

Native intra- and inter-specific reactions may cause the paradox of pest control with harvesting

Hiromi Seno

To cite this article: Hiromi Seno (2010) Native intra- and inter-specific reactions may cause the paradox of pest control with harvesting, Journal of Biological Dynamics, 4:3, 235-247, DOI: [10.1080/17513750903009169](https://doi.org/10.1080/17513750903009169)

To link to this article: <https://doi.org/10.1080/17513750903009169>



Copyright Taylor and Francis Group, LLC



Published online: 17 Jun 2009.



Submit your article to this journal [↗](#)



Article views: 538



View related articles [↗](#)



Citing articles: 1 View citing articles [↗](#)

Native intra- and inter-specific reactions may cause the paradox of pest control with harvesting

Hiromi Seno*

*Department of Mathematical and Life Sciences, Graduate School of Science, Hiroshima University,
Higashi-hiroshima, 739-8526, Japan*

(Received 7 August 2008; final version received 30 April 2009)

We analyse a general time-discrete mathematical model of host–parasite population dynamics with harvesting, in which the host can be regarded as a pest. We harvest a portion of the host population at a moment in each year. Our model involves the density effect on the host population. We investigate the condition in which the harvesting of the host results in a paradoxical increase of its equilibrium population size. Our results imply that for a family of pest–enemy systems, the paradox of pest control could be caused essentially by the interspecific relationship and the intraspecific density effect.

Keywords: population dynamics; discrete model; resurgence; harvesting; pest control

AMS Subject Classification: 92D25; 92D40; 92B99; 37N25

1. Introduction

In agriculture, one of the most serious problems has been pest outbreak. Pest management has been studied empirically and theoretically [6,8,9,13,16,18,20,21,24]. In many cases, pesticides have been used against the pest. However, in some cases, the pesticide is effective only in the early period of its introduction and results in an outbreak of the pest in the later period. Such a paradoxical phenomenon in the pest control is often called the *pest resurgence*. The resurgence was firstly defined by DeBach [3] as the unusually fast recovery of the pest population with the decrease of its natural enemy population due to the pesticide secondary effect [11,17].

Many investigations of the resurgence have been carried out [2–5,7,24]. Since various causes of the resurgence have been recognized, recently the word ‘resurgence’ is often used as the paradoxical increase of the pest population due to the application of a pest management operation. For example, it could be caused by the pesticide secondary effect such as the emergence of a pesticide-resistant strain of the pest [7,16,18,24], the preferable shift of the pesticide-applied crop condition for the pest’s predation (‘trophobiosis’) [1], or the physiological increase of the pest’s reproduction rate (‘hormesis’, ‘homoligosis’) [12,14,17].

*Email: seno@math.sci.hiroshima-u.ac.jp

In this paper, making use of a general family of host–parasite population dynamics model, we theoretically show that the pest resurgence could occur even without the above-mentioned specific effects of the pesticide: the nature of the native ecological intra- and inter-specific reactions could cause it.

2. Model

2.1. General form

We consider the following time-discrete host–parasite population dynamics:

$$\begin{aligned} h_{k+1} &= \lambda S_{\theta,\rho}(h_k)(1 - \rho)\Pi(p_k)h_k; \\ p_{k+1} &= \mu(1 - \rho)\{1 - \Pi(p_k)\}h_k, \end{aligned} \tag{1}$$

where h_k and p_k are, respectively, the population size of the host and that of the parasite at the k th season. The sufficiently smooth function Π of the parasite population size is the probability with which each host individual successfully escapes from the parasitism: $0 \leq \Pi \leq 1$. Each host individual is parasitized with probability $1 - \Pi$. The sufficiently smooth function $S_{\theta,\rho}$ of the host population size introduces the intraspecific density effect on the reproductive rate: $0 \leq S_{\theta,\rho} \leq 1$. The positive parameter λ means the intrinsic growth rate. So $\lambda S_{\theta,\rho}$ gives the per capita host reproductive rate affected by the intraspecific density effect. The parameter μ indicates the mean reproductive rate of parasite per parasitized host.

The parameter ρ indicates the strength of harvesting on the host population: $0 \leq \rho < 1$. We harvest a portion ρ of the host population at a moment indexed by the parameter θ ($0 \leq \theta \leq 1$) in the parasitism season only in which the parasite can parasitize the host (see Figure 1). In general, parasites attack only one or a few of host stages (i.e., egg, larva, and pupa) during a restricted season [18,24]. In our model, we suppose a season for the parasitism in each year. The harvesting is repeated every year. The case of $\theta = 0$ corresponds to the harvesting before the parasitism season, and that of $\theta = 1$ after it. In case of $0 < \theta < 1$, the harvesting is operated at an intermediate moment of the parasitism season. No direct effect of the harvesting is assumed on the parasite population.

As in [15], we assume that the density effect during the juvenile period determines the host’s reproductive success, that is, the cumulative density effect during the parasitism season determines it. The cumulative density effect is assumed to be determined by the proportion of the period before/after the harvesting in the parasitism season. The host population’s size is h_k before the harvesting and $(1 - \rho)h_k$ after it. Thus, the density effect is altered before and after the harvesting.

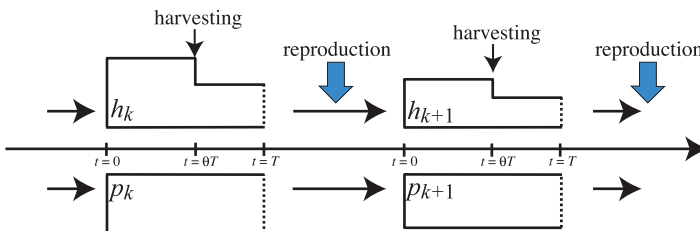


Figure 1. Scheme of the parasitism dynamics under harvesting effect in our model (1). h_k is the host population density and p_k is the parasite population density at the beginning of the k th parasitism season. The harvesting targets only the host and has no direct effect on the parasite population.

We assume that the parasitized host individuals are alive during the parasitism season (only if they successfully escape from the harvesting), so that they contribute to the density effect, though they cannot reproduce. Lastly, we introduce the cumulative density effect on the host reproductive rate as

$$S_{\theta,\rho}(h_k) = \theta R(h_k) + (1 - \theta)R((1 - \rho)h_k),$$

which is composed with the density effect weighted by the population sizes before and after the harvesting [15]. Now, h_k is the host population density and p_k is the parasite population density at the beginning of the k th parasitism season. The sufficiently smooth function $R (\geq 0)$ of the host population size introduces the strength of intraspecific density effect per unit time on the reproductive rate, satisfying that $0 < R \leq 1$.

2.2. Assumptions

In this paper, we assume that the functions R and Π are sufficiently smooth, two times continuously differentiable, and satisfy the following natures:

- $R(0) = 1$ and $\lim_{h \rightarrow \infty} R(h) = 0$;
- $R'(h) < 0$ for any $h > 0$;
- $\Pi(0) = 1$ and $\lim_{p \rightarrow \infty} \Pi(p) = 0$;
- $\Pi'(p) < 0$ and $\Pi''(p) \geq 0$ for any $p \geq 0$,

where $R'(h) = dR(h)/dh$, $\Pi'(p) = d\Pi(p)/dp$, and $\Pi''(p) = d^2\Pi(p)/dp^2$. Note that, from these assumptions for R , the density effect function $S_{\theta,\rho}$ satisfies the corresponding conditions same as those for R . These mathematical assumptions do not significantly lose the generality of the system (1) as a host–parasite population dynamics, because they represent somehow natural modelling for the host–parasite population dynamics.

When $\lambda > 1$, from the first and the second assumptions for R , there is a unique positive value of h , say h_c , such that $\lambda S_{\theta,\rho}(h_c) = 1$. With the assumptions for R , we can easily see that, in case of no parasite ($p_k \equiv 0$) and no harvesting ($\rho = 0$; $S_{\theta,0} \equiv R$), the host population approaches a stationary size given by h_c : the equilibrium state $h^* = h_c$ is globally stable for any positive initial state h_0 .

In contrast, when $\lambda < 1$, the host population eventually goes extinct independently of the existence of parasite or harvesting, because the net reproductive rate ($= h_{k+1}/h_k$) is always less than 1. When $\lambda = 1$, in the same reason, the host population eventually goes extinct if a harvesting is applied with any $\rho > 0$. In case of no harvesting ($\rho = 0$), the host extinction is not trivial even for $\lambda = 1$. However, in this case, we can easily prove that, with the parasite, the host population size is monotonically decreasing, and that the host extinction necessarily occurs. Therefore, from the biological interest, we hereafter consider our model (1) with the assumption $\lambda > 1$.

The assumption that $\Pi(0) = 1$ means that the host is never parasitized without parasite. The decreasing nature of Π in terms of the parasite population size means the negative density effect of the parasite on the success of parasitism, for instance, due to the intraspecific competition about the parasitism.

From the viewpoint of mathematical modelling for the host–parasite dynamics, the assumption that $\Pi''(h) \geq 0$ could be modified. In this paper, however, we restrict our attention on the model with this assumption, which can still cover a wide range of more concrete models, including the Nicholson–Bailey model [19].

3. Analysis

3.1. Equilibrium with parasite extinction

In this section, we consider the existence and the stability of the equilibrium $(h_0^*, 0)$, at which the parasite has gone extinct while the host survives. The equilibrium host population size h_0^* satisfies the following equation:

$$\lambda S_{\theta,\rho}(h_0^*) = \frac{1}{1-\rho}. \tag{2}$$

From the assumptions, the function $R(h)$ is monotonically decreasing toward zero in terms of $h > 0$, and so is the function $S_{\theta,\rho}(h)$. Since the left-hand side of Equation (2) must be less than λ , Equation (2) has a unique positive root only when $\lambda > 1/(1-\rho)$, that is, only when $\rho < 1 - 1/\lambda$. If $\rho \geq 1 - 1/\lambda$, it is clear that Equation (2) does not have any positive root for h_0^* . We can easily find that, in case of $\rho \geq 1 - 1/\lambda$ with the parasite, the host population size is monotonically decreasing and necessarily goes extinct.

On the other hand, from the assumption that $\lambda S_{\theta,\rho}(h_c) = 1$ for some $h_c > 0$, we can easily see that $h_0^* \leq h_c$, because the right-hand side of Equation (2) is not below 1 for $\rho \geq 0$. From these arguments and the sufficient smoothness of the function R , we can immediately get the following result:

The equilibrium $(h_0^, 0)$ uniquely exists if and only if $\rho < 1 - 1/\lambda$. If it exists, it is satisfied that $h_0^* \leq h_c$.*

We remark that $h_0^* = h_c$ if and only if $\rho = 0$.

As for the effect of harvesting on the equilibrium host population size h_0^* , we have the following result of [22]:

If the following condition is satisfied at the equilibrium $(h_0^, 0)$, the equilibrium host population size h_0^* is increasing in terms of $\rho > 0$:*

$$\theta R(h_0^*) + (1-\theta) \left. \frac{d}{dh} \{R(h)h\} \right|_{h=(1-\rho)h_0^*} < 0. \tag{3}$$

If the inequality in Equation (3) is reversed, the equilibrium host population size h_0^* is decreasing in terms of $\rho > 0$ at the equilibrium $(h_0^*, 0)$. From this result of [22], we can see that the equilibrium host population size h_0^* is decreasing in terms of $\rho > 0$ at the equilibrium $(h_0^*, 0)$ only if $d\{R(h)h\}/dh < 0$ at $h = (1-\rho)h_0^*$. As argued in [22], this necessary condition indicates that the humped reproduction curve is necessary to cause the paradoxical increase of h_0^* in terms of ρ , that is, the scramble competition is necessary.

Making use of the standard local stability analysis for the equilibrium $(h_0^*, 0)$, we can easily get the eigenvalues: $1 + \lambda S'_{\theta,\rho}(h_0^*)(1-\rho)h_0^*$, $-\mu \Pi'(0)(1-\rho)h_0^*$. If both of these eigenvalues have the absolute value less than 1, the equilibrium $(h_0^*, 0)$ is asymptotically stable. Therefore, we can get the following result:

The equilibrium $(h_0^, 0)$ is asymptotically stable if*

$$\left. \frac{d}{dh} \{h^2 S_{\theta,\rho}(h)\} \right|_{h=h_0^*} > 0 \quad \text{and} \quad \rho > 1 - \frac{1}{\mu |\Pi'(0)| h_0^*}. \tag{4}$$

It is unstable if one of these inequalities is reversed.

The first condition corresponds to one with which the equilibrium $(h_0^*, 0)$ is asymptotically stable in case of no parasite, $p_k \equiv 0$. If this condition is violated when the equilibrium $(h_0^*, 0)$ exists, the host population goes to a temporally variable state. The second condition means that the invasion of parasite fails for the equilibrium $(h_0^*, 0)$.

We remark that, when no harvesting is applied (i.e., $\rho = 0$), we have $h_0^* = h_c$. We find that the equilibrium $(h_c, 0)$ in case of $\rho = 0$ is asymptotically stable if $|R'(h_c)|h_c < 2$ and $\mu|\Pi'(0)|h_c < 1$, while it is unstable if one of these inequalities is reversed.

3.2. Existence of the coexistent equilibrium

In this section, let us consider the case when the nontrivial equilibrium (h^*, p^*) exists for given $\rho \geq 0$, where $h^* > 0$ and $p^* > 0$. From Equation (1), the following equations are satisfied:

$$\begin{aligned} \lambda S_{\theta,\rho}(h^*)\Pi(p^*) &= \frac{1}{1-\rho} \geq 1; \\ h^* &= \frac{Q(p^*)}{1-\rho}, \end{aligned} \tag{5}$$

where $Q(p) := p/[\mu(1 - \Pi(p))]$ that is monotonically increasing in terms of p .

From Equation (5), we can derive the necessary and sufficient condition for the existence of the nontrivial equilibrium (h^*, p^*) :

The nontrivial equilibrium (h^, p^*) exists if and only if*

$$\rho < 1 - \frac{1}{\mu|\Pi'(0)|h_0^*}, \tag{6}$$

where h_0^* is the unique positive root of Equation (2).

From Equation (4), this condition corresponds to that for the successful invasion of the parasite into the equilibrium state $(h_0^*, 0)$. If the condition (6) is satisfied, the equilibrium $(h_0^*, 0)$ is unstable.

The above condition for the existence of the nontrivial equilibrium (h^*, p^*) can be derived as follows: from the first equation of (5), we have a one-to-one relation:

$$h^* = U(p^*) := S_{\theta,\rho}^{-1}\left(\frac{1}{(1-\rho)\lambda\Pi(p^*)}\right), \tag{7}$$

where $S_{\theta,\rho}^{-1}$ is the inverse function of $S_{\theta,\rho}$ that is a monotonically decreasing smooth function from the assumptions. Then, the function $U(p)$ is monotonically decreasing in terms of p , since the functions $\Pi(x)$ and $S_{\theta,\rho}^{-1}(x)$ are monotonically decreasing in terms of x . Moreover, from the assumptions, we can immediately find that $U(0) = h_0^*$, and that the positive root of the equation $U(p) = 0$ is uniquely given by $p = p_c = \Pi^{-1}(1/[(1-\rho)\lambda])$ if and only if $\rho < 1 - 1/\lambda$ when $h_0^* > 0$ uniquely exists.

On the other hand, from the second equation of (5), we find that $dQ(p)/dp \geq 0$, that is, $Q(p)$ is monotonically increasing in terms of p . Moreover, we have

$$\lim_{p \rightarrow 0^+} Q(p) = \lim_{p \rightarrow 0^+} \frac{-1}{\mu\Pi'(p)} = \frac{1}{\mu|\Pi'(0)|} < \infty.$$

From these results about the nature of functions U and Q , we can easily find that, for given ρ , two curves $h = U(p)$ and $h = Q(p)/(1 - \rho)$ has a unique intersection in the positive region if and only if condition (6) is satisfied. Consequently, these arguments prove that condition (6) is necessary and sufficient for the existence of nontrivial equilibrium (h^*, p^*) for given ρ .

We remark that the existence of coexistent equilibrium (h^*, p^*) assures the existence of the equilibrium $(h_0^*, 0)$. This is because always $\Pi(p^*) < 1$ from the assumption, and the following inequality is necessary for the existence of coexistent equilibrium:

$$\frac{1}{\lambda(1-\rho)} < \Pi(p^*)$$

for $R(h^*) < 1$ from the first equation of (5) when the coexistent equilibrium (h^*, p^*) exists.

3.3. Population size at the coexistent equilibrium

Since $S_{\theta,\rho}(h)$ is monotonically decreasing in terms of h and $\Pi(p^*) < 1$ for any positive value of p^* , from Equation (2) and the first equation of (5), we find that $\lambda S_{\theta,\rho}(h^*) > 1/(1 - \rho) = \lambda S_{\theta,\rho}(h_0^*)$ and subsequently $h^* < h_0^*$. Therefore, *the host population size at the coexistent equilibrium is always below the equilibrium size in case of no parasite.*

Now, directly from Equation (5), we can obtain the following equations of ρ -derivatives for the coexistent equilibrium:

$$\frac{\partial h^*}{\partial \rho} = \frac{\Phi_{\theta,\rho}(p^*)}{(1 - \rho)^2 \Omega_{\theta,\rho}}; \tag{8}$$

$$\frac{\partial p^*}{\partial \rho} = \frac{1}{\lambda(1 - \rho)^2 \Omega_{\theta,\rho}} \left\{ 1 - R' \left(\frac{Q(p^*)}{1 - \rho} \right) \cdot \lambda \theta Q(p^*) \Pi(p^*) \right\}, \tag{9}$$

where

$$\begin{aligned} \Omega_{\theta,\rho} &= \frac{d}{dp} \left[S_{\theta,\rho} \left(\frac{Q(p)}{1 - \rho} \right) \Pi(p) \right]_{p=p^*}; \\ \Phi_{\theta,\rho}(p) &= \theta R \left(\frac{Q(p)}{1 - \rho} \right) \frac{d}{dp} \{ Q(p) \Pi(p) \} + (1 - \theta) \frac{d}{dp} \{ R(Q(p)) Q(p) \Pi(p) \}. \end{aligned} \tag{10}$$

Since $Q(p)$ is monotonically increasing in terms of p while $S_{\theta,\rho}(x)$ and $\Pi(x)$ are monotonically decreasing in terms of x , we have $\Omega_{\theta,\rho} < 0$. Therefore, from Equation (9), we find that always $\partial p^*/\partial \rho < 0$, because $R'(x)$ is negative for any $x > 0$ from the assumption. As a result *the equilibrium parasite population size is ALWAYS monotonically decreasing in terms of ρ .*

In short, the harvesting necessarily reduces the parasite population size at the equilibrium state, even though the harvesting makes no direct effect on the parasite population. This result is independent of the details of functions Π and R , and also of the harvesting timing (i.e., θ).

Next, we consider the condition for the paradox emergence in the pest control with the harvesting. In our model, we consider the paradox of pest control as the increase in the equilibrium host population size as ρ gets larger. In other words, the paradox is regarded as to emerge if $\partial h^*/\partial \rho > 0$ for some $\rho > 0$. From Equation (8), if and only if $\Phi_{\theta,\rho}(p^*) < 0$ for some $\rho > 0$, we can have the case that $\partial h^*/\partial \rho > 0$, that is, we find the following *sufficient and necessary* condition for the emergence of the paradox of pest control:

The paradox of pest control can occur if and only if $\Phi_{\theta,\rho}(p^) < 0$ for some $\rho > 0$.*

Especially, if $\Phi_{\theta,0}(p^*|_{\rho=0}) < 0$, the paradox emerges when a sufficiently weak harvesting is applied, and then the host population size at the coexistent equilibrium becomes greater than that in case of no harvesting. On the other hand, from this result, we can simultaneously have the result that, if $\Phi_{\theta,\rho}(p^*) \geq 0$ for any $p^* \geq 0$, the paradox never occurs for the population at the coexistent equilibrium.

Since $R'(x) < 0$ for any $x > 0$ from the assumption, we find that

$$R(Q(p)) \frac{d}{dp} \{ Q(p) \Pi(p) \} \geq \frac{d}{dp} \{ R(Q(p)) Q(p) \Pi(p) \} \tag{11}$$

for any $p > 0$. Hence, from Equation (10), we have the following result as a specific *sufficient* condition for the emergence of the paradox of pest control:

The paradox of pest control occurs if

$$\left. \frac{d}{dp} \{Q(p)\Pi(p)\} \right|_{p=p^*} < 0. \quad (12)$$

Although this sufficient condition (12) apparently depends only on the function Π , the equilibrium value p^* depends on the function R so that the sufficient condition (12) implicitly relates to both functions of R and Π . As a *stronger sufficient* condition for the paradox emergence, we can consider condition (12) for any $p > 0$ instead of $p = p^*$. Such stronger sufficient condition depends only on the nature of function Π . Indeed, as seen in the next section, we find that the paradox emergence is determined only by the function Π in some typical cases.

In contrast, from Equation (10), we can find the following *sufficient* condition such that the paradox never occurs:

The paradox of pest control never occurs if

$$\frac{d}{dp} \{R(Q(p))Q(p)\Pi(p)\} > 0 \quad (13)$$

for any $p > 0$.

If condition (13) is satisfied, the equilibrium host population size h^* is always monotonically decreasing in terms of ρ . So the harvesting always results in the successful suppression of the pest (= host) density in this case.

Furthermore, from Equation (10) and the above arguments, we can easily find the following *necessary* condition for the paradox emergence:

The paradox of pest control occurs only if

$$\left. \frac{d}{dp} \{R(Q(p))Q(p)\Pi(p)\} \right|_{p=p^*} < 0. \quad (14)$$

So, from Equations (10) and (11), we can see that the paradox is more likely to occur with the smaller θ , that is, *the paradox is more likely to occur with the harvesting before or earlier in the parasitism season*.

This result indicates that, to satisfy the condition for the paradox emergence, the sufficiently small θ is *necessary*.

In summary, when the application of harvesting with the parameter ρ for the system results in the coexistent equilibrium with the parasite population size p^* , if the condition $\Phi_{\theta,\rho}(p^*) < 0$ defined by Equation (10) is satisfied, the paradox of pest control occurs so that the increase of ρ makes the equilibrium host population size greater. Moreover, there is the host–parasite system in which the emergence of the paradox of pest control is determined only by the nature of function Π that gives the relationship between host and parasite populations in terms of the parasitism dynamics. In contrast, the host–parasite system in which such paradox never occurs requires specific natures of both functions Π and R . Further, the paradox of pest control is more likely to emerge with a sufficiently early application of harvesting in the parasitism season. Thus, in some cases, the application of harvesting at an appropriately late moment in the parasitism season is necessary for the successful suppression of the pest (= host) density, while that at too early moment may fail and cause the paradox of pest control.

3.4. Application for some typical cases

3.4.1. Exponential function

In case of the exponential function Π ,

$$\Pi(p) = e^{-\alpha p}, \tag{15}$$

where α is a positive constant, which is corresponding to the well-known Nicholson–Bailey model [19], we can easily prove that $d\{Q(p)\Pi(p)\}/dp < 0$ for any $p > 0$. Therefore, the condition that $\Phi_{\theta,\rho}(p^*) < 0$ is satisfied independently of the value of p^* also in this case. Thus, the paradox of pest control occurs. Numerical illustrations are given in Figure 2, where

$$R(h) = \frac{1}{1 + bh} \tag{16}$$

with a positive constant b [15].

We remark that, in this case with the growth function R given by Equation (16), the host population has a monotonically increasing reproduction curve when the parasite is absent. The host population is under a contest type of intra-specific competition. So, from the result of [22], the equilibrium host population size h_0^* in case of no parasite is always decreasing in terms of ρ [22]. However, even in this case, the above result shows that the paradox of pest control can

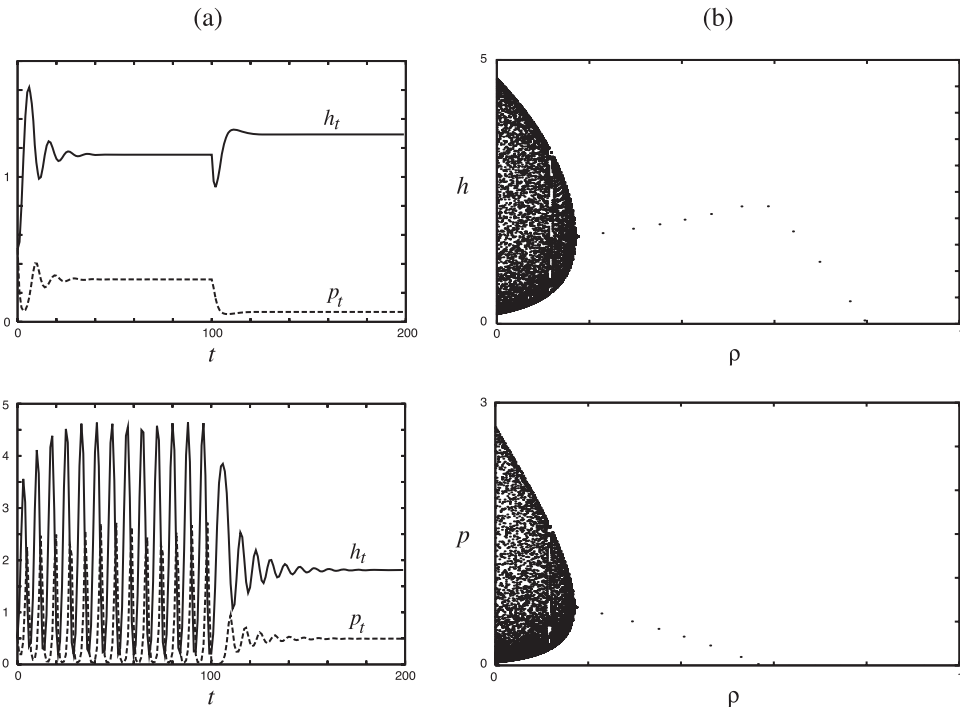


Figure 2. Numerical illustrations of the paradox emergence for the model (1) with an exponential function Π and the Beverton–Holt type function R , given by (15) and (16). After [15]. (a) population size transition by the introduction of harvesting for the host. $\alpha = 1$; $\mu = 1$; $b = 0.75$; $\theta = 0.5$. Upper: $\lambda = 2.5$ and $\rho = 0.2$, lower: $\lambda = 5.0$ and $\rho = 0.3$. The harvesting starts after $t = 100$. In the lower case, the chaotic oscillation transits to a dumping oscillation toward an equilibrium. (b) Numerically obtained bifurcation diagram: ρ -dependence of the limit state as $t \rightarrow \infty$. $\alpha = 1$; $\mu = 1$; $\lambda = 5.0$; $b = 0.75$; $\theta = 0.5$.

occur. Therefore, we can conclude that the paradox of pest control may be essentially caused by an inter-specific reaction.

3.4.2. *A concave polynomial function*

In this section, let us consider the following concave function Π :

$$\Pi(p) = \begin{cases} 1 - \left(\frac{p}{p_e}\right)^a & \text{for } 0 \leq p < p_e; \\ 0 & \text{for } p \geq p_e, \end{cases}$$

where p_e is a positive constant beyond which every host cannot escape from being parasitized. Although this function does not satisfy all our assumptions for the function Π because it is not differentiable at $p = p_e$, every assumption is satisfied in $[0, p_e)$ with any positive parameter $a \leq 1$. Since any positive p^* must be in $[0, p_e)$, we focus p in $[0, p_e)$.

In this case, we obtain

$$\frac{d}{dp}\{Q(p)\Pi(p)\} = (1 - a) \left(\frac{p_e}{p}\right)^a - 1. \tag{17}$$

Therefore, the sign of $d\{Q(p)\Pi(p)\}/dp$ at $p = p^*$ depends on the value of p^* , necessarily depending on the function R .

At first, let us consider the simplest case with $a = 1$, when Π is a piecewise linear function. In this case, we can easily find that $d\{Q(p)\Pi(p)\}/dp = -1$ for any p in $[0, p_e)$. Therefore, from the sufficient condition (12), the condition that $\Phi_{\theta,\rho}(p^*) < 0$ is satisfied independently of the value of p^* , so that the paradox can occur. Now we additionally assume a similar general concave function for R :

$$R(h) = \begin{cases} 1 - \left(\frac{h}{h_e}\right)^b & \text{for } 0 \leq h < h_e; \\ 0 & \text{for } h \geq h_e, \end{cases}$$

where h_e and b are positive constants. For $h > h_e$, the reproduction of host population fails at all, and the host population goes extinct. This is a case of scramble competition in the host population. To satisfy every assumption in our model, we consider only the case of $b \leq 1$ and focus h in $[0, h_e)$. Especially in case of $a = 1$ and $b = 1$ for Π and R given above, we can explicitly obtain the population sizes at the coexistent equilibrium:

$$(h^*, p^*) = \left(\frac{p_e}{\mu(1 - \rho)}, p_e - \frac{p_e}{\lambda(1 - \rho)\{1 - p_e/(\mu h_e)\}} \right).$$

Indeed, the equilibrium host population size h^* is monotonically increasing in terms of ρ , while the equilibrium parasite population size p^* is monotonically decreasing.

In this case with the piecewise linear growth function R with $b = 1$, the host population has a humped reproduction curve when the parasite is absent. The host population is under a scramble type of intra-specific competition. So, in accordance with the result of [22], the equilibrium host population size h_0^* in case of no parasite is increasing in terms of ρ , because we indeed have

$$h_0^* = \frac{1 - 1/\{\lambda(1 - \rho)\}}{\theta + (1 - \theta)(1 - \rho)} \cdot h_e,$$

and can easily get the necessary and sufficient condition for the paradoxical increase of h_0^* in terms of ρ at the stable equilibrium $(h_0^*, 0)$ [22].

Next, let us consider the case of $a \neq 1$ and $b \neq 1$ for Π and R given above. For mathematical simplicity, we consider the case of $\theta = 1$, when the sign of $\Phi_{\theta,\rho}(p)$ is determined only by that of $d\{Q(p)\Pi(p)\}/dp$. From Equation (5), we have the following equation to determine the value of p^* :

$$U(P^*) = (1 - P^*) \left\{ 1 - \left(\frac{P^*}{M} \right)^{b(1-a)/a} \right\} = \frac{1}{\lambda(1 - \rho)},$$

where $P^* = (p^*/p_e)^a$ and $M = (\mu h_e/p_e)^{a/(1-a)}$. From this equation, we can easily prove that the condition for the existence of coexistent equilibrium (h^*, p^*) is to satisfy that $\lambda(1 - \rho) > 1$, and that P^* is monotonically decreasing in terms of the value of $\lambda(1 - \rho)$.

From Equation (17), $d\{Q(p)\Pi(p)\}/dp < 0$ at $p = p^*$ if and only if $P^* > 1 - a$. The condition that $P^* > 1 - a$ is now equivalent to $U(1 - a) > 1/\{\lambda(1 - \rho)\}$, that is,

$$a \left\{ 1 - \left(\frac{1 - a}{M} \right)^{b(1-a)/a} \right\} > \frac{1}{\lambda(1 - \rho)}.$$

This inequality brings the following condition for the value of b :

$$b > \frac{a}{1 - a} \frac{\log [1 - 1/\{a\lambda(1 - \rho)\}]}{\log\{(1 - a)/M\}},$$

where it is necessary that $a\lambda(1 - \rho) > 1$ and $M > 1 - a$, that is,

$$a > \max \left[\frac{1}{\lambda(1 - \rho)}, 1 - M \right].$$

Consequently, in this case, the emergence of the paradox requires both the sufficiently strong density dependence of the probability of successful escape from the parasitism and the sufficiently strong density effect on the host population growth.

3.4.3. A concave rational function

In this section, let us consider the following rational function Π :

$$\Pi(p) = \frac{1}{(1 + Cp^\alpha)^\beta}, \tag{18}$$

where C, α, β are positive constants, and $\alpha \leq 1$. This function satisfies all assumptions for Π in our model.

In case of $\alpha = 1, \beta = k$ and $C = 1/k$, Equation (18) gives the negative binomial function for Π . In this case, we can easily prove that

$$\frac{d}{dp} \{Q(p)\Pi(p)\} \begin{cases} > 0 & \text{for } k < 1; \\ < 0 & \text{for } k > 1, \end{cases}$$

for any positive value of p . Therefore, the paradox occurs independently of the value of p^* for $k > 1$. The larger value of k means the strong density dependence of the probability of successful escape from the parasitism: As k gets larger, the probability more steeply decreases for increasing parasite population density. This result implies that the paradox is more likely to occur in such a situation as the strong density dependence of the probability of successful escape from the parasitism. Strong parasitism is likely to cause the paradox.

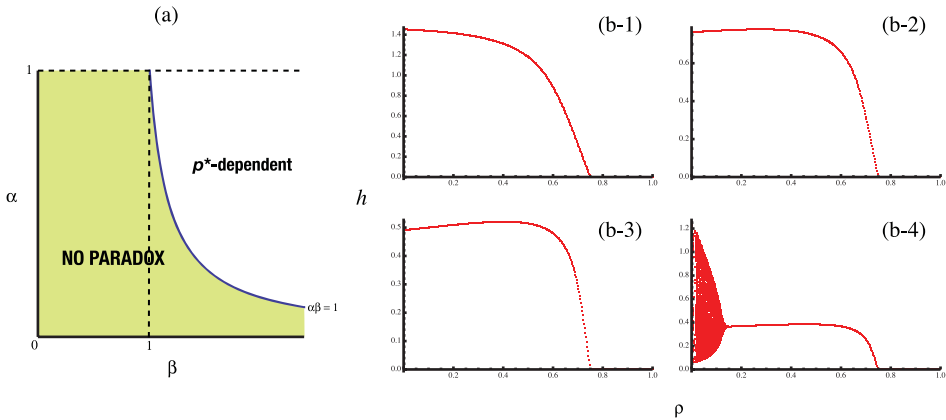


Figure 3. (a) Analytical result about the paradox emergence for (1) with the general concave rational function (18) in case of $\theta = 1$. For (α, β) of the region indicated by “NO PARADOX”, the paradox never occurs. For (α, β) of the white region indicated by “ p^* -dependence”, the paradox emergence depends on the features of the density effect function R and on the other parameter values. The nontrivial equilibrium (h^*, p^*) always exists. (b) Numerically drawn ρ -dependence of the limiting state of h_k ($k \gg 1$) for (1) with the general concave rational function (18) and the Beverton–Holt type density effect function (16). $\theta = 0.5; \lambda = 4.0; \mu = 1.0; b = 1.0; C = 1.0; \alpha = 0.8$. (b-1) $\beta = 1.0$; (b-2) $\beta = 2.0$; (b-3) $\beta = 3.0$; (b-4) $\beta = 4.0$.

As for the general case of Equation (18), again for mathematical simplicity, we focus the case of $\theta = 1$, when the sign of $\Phi_{\theta, \rho}(p)$ is determined only by that of $d\{Q(p)\Pi(p)\}/dp$. We can immediately obtain the (α, β) -dependence of the paradox emergence as shown in Figure 3a. We remark that there is a case that only the features of Π ensures the non-emergence of paradox, as indicated by the region of $\alpha\beta < 1$ in Figure 3a. The paradox emergence requires the condition that $\alpha\beta > 1$. Indeed, numerical calculations show the paradoxical increase of the equilibrium host population size as ρ gets larger in case of $\alpha\beta > 1$ (see Figure 3b).

4. Concluding remarks

In this paper, we show that, for a family of host–parasite systems, the host harvesting at the coexistent equilibrium is likely to make the equilibrium host population density larger, while it makes the equilibrium parasite population density smaller. We analytically proved that such a paradoxical increase of the equilibrium host density occurs even when the harvesting does not directly affect the parasite population at all. This result suggests that such a paradox would not be necessarily caused by the reduction of the parasite (natural enemy) population due to the harvesting itself, for example, by a pesticide. The host population is reduced by the harvesting, and simultaneously the intraspecific density effect is weakened. At the same time, the decrease of the host density causes the reduction of the net reproduction rate of the parasite. Since the parasite population eventually decreases under the repetitive harvesting operation targeted to the host, the paradox could emerge if the reduction of the parasite’s reproduction rate would be so serious that the parasite population cannot compensate it with parasitizing the host population successfully escaping from the harvesting.

As seen for model (1) with the negative binomial function Π , (18) with $\alpha = 1, \beta = k$ and $C = 1/k$, the emergence of the paradox depends on the intensity of parasitism. In case of a sufficiently strong parasitism, the decrease of the host population by the harvesting would significantly reduce the parasite’s reproductive success and eventually make the equilibrium parasite population density smaller, which could subsequently enhance the paradoxical increase of the host population density.

In our model, we have analytically shown that the parasite equilibrium population size is monotonically decreasing in terms of the strength of harvesting, represented by the parameter ρ . This means that the natural enemy (= parasite) population size is necessarily decreased by the pest (= host) control operation, even when the operation does not directly affect the natural enemy at all. Therefore, even though the natural enemy population density would decrease after a pesticide application against a pest, it is likely that it would not be caused by the pesticide effect, and instead would be resulted in with the native interspecific reaction between the pest and the natural enemy.

We conclude that a combined effect of the reduction of the host's intraspecific density effect and that of the parasite's reproduction rate could enhance the emergence of the paradox. Therefore, the emergence of the paradox in the pest control would not necessarily require the direct effect on the enemy population, the appearance of some pesticide-resistance, the trophobiosis or the pest hormesis due to the pest control operation. The purely ecological balance in the native population dynamics may do cause it, as Huffaker [10] emphasized the importance of 'balance of nature' and 'density-dependent' population regulation in the system involving the pest. For the pest control, the native species interactions are important as the key factors to determine the success/failure of additional control operation on the system. Therefore, in this reason, some integrated pest management (IPM) designed case by case would be necessary for the practical pest control [18,20,21,23–25].

In our model, harvesting before or earlier in the parasitism season is more likely to cause the paradoxical increase of the host population density. This result implies that the success of a pest control operation would depend on its schedule. The design of IPM should pay attention to how and when the pest control operations are scheduled.

Until now we have not found any experimental or observational report properly corresponding to our model, although there have been a number of researches on the resurgence. This may be because the studied resurgences in the previous works were mostly for the outbreak of a pest population after the application of a pesticide, instead of for simply an increase of the pest population size. We expect that some experiments in laboratory with a periodic partial reduction of a feeding population (e.g., of an insect, or of a fish in the fishery) could be conducted to show the paradoxical increase of the equilibrium population size which we have shown in this paper.

References

- [1] F. Chaboussou, *Nouveaux aspects de la phytiairie et de la phytopharmacie. Le phénomène de la trophobiose*, Proc. FAO Symp. Integrated Pest Control, Rome I (1966), pp. 33–61.
- [2] E. Cohen, *Pesticide-mediated homeostatic modulation in arthropods*, Pestic. Biochem. Physiol. 85 (2006), pp. 21–27.
- [3] P. DeBach (ed.), *Biological Control of Insect Pests and Weeds*, Chapman and Hall, London, 1964.
- [4] P. DeBach, D. Rosen, and C.E. Kennett, *Biological control of coccid by introduced natural enemies*, in *Biological Control*, C.B. Huffaker, ed., Plenum Press, New York, 1971, pp. 165–194.
- [5] U. Gerson and E. Cohen, *Resurgence of spider mites (Acari: Tetranychidae) induced by synthetic pyrethroids*, Exp. Appl. Acarol. 6 (1989), pp. 29–46.
- [6] A.E. Hajek, M.L. McManus, and I. Delalibera Jr., *A review of introductions of pathogens and nematodes for classical biological control of insects and mites*, Biol. Control 41 (2007), pp. 1–13.
- [7] M.R. Hardin, B. Benrey, M. Coll, W.O. Lamp, G.K. Roderick, and P. Barbosa, *Arthropod pest resurgence: an overview of potential mechanisms*, Crop Prot. 14 (1995), pp. 3–18.
- [8] M.E. Hochberg and R.I. Anthony (eds.), *Parasitoid Population Biology*, Princeton University Press, Princeton, 2000.
- [9] C.B. Huffaker (ed.), *New Technology of Pest Control*, Wiley-Interscience, New York, 1980.
- [10] C.B. Huffaker, F.J. Simmons, and J.E. Laing, *The theoretical and empirical basis of biological control*, in *Theory and Practice of Biological Control*, C.B. Huffaker and P.S. Messenger, eds., Academic Press, New York, 1976, pp. 41–78.
- [11] Y. Ito, K. Miyashita, and K. Sekiguchi, *Studies on the predators of the rice crop insect pests, using the insecticidal check method*, Jpn. J. Ecol. 12 (1962), pp. 1–11.
- [12] D.G. James and T.S. Price, *Fecundity in twospotted spider mite (Acari: Tetranychidae) is increased by direct and systemic exposure to imidacloprid*, Ecotoxicology 95 (2002), pp. 729–732.

- [13] S.D. Lane, N.J. Mills, and W.M. Getz, *The effects of parasitoid fecundity and host taxon on the biological control of insect pests: the relationship between theory and data*, *Ecol. Entomol.* 24 (1999), pp. 181–190.
- [14] T.D. Luckey, *Insecticide hormoligosis*, *J. Econ. Entomol.* 61 (1968), pp. 7–12.
- [15] T. Matsuoka and H. Seno, *Ecological balance in the native population dynamics may cause the paradox of pest control with harvesting*, *J. Theor. Biol.* 252 (2008), pp. 87–97.
- [16] R.L. Metcalf and W.H. Luckmann (eds.), *Introduction to Insect Pest Management*, Wiley-Interscience, New York, 1975.
- [17] J.G. Morse, *Agricultural implications of pesticide-induced hormesis of insects and mites*, *Hum. Exp. Toxicol.* 17 (1998), pp. 266–269.
- [18] W.W. Murdoch and C.J. Briggs, *Theory for biological control: Recent developments*, *Ecology* 77 (1996), pp. 2001–2013.
- [19] A.J. Nicholson and V.A. Bailey, *The balance of animal populations*, *Proc. Zool. Soc. Lond.* 3 (1935), pp. 551–598.
- [20] J.H. Perkins, *Insects, Experts, and the Insecticide Crisis*, Plenum Press, New York, 1982.
- [21] R.E. Plant and M. Mangel, *Modeling and simulation in agricultural pest management*, *SIAM Rev.* 29 (1987), pp. 235–261.
- [22] H. Seno, *A paradox in discrete single species population dynamics with harvesting/thinning*, Preprint.
- [23] V.M. Stern, R.F. Smith, R. van den Bosch, and K.S. Hogan, *The integrated control concept*, *Higardia* 29 (1959), pp. 81–101.
- [24] M. Takagi, *Perspective of practical biological control and population theories*, *Res. Popul. Ecol.* 41 (1999), pp. 121–126.
- [25] S. Tang, Y. Xiao, L. Chen, and R.A. Cheke, *Integrated pest management models and their dynamical behaviour*, *Bull. Math. Biol.* 67 (2005), pp. 115–135.