  is a linear function for simplicity. This assumption leads to the following function:

$$H(N_{inf}) = (H_{max} - H_{min}) \frac{N_{inf}}{N - 1} + H_{min}. \quad (1)$$

Note that the above function satisfies  $H(0) = H_{min}$  and  $H(N - 1) = H_{max}$ .

### 3. Results

When the patch size is 2 ( $N = 2$ ), there are three strategies, i.e. strategies 0, 1, and 2. Fig. 1 shows a result under infinite  $T$  (the number of time steps) for  $N = 2$ . The vertical axes denote the ratio of the signal cost to the damage cost  $c_{sig}/c_{dam}$  in all three graphs. In Figs. 1A–C, the horizontal axes denote  $P$  (the probability of recruiting bodyguards for signaling individuals),  $H_{max}$  (the maximum attack probability), and  $H_{min}$  (the minimum attack probability), respectively. Note that in all graphs, the whole space is divided into five regions by four solid lines. In the regions indicated by numbers 0, 1, and 2, strategies 0, 1, and 2 are ESS, respectively. Likewise, in the region indicated by  $B_{01}$ , both strategies 0 and 1 are evolutionarily stable; which of these strategies is actually established, depends on their initial frequencies, although we do not explore this dependence in detail. In region  $C_{12}$ , there is no monomorphic ESS. In this region, strategies 1 and 2 can invade each other, but strategy 0 can invade neither strategy 1 nor strategy 2. In Appendix B, we prove that a polymorphism of strategies 1 and 2 is stable against invasion by strategy 0 in region  $C_{12}$ . Thus, in this region, the evolutionary consequence is an ES polymorphism of strategies 1 and 2. As a whole, Fig. 1 shows that the regions for polymorphism and bistability are very limited; we checked that this tendency holds regardless of parameter values. This means that stable polymorphism or bistability seldom occur; in other words, only one ESS is likely to exist for any parameter values.

As shown in Fig. 1, strategy 0, then strategy 1, and then finally strategy 2 become evolutionarily stable, as the relative signal cost  $c_{sig}/c_{dam}$  increases, which is reasonable for the following two reasons. First, individuals with low thresholds of signaling (small  $n$ ) have ample opportunity to signal, as compared to those with large  $n$ . Therefore, large

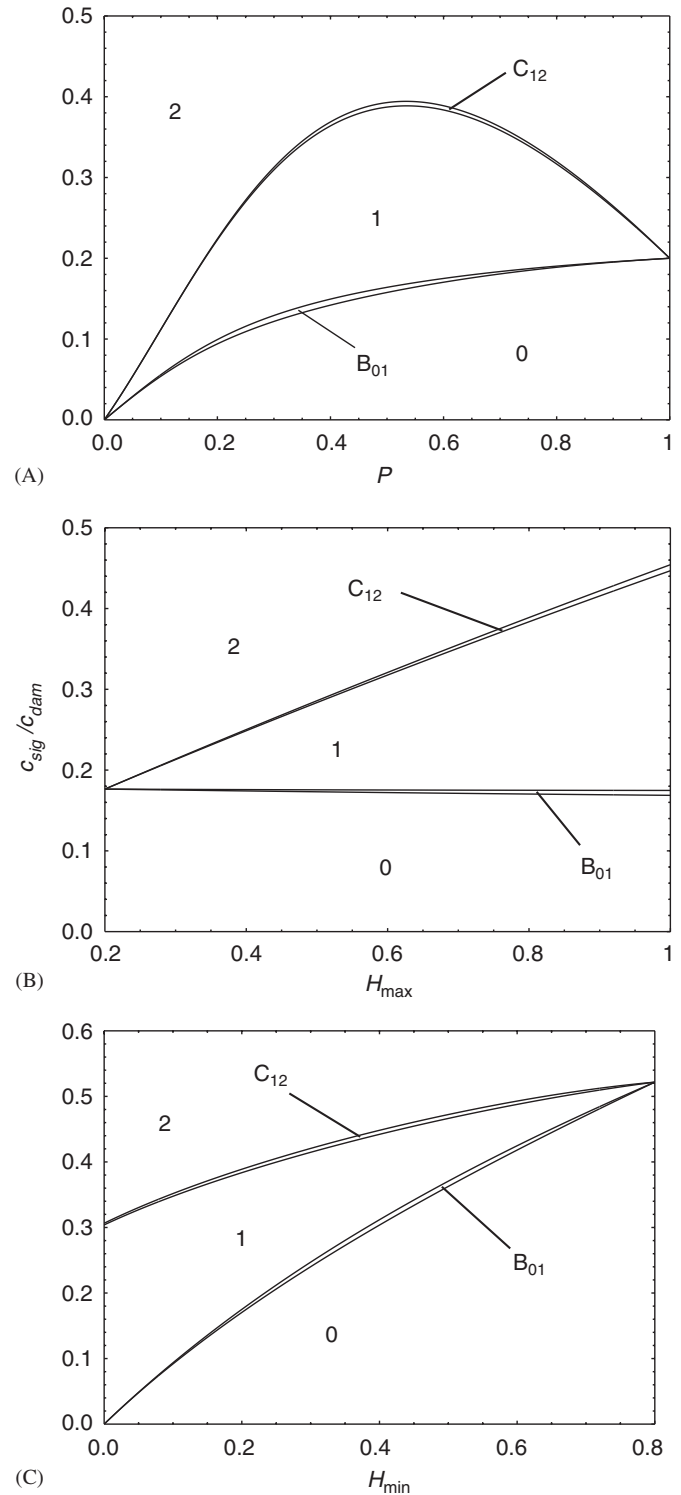


Fig. 1. Regions in which strategies are evolutionarily stable in (A)  $P - c_{sig}/c_{dam}$ , (B)  $H_{max} - c_{sig}/c_{dam}$ , and (C)  $H_{min} - c_{sig}/c_{dam}$  space under  $N = 2$  and  $T \rightarrow \infty$ . Values of fixed parameters are  $P = 0.6$ ,  $H_{min} = 0.2$ , and  $H_{max} = 0.8$ . In all figures, strategies 0, 1, and 2 are evolutionarily stable in regions indicated by 0, 1, and 2. In the region  $B_{01}$ , both 0 and 1 are evolutionarily stable, while in region  $C_{12}$ , strategies 1 and 2 compose an evolutionarily stable polymorphism.

$c_{sig}$  is disadvantageous to individuals with small  $n$ . Second, individuals with small  $n$  have less opportunity to be infested than those with large  $n$ , as they protect themselves better initially. Therefore, large  $c_{dam}$  is relatively disadvantageous to individuals with large  $n$ . Thus, as the ratio of the signal cost to the damage cost  $c_{sig}/c_{dam}$  decreases, small  $n$  becomes relatively advantageous.

When the probability of recruiting bodyguards for signaling individuals is zero ( $P = 0$ ), strategy 2 is evolutionarily stable regardless of the value of  $c_{sig}/c_{dam}$  (Fig. 1A), because there is a cost but no profit in signaling under  $P = 0$ ; in this case, strategy 2, which have the least opportunity to signal, represent the best strategy. In contrast, when  $P = 1$ , strategy 1 can never be evolutionarily stable. This result may seem counterintuitive, because high  $P$  means a high effectiveness of secondary signaling. However, it is intuitively explainable as follows. Note that infested individuals immediately recover in the next defense step under  $P = 1$ , since  $P$  is also the recovery probability of infested individuals. Therefore, the infestation of an individual does not affect the attack probability of the partner in the next attack step. Hence, secondary signaling does not make sense. Under  $P = 1$ , as shown in Appendix B, strategy 2 is evolutionarily stable if the relative signal cost is larger than the minimum attack probability ( $c_{sig}/c_{dam} > H_{min}$ ); otherwise, strategy 0 is evolutionarily stable. This condition is easy to derive intuitively as follows. Since infestation does not continue over one time step, the expected per-step cost due to infestation for uninfested individuals is simply given by  $H_{min}c_{dam}$ . Strategy 2 would be favored when the signal cost is larger than the expected cost of infestation, i.e. when  $c_{sig} > H_{min}c_{dam}$ ; otherwise, strategy 0 would be favored. Thus, signaling makes sense only when the probability of recruiting bodyguards for signaling individuals  $P$  is sufficiently larger than 0; at the same time, secondary signaling makes sense only when  $P$  is sufficiently smaller than 1. From these, strategy 1 is likely to be evolutionarily stable only with intermediate  $P$  (Fig. 1A).

Strategy 1 becomes likely to be evolutionarily stable as the maximum attack probability  $H_{max}$  increases or the minimum attack probability  $H_{min}$  decreases (Figs. 1B and C). In contrast, when  $H = H_{max} = H_{min}$ , strategy 1 is never evolutionarily stable (left boundary in Fig. 1B and right boundary in Fig. 1C). These results can easily be explained as follows. When  $H_{max}$  is large but  $H_{min}$  is small, uninfested individuals are in great danger only if they have infested partners. Therefore, in this case, uninfested individuals should signal only in the presence of infested neighbors, i.e. strategy 1 is selected for. Note that the risk to uninfested individuals does not depend on the states of partners when  $H = H_{max} = H_{min}$ . Therefore, secondary signaling does not make sense, so that strategy 1 never evolves. As shown in Appendix B, when  $H = H_{max} = H_{min}$ , the strategy 0 is evolutionarily stable when  $c_{sig}/c_{dam} < PH/(P + H - PH)$ , while the strategy 2 is evolutionarily stable when  $c_{sig}/c_{dam} > PH/(P + H - PH)$ .

As shown in Appendix C, the case where the patch size is larger than 2 ( $N > 2$ ) is not analytically tractable. Figs. 2A–C show the numerical results for  $N = 10$  and  $T$  (the number of time steps) = 200 in  $P$ – $c_{sig}/c_{dam}$ ,  $H_{max}$ – $c_{sig}/c_{dam}$ , and  $H_{min}$ – $c_{sig}/c_{dam}$  spaces. In this figure, increasing shades of gray (white to black) indicate larger

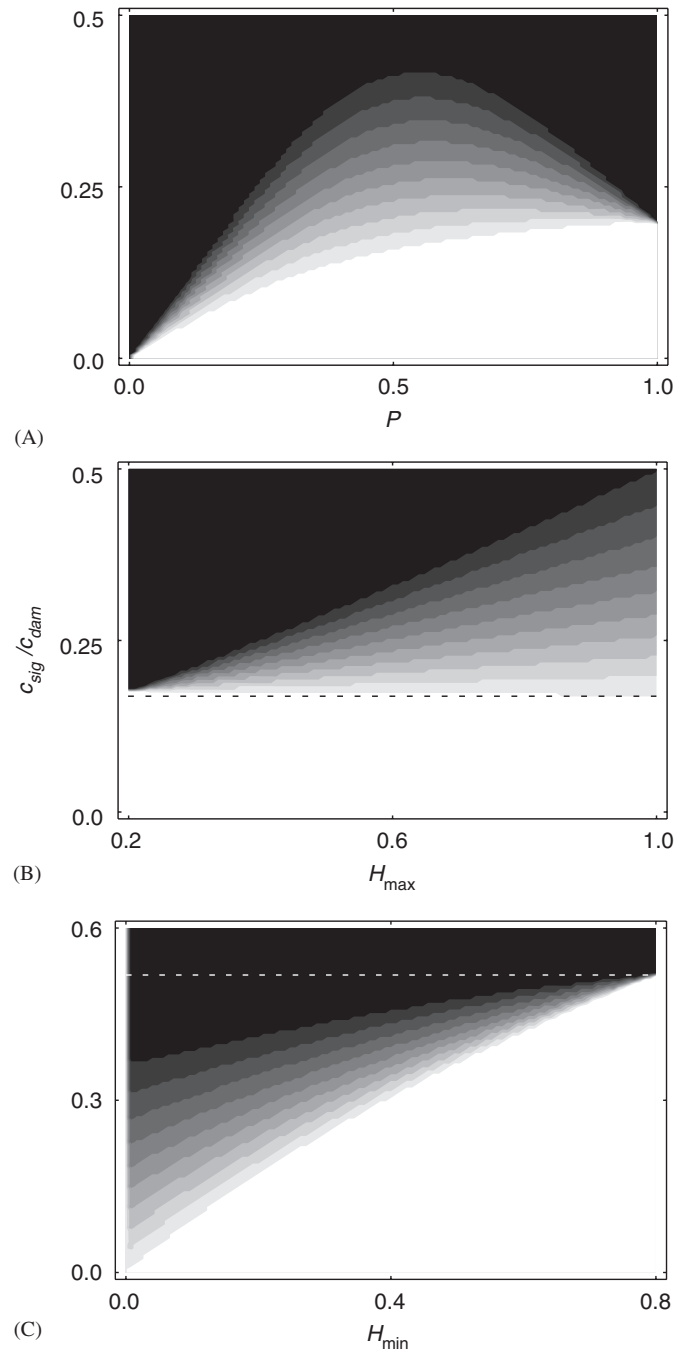


Fig. 2. Evolutionarily stable  $n$  in (A)  $P$ – $c_{sig}/c_{dam}$  space, (B)  $H_{max}$ – $c_{sig}/c_{dam}$  space, and (C)  $H_{min}$ – $c_{sig}/c_{dam}$  space under  $N = 10$ . The values of fixed parameters are  $P = 0.6$ ,  $H_{min} = 0.2$ ,  $H_{max} = 0.8$ , and  $T = 200$ . The color of a region indicates the value of the evolutionarily stable  $n$ . Thus, black and white indicate  $n = 10$  and  $n = 0$ , respectively, while gray regions concern the case where the ESS threshold  $n$  changes from 1 (light gray) to 9 (dark gray). Broken lines in (B) and (C) show the value of  $PH_{min}/(P + H_{min} - PH_{min})$  and  $PH_{max}/(P + H_{max} - PH_{max})$ , respectively.

values of evolutionarily stable  $n$ . In particular, strategy 0 and strategy 10 are evolutionarily stable in white and black regions, respectively. In gray regions, intermediate strategies ( $1 \leq n \leq 9$ ) are evolutionarily stable. As mentioned in Appendices A and B, the power of our analyses is limited under general  $N$ , because these cannot explore polymorphism in detail. Therefore, to draw Fig. 2, we made the following simplifications. When polymorphisms are evolutionarily stable, the figure shows the strategy with the largest  $n$  among the strategies that are part of stable polymorphisms. Furthermore, when there are multiple ESS, Fig. 2 shows the ESS with the largest  $n$  among them. This is a rational approach if evolution starts with strategy  $N$ , progresses by stepwise mutation, and ends up with the first encountered ESS. As shown in Fig. 2, the evolutionarily stable  $n$  becomes large as  $c_{sig}/c_{dam}$  increases. It is noteworthy that the shapes of regions where intermediate strategies are favored are similar to those under  $N = 2$  (see Fig. 1). Thus, the same arguments explain these shapes.

In Figs. 2B and C, broken lines show the value of  $PH_{min}/(P+H_{min}-PH_{min})$  and  $PH_{max}/(P+H_{max}-PH_{max})$ . Figs. 2B and C suggest that the condition for the evolution of strategy 0 [strategy 10] converges on  $c_{sig}/c_{dam} < PH/(P+H-PH)$  [ $c_{sig}/c_{dam} > PH/(P+H-PH)$ ] under  $H = H_{max} = H_{min}$  and  $T \rightarrow \infty$ , although we cannot mathematically prove this. This convergence suggests that the condition for the evolution of strategy 0 and strategy  $N$  is independent of the patch size  $N$  under  $H = H_{max} = H_{min}$  and  $T \rightarrow \infty$  (remember the result for  $N = 2$ ). When  $H = H_{max} = H_{min}$ , intermediate strategies can never be evolutionarily stable. This is because the risk to uninfested individuals does not depend on the states of patch mates when  $H = H_{max} = H_{min}$ , as mentioned earlier.

#### 4. Discussion

Our work was prompted by a paper of Järemo et al. (1999), who described a one-shot matrix model of an asymmetric communication game between two plants in a single patch. They assessed the strategy of a focal plant given the strategy of their neighbor opponent. Our model is an extension in that it allows for tracking the frequencies in which each of the strategies occurs in an environment with an infinite number of patches, harboring an arbitrary fixed number of plants. In this way, our model keeps track of the within-patch environments that each plant may encounter. This model structure enables us to perform invasion analyses for determining the ESS. These ingredients, i.e. frequency dependence and ESS analysis, warrant the work presented in this article.

We modeled a game involving two extreme strategies of plant defense and a set of intermediate strategies. In one of the extremes ( $n = 0$ ), plants always emit a signal whether they are infested or not, and in the other ( $n = N$ ), plants emit a signal only when they are infested. Plants of intermediate strategies ( $1 \leq n \leq N - 1$ ) emit a signal not only when they are infested but also when the number of

infested neighbors is above an arbitrary threshold  $n$  (i.e. secondary signaling). We assessed the conditions for which each strategy is favored. When the expected damage cost is sufficiently high relative to the signal cost, strategy 0 is favored and, when sufficiently low, strategy  $N$  is favored. For the intermediate cases, intermediate strategies are favored. The intermediate strategies will not evolve when the signals released by infested plants lure the bodyguards too effectively (high  $P$ ; Figs. 1A and 2A). The reason is straightforward because uninfested plants incur a lower risk of being attacked by herbivores currently attacking another plant in the neighborhood. This indirect effect may be interpreted as an “associational refuge” (Pfister and Hay, 1988).

The results are different from those of the PEH model especially at two points. First, under PPH, the relative signaling cost  $c_{sig}/c_{dam}$  cannot be very low for intermediate strategies to evolve, because strategy 0 can invade. On the other hand, strategy 0 is never adaptive under PEH regardless of the relative cost; therefore, we did not even include strategy 0 in the strategy set. Second, we found strong effect of associational refuge in the PPH model, whereas not in the PEH model. This is because the recovery probability of infested individuals is always positively correlated with the number of signaling individuals in the same patch in the PEH model. The maximum recovery probability is attained only when all the members of the patch are signaling. Therefore, even when the maximum recovery probability is very high, signaling by several infested individuals cannot attain it and is not enough to make associational refuge; in other words, there is always room to improve the recovery probability by secondary signaling.

In the present model, we assumed that the probability of recruiting bodyguards  $P$  is independent of the number of signaling patch-mates. This is for excluding the mechanism of PEH from the model to see whether PPH can solely promote the evolution of secondary signaling. However, in reality, the recovery probability may be positively correlated with the number of signaling patch-mates as assumed in the model of PEH. We have investigated what happens if this assumption is put into the present model (Appendix E). Such a model has features of both PEH and PPH models. That is, there is no strong associational refuge as in the PEH model, but there is room for strategy 0 to evolve as in the PPH model.

In our model, we assumed that the efficiency of attraction and the signal costs were equal for infested and uninfested plants. Hence, one may wonder how our results are affected by making these parameters unequal. Empirically, the most likely case is that uninfested plants produce less chemical signals, are therefore less attractive and, perhaps, pay lower costs. The consequences of attributing lower attraction efficiency and lower signal costs to uninfested plants are, however, mainly of a quantitative nature. Lower signal costs favor selection for strategy 0 and intermediate strategies at the expense of

strategy  $N$ . Lower efficiency of attraction favors strategy  $N$  at the expense of intermediate strategies and strategy 0. Yet, the qualitative conclusions drawn above are robust to these parameter modifications.

To translate the predictions of our model into experimentally testable hypotheses it is crucial to estimate the cost of signal emission (relative to the expected cost of herbivore damage). Dicke and Sabelis (1989) argued that the instantaneous energy cost of signal emission (in terms of ATP required) is very low compared to that of leaf production in plants. However, costs paid early in growth can exponentially increase with growth and the costs of infrastructure required for biosynthesis of the chemical signals are entirely unknown. Moreover, there is an even stronger reason to expect signal costs to be higher than biosynthetic costs alone, because signal emission entails so-called “ecological costs” due to increased conspicuousness to other herbivores (Sabelis et al., 1999a, b; Horiuchi et al., 2003; Heil, 2004). Such an increased signal cost, may prevent the evolution of plants that always emit a signal (strategy 0). However, ecological costs are caused by herbivores, which are evolving organisms; therefore, their effect may differ from that of simple energy costs. For this reason, ecological costs should be explicitly considered in future work extending our model to a food web context.

The most crucial assumption in our model is that even herbivore-free plants can attract and retain bodyguards by secondary signaling to an extent that they are better protected from future herbivory. Is this assumption realistic? There are two arguments in favor. First, arthropod predators have no means to assess herbivore density on a plant from a distance. They have to visit the plant and spend some time to explore the plant surface for the presence of potential prey. From the plant’s perspective, this time expenditure by the predators can be viewed as time ‘invested in plant protection’. Second, herbivore-free plants can challenge the visiting predators to stay even longer by offering alternative food, such as extrafloral nectars (Wäckers et al., 2005). Interestingly, there is evidence that herbivore-free plants provision more alternative food after exposure to HIPV emanating from a neighbor plant (Choh, 2005; Kost and Heil, unpublished manuscript; Choh et al., 2006). However, it must be noted that such food provisioning may impose some costs on plants and may be an evolutionary trait; it may be interesting to explicitly incorporate the food provisioning in the model as a strategy of plants in a future work.

There are several assumptions that need to be relaxed in future works to test the robustness of its predictions. For example, our model ignores the evolution of the response of bodyguards to the signal. Since biological signaling is a consequence of the coevolution of the sender and the receiver, incorporating the evolution of bodyguards into the model may change the results. Although we did not conduct such analyses, the following scenario is possible with the evolution of bodyguards. As shown in the present model, when the signal cost is very low relative to the damage cost,

plants may evolve to always emit a signal. However, in such a population, the quality of information conveyed by the signal is very low, because the signal and the presence of prey are not correlated. In this case, bodyguards may evolve to ignore such a useless signal, which can further result in the breakdown of the signaling system. This scenario is likely, but we need to model it mathematically in order to know the condition of the breakdown. Another extension may be to assume that the strategy of plants is the strength of the signal rather than whether they emit a signal or not; that is, the strategy may be continuous and quantitative rather than discrete and qualitative. If the quantitative strategy is assumed, the evolutionarily stable signal strength may be dependent on the risk of attack that the plant is facing; that is, e.g. plants may evolve to gradually increase the signal strength with increasing the number of infested neighbors. However, these arguments are speculative and require confirmation by future modeling.

Moreover, one may wish to allow uninfested plants to respond to signals from other uninfested plants. We ignored this possibility because uninfested plants release much less volatiles than infested plants, so that there must be a limit to communication among uninfested plants. Also, one may wish to consider the role of kin selection in promoting plant-plant communication. Another relevant extension is to include population dynamics of the full tritrophic system, thereby allowing plants to compete for protection by bodyguards. Competition for predators is essential to answer question whether uninfested plants should keep predators for their own protection (i.e. PPH) or to act as a guidepost for predators to visit their infested neighbor, thereby indirectly reducing their own future risk on herbivory (i.e. PEH). In the first case (PPH), uninfested plants producing a secondary signal invest in alternative food to arrest the predators lured by the signal, at the expense of predator visitation to the infested plant. In the second case (PEH), secondary signals benefit the uninfested plant only by reducing the risk of herbivore migration from the infested plant. This also highlights the need for a crucial empirical test: Do predators tend to stay on a HIPV-exposed and uninfested plant or do they move on to the HIPV producing plant? To our best knowledge such a pivotal experiment has not yet been carried out.

### Acknowledgements

We greatly thank T. Miki, and A. Telschow for reading the manuscript and many helpful comments. We also thank M. Kidokoro and R. Wagai for reading part of the manuscript. K. Kikuzawa, T. Ohgushi, J. Takabayashi, A. Yamauchi, and many other researchers in CER helped us through valuable discussions. We thank anonymous reviewers for many valuable comments. This work was supported by JSPS Research Fellowships for Young Scientists. This research was also partly supported by the Grant for the Biodiversity Research of the 21st Century COE (A14).

**Appendix A. Conditions for invasion**

In this appendix, we derive the condition on which a given strategy can invade another strategy. For the analysis, we introduce several pieces of notation. Imagine that we “mark” one individual chosen at random in each patch. We define type- $n/n^*$  patches as patches in which the marked individual is strategy  $n$  and the unmarked individuals are all strategy  $n^*$ . A patch is in state  $ij$  if the marked individual is in state  $i$  ( $i = 0$  for uninfested individuals and  $i = 1$  for infested individuals) and the number of infested unmarked individuals is  $j$ . From the definition,  $i + j$  is the number of infested individuals in a patch in state  $ij$ . Let  $\gamma_{n/n^*,ij}(t)$  denote the probability that a type- $n/n^*$  patch is in state  $ij$  just before the  $(t + 1)$ th defense step. Below, we describe the conditions for invasion between strategies using these symbols.

For given pairs of strategies, we wish to investigate when one is or is not resistant to invasion by the other. To do so, we must compare the average payoff for a resident and for a mutant. However, from the symmetry among different individuals within a patch, it is enough to compare the average payoff for a marked resident to that for a marked mutant. Furthermore, we can assume that a marked individual is always surrounded by  $N - 1$  residents, since mutants are rare. Therefore, provided that  $n^*$  is the resident strategy and  $n$  is a mutant strategy, we compare the average payoff for a marked individual of strategy  $n^*$  in a type- $n^*/n^*$  patch to that for a marked individual of strategy  $n$  in a type- $n/n^*$  patch. If the former payoff is higher than the latter,  $n^*$  is resistant to the invasion by  $n$ ; otherwise,  $n$  can invade the population of  $n^*$ . Below, we derive the average payoff for each strategy to perform this analysis.

Any individual emits a signal regardless of its strategy when infested; therefore, a marked individual in a patch in state  $1|j$ , where  $0 \leq j \leq N - 1$ , gains payoff  $-(c_{sig} + c_{dam})$  per time step, regardless of its strategy. Since the mutant emits a signal when the number of infested patch mates is larger than or equal to  $n$ , a marked mutant gains payoff  $-c_{sig}$  in a patch in state  $0|j$ , if  $j \geq n$ . From the above, the average payoff to a marked mutant between the  $t$ th step and the  $(t + 1)$ th step is given by

$$-(c_{sig} + c_{dam}) \sum_j \gamma_{n/n^*,1|j}(t) - c_{sig} \sum_{j \geq n} \gamma_{n/n^*,0|j}(t). \tag{A.1}$$

In the above equation, the first term represents the payoff for infested mutants and the second term is the payoff for uninfested but signaling mutants. We define  $C_{n/n^*}$  as the per-step average payoff for a marked individual of mutant strategy  $n$  in the population of strategy  $n^*$ . From Eq. (A.1),  $C_{n/n^*}$  is given by

$$C_{n/n^*} = -(c_{sig} + c_{dam}) \sum_j \bar{\gamma}_{n/n^*,1|j} - c_{sig} \sum_{j \geq n} \bar{\gamma}_{n/n^*,0|j}, \tag{A.2}$$

where  $\bar{\gamma}_{n/n^*,ij} = (1/(T + 1)) \sum_{t=0}^T \gamma_{n/n^*,ij}(t)$ . Throughout this paper, the bar over a symbol represents the per-step

average of the value. We can obtain the average per-step payoff  $C_{n^*/n^*}$  for a marked resident by replacing  $n$  in Eq. (A.2) by  $n^*$ :

$$C_{n^*/n^*} = -(c_{sig} + c_{dam}) \sum_j \bar{\gamma}_{n^*/n^*,1|j} - c_{sig} \sum_{j \geq n^*} \bar{\gamma}_{n^*/n^*,0|j}. \tag{A.3}$$

If residents have a higher average per-step payoff than mutants,  $n^*$  resists the invasion by  $n$ , as mentioned above. Therefore,  $n^*$  resists the invasion by  $n$  when  $C_{n^*/n^*} > C_{n/n^*}$ , that is,

$$-(c_{sig} + c_{dam}) \sum_j \bar{\gamma}_{n/n^*,1|j} - c_{sig} \sum_{j \geq n^*} \bar{\gamma}_{n/n^*,0|j} > -(c_{sig} + c_{dam}) \sum_j \bar{\gamma}_{n^*/n^*,1|j} - c_{sig} \sum_{j \geq n} \bar{\gamma}_{n^*/n^*,0|j}. \tag{A.4}$$

From  $\sum_j \bar{\gamma}_{n/n^*,ij} = (1/(T + 1)) \sum_{t=0}^T \sum_j \gamma_{n/n^*,ij}(t) = 1$  and  $\sum_j \bar{\gamma}_{n/n^*,0|j} + \sum_j \bar{\gamma}_{n/n^*,1|j} = 1$ , we have  $\sum_j \bar{\gamma}_{n/n^*,0|j} + \sum_j \bar{\gamma}_{n^*/n^*,1|j} = 1$ . Noting this relationship and rearranging the above equation, we have

$$c_{sig} \left( \sum_{j < n} \bar{\gamma}_{n/n^*,0|j} - \sum_{j < n^*} \bar{\gamma}_{n^*/n^*,0|j} \right) < c_{dam} \left( \sum_j \bar{\gamma}_{n/n^*,1|j} - \sum_j \bar{\gamma}_{n^*/n^*,1|j} \right). \tag{A.5}$$

We define  $F_{n/n^*}$  as  $\sum_{j < n} \bar{\gamma}_{n/n^*,0|j}$ , which gives the per-step average of the probability that a marked individual of strategy  $n$  is not signaling. The expression in parentheses on the left-hand side of Eq. (A.5) is equivalent to  $F_{n/n^*} - F_{n^*/n^*}$ . Thus, Eq. (A.5) is rewritten as follows:

$$\frac{c_{sig}}{c_{dam}} < \Theta_N(n|n^*), \tag{A.6a}$$

when  $F_{n/n^*} > F_{n^*/n^*}$  and

$$\frac{c_{sig}}{c_{dam}} > \Theta_N(n|n^*), \tag{A.6b}$$

when  $F_{n/n^*} < F_{n^*/n^*}$ , where

$$\Theta_N(n|n^*) = \frac{\sum_j \bar{\gamma}_{n/n^*,1|j} - \sum_j \bar{\gamma}_{n^*/n^*,1|j}}{\sum_{j < n} \bar{\gamma}_{n/n^*,0|j} - \sum_{j < n^*} \bar{\gamma}_{n^*/n^*,0|j}}. \tag{A.6c}$$

The above Eq. (A.6) gives the condition in which  $n^*$  resists invasion by  $n$ . Obviously, reversing the direction of the inequality Eqs. (A.6a) and (A.6b), we obtain the condition in which strategy  $n$  can invade the population of strategy  $n^*$ .

Suppose two strategies  $n$  and  $n^*$  satisfy  $c_{sig}/c_{dam} < \Theta_N(n|n^*)$ . If  $F_{n/n^*} > F_{n^*/n^*}$ ,  $n^*$  is resistant to invasion by  $n$  from Eq. (A.6a). In contrast, if  $F_{n/n^*} < F_{n^*/n^*}$ ,  $n$  can invade the population of  $n^*$  from Eq. (A.6b). Here, note that the strategy with smaller  $F$  always fares better than the other if  $c_{sig}/c_{dam} < \Theta_N(n|n^*)$ . This implies that strategies with small  $F$  are favored when  $c_{sig}/c_{dam}$  is small, which can be explained as follows. First, since individuals with small  $F$  have many opportunities to signal, small  $c_{sig}$  is advantageous to these individuals. Second, individuals with large  $F$



have many opportunities to be infested, since they have relatively less opportunity to signal; therefore, large  $c_{dam}$  is disadvantageous to them. Thus, small  $c_{sig}/c_{dam}$  is relatively advantageous to strategies with small  $F$ .

When a strategy is resistant to the invasions by all other strategies, the strategy represents an ESS. Therefore, a strategy  $n^*$  is an ESS when  $c_{sig}/c_{dam} < \Theta_N(n|n^*)$  for any  $n$  satisfying  $F_{n/n^*} > F_{n^*/n^*}$  and  $c_{sig}/c_{dam} > \Theta_N(n|n^*)$  for any  $n$  satisfying  $F_{n/n^*} < F_{n^*/n^*}$ . Let  $n_0, n_1, \dots, n_i$  denote  $n$  satisfying  $F_{n/n^*} < F_{n^*/n^*}$ , and  $n_{i+1}, n_{i+2}, \dots, n_{N-1}$  denote  $n$  satisfying  $F_{n/n^*} > F_{n^*/n^*}$ . From the above,  $n^*$  is an ESS when the following condition is met:

$$\begin{aligned} & \max\{0, \Theta_N(n_0|n^*), \Theta_N(n_1|n^*), \dots, \Theta_N(n_i|n^*)\} \\ & < \frac{c_{sig}}{c_{dam}} < \min\{\Theta_N(n_{i+1}|n^*), \\ & \Theta_N(n_{i+2}|n^*), \dots, \Theta_N(n_N|n^*), \infty\}, \end{aligned} \tag{A.7}$$

where ‘max’ and ‘min,’ respectively, denote the maximum and minimum values of given sets.

Note that we only considered invasion of one strategy by another above. For simplicity, we refer to such analyses as ‘‘simple pair-wise invasibility analyses’’ (SPIA). Although SPIA have the great advantage of simplicity, they cannot predict evolutionary consequences in some cases. For example, when there is no monomorphic ESS, we expect an evolutionarily stable polymorphism (ES polymorphism) of two or more strategies. However, to assess the stability of a polymorphism, we must consider invasions of mutant strategies into the polymorphic population (Geritz et al., 1998), which is not considered by SPIA. When  $N = 2$ , we can overcome this problem and we can determine whether a stable polymorphism of given strategies is possible, as discussed in Appendix B. However, for larger  $N$ , SPIA are unsuitable. However, for the purposes of this study, we use only SPIA and do not investigate the stability of polymorphisms in detail for large  $N$ , because it is beyond the scope of this study.

In Appendix B, we apply the above analysis to case  $N = 2$ . This case is analytically tractable and also has the advantage regarding polymorphisms as mentioned above. In Appendix C, we show how to numerically analyse the case of any value of  $N$ .

### Appendix B. ESS analysis for $N = 2$

In this appendix, we apply the analysis in Appendix A to case  $N = 2$  to obtain the ESS. To obtain the per-step payoff for an individual, we must track the state change of the individual. Although state changes of individuals in a patch are interdependent, state changes of patches are independent of each other and follow Markovian processes. Therefore, tracking the state change of a patch, we can also track the state change of individuals in the patch.

We first derive the transition probability matrix for the changes in patch states to calculate the probability distribution of patch states in arbitrary time steps. For

convenience, we refer to states  $0|0, 1|0, 0|1$ , and  $1|1$  as states 1, 2, 3, and 4, respectively. We also let  $\gamma_{n/n^*,i}(t)$  denote the probability that a type- $n/n^*$  patch is in state  $i$  just before the  $(t+1)$ th defense step. The transition probability matrix  $\mathbf{V}_{n/n^*}$  is defined as a matrix whose  $(i,j)$  element is the probability that the state of a type- $n/n^*$  patch changes from state  $j$  to state  $i$  in one step. Hence,  $\mathbf{V}_{n/n^*}$  obviously depends on the strategy  $n$  of the marked individuals and the strategy  $n^*$  of the unmarked individuals in the patch.  $Q_n(N_{inf})$  denotes the probability that an uninfested strategy- $n$  individual with  $N_{inf}$  infested patch mates is visited by bodyguards in a defense step. From the definition,  $Q_n(N_{inf}) = 0$  under  $N_{inf} < n$ , while  $Q_n(N_{inf}) = P$  under  $N_{inf} \geq n$ . We also use this notation in Appendix C, where we consider general  $N$ . Using this notation, the transition probability matrix under  $N = 2$  is given by

$$\mathbf{V}_{n/n^*} = \begin{pmatrix} \kappa_0 \kappa_0^* & P \kappa_1^* & \kappa_1 P & P^2 \\ (1 - \kappa_0) \kappa_0^* & (1 - P) \mu_1^* & (1 - \kappa_1) P & P(1 - P) \\ \kappa_0 (1 - \kappa_0^*) & P(1 - \kappa_1^*) & \mu_1 (1 - P) & P(1 - P) \\ (1 - \kappa_0)(1 - \kappa_0^*) & (1 - P)(1 - \mu_1^*) & (1 - \mu_1)(1 - P) & (1 - P)^2 \end{pmatrix}, \tag{B.1a}$$

where

$$\kappa_0 = Q_n(0) + (1 - Q_n(0))(1 - H_{\min}), \tag{B.1b}$$

$$\kappa_0^* = Q_{n^*}(0) + (1 - Q_{n^*}(0))(1 - H_{\min}), \tag{B.1c}$$

$$\kappa_1 = Q_n(1) + (1 - Q_n(1))(1 - H_{\min}), \tag{B.1d}$$

$$\kappa_1^* = Q_{n^*}(1) + (1 - Q_{n^*}(1))(1 - H_{\min}), \tag{B.1e}$$

$$\mu_1 = Q_n(1) + (1 - Q_n(1))(1 - H_{\max}), \tag{B.1f}$$

$$\mu_1^* = Q_{n^*}(1) + (1 - Q_{n^*}(1))(1 - H_{\max}). \tag{B.1g}$$

We demonstrate the derivations of several elements of  $\mathbf{V}_{n/n^*}$  in Eq. (B.1a). For example, a patch in state 1 (state  $0|0$ ) remains in state 1 after one step if both individuals remain uninfested in that step. An uninfested individual remains uninfested if it obtains bodyguards or if it is not attacked in the attack step, despite the absence of bodyguards. In a type- $n/n^*$  patch in state 1, this probability is given by  $Q_n(0) + (1 - Q_n(0))(1 - H_{\min}) = \kappa_0$  for the marked individuals and  $Q_{n^*}(0) + (1 - Q_{n^*}(0))(1 - H_{\min}) = \kappa_0^*$  for the unmarked individuals. Therefore, both marked and unmarked individuals remain uninfested with probability  $\kappa_0 \kappa_0^*$ , which is equivalent to the transition probability of the patch from state 1 to state 1. The next example is the transition from state 2 to state 2. A patch in state 2 (state  $1|0$ ) remains in state 2 if the marked individual remains infested and the unmarked individual remains uninfested. Since the marked individual is infested in a patch in state 2, it signals to attract bodyguards, regardless of its strategy. Therefore, it recovers with probability  $P$  and it remains infested with probability  $1 - P$ . On the other hand, the unmarked individual remains uninfested if it acquires bodyguards in the defense step or if it is not attacked in the attack step. This probability is given by

$Q_{n^*}(1) + (1 - Q_{n^*}(1))(1 - H_{\max}) = \mu_1^*$ ; it must be noted that the second term of this expression is  $(1 - Q_{n^*}(1))(1 - H_{\max})$  and not  $(1 - Q_{n^*}(1))(1 - H_{\min})$ , because the marked individual is infested. From the above, the transition probability from state 2 to state 2 is given by  $(1 - P)\mu_1^*$ . The other elements of  $V_{n/n^*}$  are derived as well.

We define  $\gamma_{n/n^*}(t)$  as a column vector whose  $i$ th element is  $\gamma_{n/n^*,i}(t)$ .  $\gamma_{n/n^*}(t + 1)$  is given by the product of  $V_{n/n^*}$  and  $\gamma_{n/n^*}(t)$ :

$$\gamma_{n/n^*}(t + 1) = V_{n/n^*}\gamma_{n/n^*}(t). \tag{B.2}$$

Unfortunately, we cannot analytically obtain  $\gamma_{n/n^*}(t)$  for general  $t$ ; however, we can obtain the stationary distribution  $\tilde{\gamma}_{n/n^*} = \lim_{t \rightarrow \infty} \gamma_{n/n^*}(t)$  as the leading eigenvector of  $V_{n/n^*}$ :

$$\tilde{\gamma}_{n/n^*,1} = \frac{1 - (1 - P)^2 + PA^*C^* + PAC}{(1 - \kappa_0)(1 - \kappa_0^*) - (1 - P)^2 + 1 + (1 + P - \kappa_0^*)A^*C^* + (1 + P - \kappa_0)AC}, \tag{B.3a}$$

$$\tilde{\gamma}_{n/n^*,2} = A^*[-P + (1 + P - \kappa_0^*)\tilde{\gamma}_{n/n^*,1}], \tag{B.3b}$$

$$\tilde{\gamma}_{n/n^*,3} = A[-P + (1 + P - \kappa_0)\tilde{\gamma}_{n/n^*,1}], \tag{B.3c}$$

$$\tilde{\gamma}_{n/n^*,4} = 1 - \tilde{\gamma}_{n/n^*,1} - \tilde{\gamma}_{n/n^*,2} - \tilde{\gamma}_{n/n^*,3}, \tag{B.3d}$$

where

$$A = \frac{1}{P\kappa_1 + (1 - P)\mu_1 - 1 - P}, \tag{B.3e}$$

$$C = (1 - P)(1 - \mu_1) - (1 - P)^2 + 1, \tag{B.3f}$$

$$A^* = \frac{1}{P\kappa_1^* + (1 - P)\mu_1^* - 1 - P}, \tag{B.3g}$$

$$C^* = (1 - P)(1 - \mu_1^*) - (1 - P)^2 + 1. \tag{B.3h}$$

Substituting  $n = n^*$  for Eq. (B.3), we can also obtain  $\tilde{\gamma}_{n^*/n^*,i}$ . Thus, we can obtain the value of  $\tilde{\Theta}_2$  from Eqs. (A.6c) and (B.3). Especially when  $P = 1$ , we have

$$\tilde{\Theta}_2(n|n^*) = H_{\min}. \tag{B.4}$$

Thus,  $\tilde{\Theta}_2$  does not depend on  $n$  and  $n^*$  under  $P = 1$ . This means that all four lines in Fig. 1 coincide, so that the region in which strategy 1 is the ESS disappears. Likewise, when  $H = H_{\max} = H_{\min}$ , we have

$$\tilde{\Theta}_2(n|n^*) = \frac{PH}{P + H - PH}. \tag{B.5}$$

In Eq. (B.5),  $\tilde{\Theta}_2$  does not depend on strategies. That is, all lines in Fig. 1 coincide, so that the region in which strategy 1 is the ESS disappears.

In the rest of this appendix, we show that the following statement is true under  $N = 2$ : if strategies  $i$  and  $j$  can invade each other, and strategy  $k$  can invade neither  $i$  nor  $j$ , a polymorphism of  $i$  and  $j$  is stable against  $k$ . This

guarantees that strategies 1 and 2 can compose a stable polymorphism in the region indicated by  $C_{12}$  in Fig. 1.

Assume that the condition of the above statement is satisfied. Then, we have

$$C_{i/j} > C_{j/j}, \tag{B.6a}$$

$$C_{j/i} > C_{i/i}, \tag{B.6b}$$

$$C_{k/i} < C_{i/i}, \tag{B.6c}$$

$$C_{k/j} < C_{j/j}. \tag{B.6d}$$

Imagine a polymorphic population composed of strategies  $i$  and  $j$ , and let  $f$  and  $1 - f$  denote the frequency of strategies  $i$  and  $j$ , respectively. In such a population, since

each individual has a strategy- $i$  partner and strategy- $j$  partner with probability  $f$  and  $1 - f$ , respectively, the per-step payoff for an individual of the arbitral strategy  $a$  is given by

$$fC_{a/i} + (1 - f)C_{a/j}. \tag{B.7}$$

Now, we determine whether strategy  $k$  can invade this population. Strategy  $k$  cannot invade the population if the payoff for strategy  $k$  is smaller than that for strategy  $i$  and  $j$ . The difference in the payoff between  $k$  and  $i$  is given by

$$fC_{k/i} + (1 - f)C_{k/j} - \{fC_{i/i} + (1 - f)C_{i/j}\}. \tag{B.8}$$

Rearranging the above expression, we have

$$f(C_{k/i} - C_{i/i}) + (1 - f)(C_{k/j} - C_{i/j}). \tag{B.9}$$

From Eq. (B.6c), the first term of (B.9) is negative, and from Eqs. (B.6a) and (B.6d), the second term is also negative. Therefore, the expression (B.9) is negative. Likewise, the payoff for  $k$  is also smaller than that for  $j$ . Therefore,  $k$  cannot invade the population of  $i$  and  $j$ .

It must be noted that such an analysis is possible only when  $N = 2$ . Under  $N = 2$ , we can regard the model as a symmetric matrix game with three strategies between two players, because the fitness of an individual depends only on its own strategy and that of its partner, but not on strategies of individuals in other patches. That is, in this game, each individual forms a pair with another individual at random once in its life and engages in a game with the partner, as in the original hawk–dove game. In our model,  $C_{i/j}$  corresponds to the  $(i, j)$  element of the payoff matrix. In such a matrix game, the payoff of an arbitral strategy is given by Eq. (B.7). This linearity makes the above analysis possible.

**Appendix C. ESS analysis for arbitral  $N$**

In this appendix, we show a general method to numerically calculate the probability distribution of patch states for a given time step. Following Appendix B, we let  $Q_n(N_{inf})$  denote the probability that a strategy- $n$  individual with  $N_{inf}$  infested patch-mates receives the visit of bodyguards in a defense step. We also define a function  $\beta$  as follows:

$$\beta(x, y, z) = \binom{x}{y} z^y (1 - z)^{x-y}. \tag{C.1}$$

This function yields binary probabilities with the probability of occurrence  $z$ .

To see how the states of patches change in one step, we separately consider a defense step and the subsequent attack step. At the start of each step, all individuals in the population are not protected by bodyguards, because bodyguards disperse at the end of the previous step. However, between a defense step and the subsequent attack step, individuals may be protected by bodyguards; therefore, we must distinguish between individuals that are protected and those that are not. For this purpose, we temporally use special notation to describe the states of patches between a defense step and the subsequent attack step, i.e. an individual is in state  $i.l$  when the individual is in state  $i$  and is protected by bodyguards. Likewise, an individual is in state  $i.0$  when the individual is in state  $i$  and is not protected. From these definitions, an individual in state  $i.j$  is also in state  $i$ . Since an infested individual recovers as soon as it obtains bodyguards, a protected individual can never be infested. Therefore, provided an individual is in state  $i.j$ ,  $i$  or  $j$  must be zero. We denote the state of a patch between a defense step and an attack step by  $i.j|m.l$ , where  $i.j$  is the state of the marked individual,  $m$

is the number of infested unmarked individuals, and  $l$  is the number of protected unmarked individuals. Note that  $i + m$  and  $j + l$  represent the number of infested individuals and the number of protected individuals, respectively, in a patch in state  $i.j|m.l$ . Thus,  $N - (i + j + m + l)$  is the number of uninfested but non-protected individuals.

We first consider state changes in a defense step. Imagine a type- $n/n^*$  patch. Possible state changes and corresponding transition probabilities in one defense step in this patch are summarized in Table 1. As an example, we show the derivation of the transition probability from state  $0|m$  to  $0.1|k.l$  (the second row in Table 1). Note that  $k \leq m$ , because no attack occurs in a defense step; also note that  $l \geq m - k$ , because the individuals that have recovered are always protected. In this transition, the state of the marked individual changes from  $0$  to  $0.1$ ; that is, the marked individual obtains the guard. This occurs with probability  $Q_n(m)$ , because  $m$  individuals are infested in the patch. On the other hand,  $m - k$  infested unmarked individuals recover in this transition. This occurs with probability  $\beta(m, m - k, P)$ , since an infested individual recovers with probability  $P$  and the recoveries of different individuals are independent of each other. Lastly,  $l - (m - k)$  uninfested unmarked individuals acquire bodyguards. This occurs with probability  $\beta(N - 1 - m, l - (m - k), Q_{n^*}(m))$ , because the number of uninfested unmarked individuals is  $N - 1 - m$  and each unmarked individual is visited by bodyguards with probability  $Q_{n^*}(m)$ . From the above, the transition probability from state  $0|m$  to state  $0.1|k.l$  is given by

$$Q_n(m)\beta(m, m - k, P)\beta(N - 1 - m, l - (m - k), Q_{n^*}(m)).$$

The other transition probabilities in a defense step are derived as well.

Let  $\eta_{n/n^*, i.j|k.l}(t)$  denote the probability that a type- $n/n^*$  patch is in state  $i.j|k.l$  just before the  $(t + 1)$ th attack step.

Table 1  
Possible transitions and transition probabilities

	Transition	Probability
Defense step	$0 m \rightarrow 0.0 k.l$	$(1 - Q_n(m))\beta(m, m - k, P)$ $\beta(N - 1 - m, l - (m - k), Q_{n^*}(m))$
	$0 m \rightarrow 0.1 k.l$	$Q_n(m)\beta(m, m - k, P)\beta(N - 1 - m, l - (m - k), Q_{n^*}(m))$
	$1 m \rightarrow 0.1 k.l$	$P\beta(m, m - k, P)\beta(N - 1 - m, l - (m - k), Q_{n^*}(m + 1))$
	$1 m \rightarrow 1.0 k.l$	$(1 - P)\beta(m, m - k, P)$ $\beta(N - 1 - m, l - (m - k), Q_{n^*}(m + 1))$
	$(k \leq m \leq k + l)$	
Attack step	$0.0 m.l \rightarrow 0 k$	$(1 - H(m))\beta(N - 1 - m - l, k - m, H(m))$
	$0.0 m.l \rightarrow 1 k$	$H(m)\beta(N - 1 - m - l, k - m, H(m))$
	$0.1 m.l \rightarrow 0 k$	$\beta(N - 1 - m - l, k - m, H(m))$
	$1.0 m.l \rightarrow 1 k$	$\beta(N - 1 - m - l, k - m, H(m + 1))$
	$(m \leq k)$	

From Table 1, we have

$$\begin{aligned} \eta_{n/n^*,0.0|k.l}(t) &= \sum_{m=k}^{k+l} (1 - Q_n(m)) \beta(m, m-k, P) \\ &\quad \times \beta(N-1-m, l-(m-k), Q_{n^*}(m)) \\ &\quad \times \gamma_{n/n^*,0|m}(t), \end{aligned} \quad (\text{C.2a})$$

$$\begin{aligned} \eta_{n/n^*,1.0|k.l}(t) &= \sum_{m=k}^{k+l} (1 - P) \beta(m, m-k, P) \\ &\quad \times \beta(N-1-m, l-(m-k), Q_{n^*}(m+1)) \\ &\quad \times \gamma_{n/n^*,1|m}(t), \end{aligned} \quad (\text{C.2b})$$

$$\begin{aligned} \eta_{n/n^*,0.1|k.l}(t) &= \sum_{m=k}^{k+l} Q_n(m) \beta(m, m-k, P) \\ &\quad \beta(N-1-m, l- \\ &\quad (m-k), Q_{n^*}(m)) \gamma_{n/n^*,0|m} \\ &\quad (t) + \sum_{m=k}^{k+l} P \beta(m, m-k, P) \\ &\quad \times \beta(N-1-m, l-(m-k), \\ &\quad Q_{n^*}(m+1)) \gamma_{n/n^*,1|m}(t). \end{aligned} \quad (\text{C.2c})$$

Next we consider the state change of a type- $n/n^*$  patch in an attack step. Possible state changes and corresponding transition probabilities in one attack step are also summarized in Table 1. As an example, we show the derivation of the transition probability from state  $0.0|m.l$  to  $1|k$  (the sixth row in Table 1). Note that  $k \geq m$ , because no recovery occurs in an attack step. The marked individual is attacked with probability  $H(m)$ , since  $m$  individuals are infested in the patch. In the transition,  $k-m$  unmarked individuals are newly attacked. Noting that protected individuals are not attacked, this probability is given by  $\beta(N-1-m-l, k-m, H(m))$ . Therefore, the transition probability from state  $0.0|m.l$  to  $1|k$  is given by  $H(m)\beta(N-1-m-l, k-m, H(m))$ . The other transition probabilities in an attack step are obtained as well. Thus, from Table 1, we have

$$\begin{aligned} \gamma_{n/n^*,0|k}(t+1) &= \sum_{l=0}^{N-1-k} \sum_{m=0}^k (1 - H(m)) \\ &\quad \times \beta(N-1-m-l, k \\ &\quad - m, H(m)) \eta_{n/n^*,0.0|m.l} \\ &\quad + \sum_{l=0}^{N-1-k} \sum_{m=0}^k \beta(N-1-m-l, \\ &\quad k-m, H(m)) \eta_{n/n^*,0.1|m.l}, \end{aligned} \quad (\text{C.3a})$$

$$\begin{aligned} \gamma_{n/n^*,1|k}(t+1) &= \sum_{l=0}^{N-1-k} \sum_{m=0}^k H(m) \beta(N-1-m-l, \\ &\quad k-m, H(m)) \eta_{n/n^*,0.0|m.l} \\ &\quad + \sum_{l=0}^{N-1-k} \sum_{m=0}^k \beta(N-1-m-l, \\ &\quad k-m, H(m+1)) \eta_{n/n^*,1.0|m.l}. \end{aligned} \quad (\text{C.3b})$$

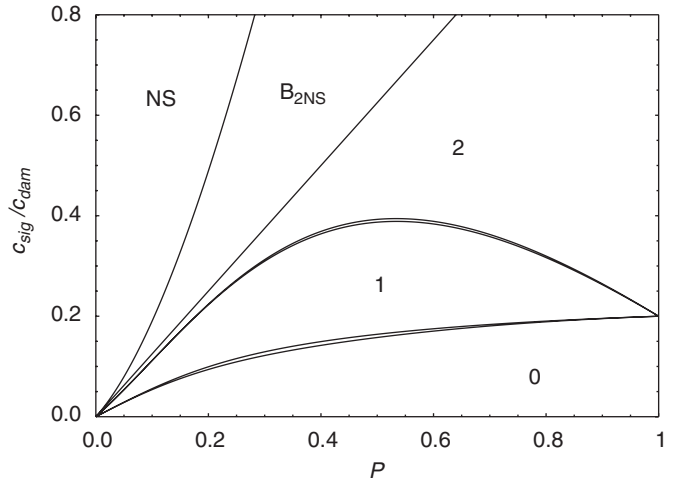


Fig. 3. Regions in which strategies are evolutionarily stable in  $P-c_{sig}/c_{dam}$  space under  $N=2$  and  $T \rightarrow \infty$ . The strategy set includes the non-signaler. Values of fixed parameters are  $H_{min}=0.2$ , and  $H_{max}=0.8$ . Strategies 0, 1, 2, and the non-signaler are evolutionarily stable in regions indicated by 0, 1, 2, and NS, respectively. In the region  $B_{2NS}$ , both the non-signaler and strategy 2 are evolutionarily stable.

Numerically iterating Eqs. (C.2) and (C.3), we can calculate  $\gamma_{n/n^*,i|m}(t)$  for any  $t$ ; hence, we can also calculate  $\bar{\gamma}$  for any  $T$ . Substituting numerically obtained  $\bar{\gamma}$  for Eq. (A.6c), we obtain conditions for resistance and invasibility for all  $N$ .

#### Appendix D. Case including non-signalers

In this appendix, we show the effect of including non-signalers into the strategy set under  $N=2$ . Non-signalers never signal regardless of their own states and of their neighbors' states. We only graphically show part of the results, and do not show the details of the analysis. Fig. 3 shows where each strategy is the ESS in  $P-c_{sig}/c_{dam}$  space. Parameter values are the same as those in Fig. 1A. In region NS, non-signalers are evolutionarily stable, whereas in region  $B_{2NS}$ , both non-signalers and strategy 2 are evolutionarily stable (bistable). As shown in the figure, when  $P$  is very small or when  $c_{sig}/c_{dam}$  is sufficiently large, strategy 2 becomes unstable and instead non-signalers evolve. This is reasonable, because  $P$  and  $c_{sig}/c_{dam}$  represent the efficiency and the relative cost of signaling, respectively; i.e. plants should stop signaling when the efficiency is too low or the cost is too high.

#### Appendix E. The probability of recruiting bodyguards increases with the number of signaling patch mates

In this appendix, we investigate what happens if the probability of recruiting bodyguards increases with the number of signaling individuals in the patch, as in the PEH model. We do not show the details of the analysis, but briefly discuss part of the results. Following Kobayashi and Yamamura (2003), for simplicity, we assume that all the individuals in the patch recover from infestation and

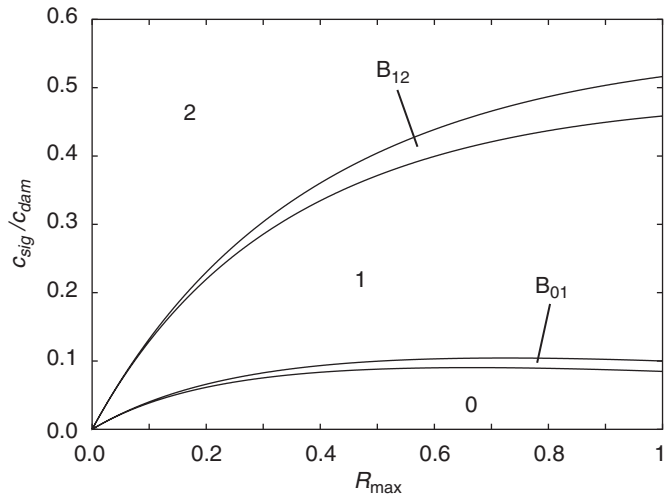


Fig. 4. Regions in which strategies are evolutionarily stable in  $R_{\max}-c_{sig}/c_{dam}$  space under  $N = 2$  and  $T \rightarrow \infty$ . The probability that a patch recruits bodyguards is assumed to increase with the number of signaling individuals in the patch. Values of fixed parameters are  $H_{\min} = 0.2$ , and  $H_{\max} = 0.8$ . Strategies 0, 1, and 2 are evolutionarily stable in regions indicated by 0, 1, and 2, respectively. In the region  $B_{01}$ , both 0 and 1 are evolutionarily stable, while in region  $B_{12}$ , both 1 and 2 are evolutionarily stable.

obtain protection, when bodyguards visit the patch. We let  $R(N_{sig})$  denote the probability that a patch gains bodyguards, where  $N_{sig}$  is the number of signaling individuals in the patch. For simplicity, we assume the following linear function for  $R$ :

$$R(N_{sig}) = R_{\max} \frac{N_{sig}}{N}, \quad (\text{E.1})$$

where  $R_{\max}$  is the maximum value of  $R$ . Fig. 4 shows where each strategy is the ESS in  $R_{\max}-c_{sig}/c_{dam}$  space under  $N = 2$  and  $T \rightarrow \infty$ . Parameter values are the same as those in Fig. 1A. Notation is the same as in Fig. 1. As shown in the figure, there is no strong effect of associational refuge, as in the PEH model (Kobayashi and Yamamura, 2003). However, when  $c_{sig}/c_{dam}$  is low, strategy 0 can be evolutionarily stable, as in the PPH model.

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