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Ecological balance in the native population dynamics may cause the paradox of pest control with harvesting

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Abstract

We analyze a 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 parasitism season. The principal target of the harvesting is the host; however, the parasite population may also be affected and reduced by a portion. Our model involves the Beverton–Holt type density effect on the host population. We investigate the condition in which the harvesting of the host results in an eventual increase of its equilibrium population size, analytically proving that the paradoxical increase could occur even when the harvesting does not directly affect the parasite population at all. We show that the paradox of pest control could be caused essentially by the interspecific relationship and the intraspecific density effect.

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1. Introduction

In agriculture, one of the serious problems has been the pest outbreak. So pest management has been studied empirically and theoretically (for reviews, see Metcalf and Luckmann, 1975; Huffaker, 1980; Plant and Mangel, 1987; Lane et al., 1999; Hochberg and Anthony, 2000; Hajek et al., 2007). 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*. Many investigations of the resurgence have been carried out (for instance, see DeBach et al., 1971; Gerson and Cohen, 1989; Hardin et al., 1995; Cohen, 2006). It could be caused by the emergence of a pesticide-resistant strain of the pest or by the decrease of its enemy population affected by the pesticide (Morse, 1998).

Ito et al. (1962) experimentally investigated such a case: a pest insect coexists with some species of spider as its

predators. The experimental field was divided into two regions, one of which was sprayed with an insecticide, while the other remained unsprayed. As a result, this chemical treatment decreased not only the pest population but also the spider population. The pest population increased by a remarkable amount in several weeks after spraying the insecticide. The primary cause of this phenomenon was suggested to be the decline of the predation pressure due to the reduction of the spider population by the insecticide.

Some other researches showed that a small amount of pesticide could increase the pest fecundity, whereas a large amount of pesticide decreases the pest population (Morse, 1998; James and Price, 2002). Such a phenomenon is called the *hormesis* or the *homoligosis* (Luckey, 1968; Morse, 1998). The hormesis would be the essential cause of some resurgence (Morse, 1998).

One of the most well-known time-discrete models for the host–parasite population dynamics is the Nicholson–Bailey model (Nicholson and Bailey, 1935):

$$\begin{aligned} h_{t+1} &= \lambda h_t e^{-\alpha p_t}, \\ p_{t+1} &= \mu h_t (1 - e^{-\alpha p_t}), \end{aligned} \quad (1)$$

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where h_t and p_t are the host and the parasite population densities at the t th generation. λ is the host (intrinsic) per capita growth rate, α the parasitism efficiency, and μ the parasite reproductive rate by the parasitism. This system has two equilibria: one at which both of host and parasite go extinct and another at which they coexist. The former is globally stable if $\lambda < 1$, and unstable if $\lambda > 1$. The latter is always unstable. If $\lambda > 1$, the model is unstable and non-permanent, since the host and the parasite populations show excited oscillations with infinitely increasing amplitude, asymptotically approaching an infinitesimally small population size at their minimal extremum in time (Hassell and May, 1973). The Nicholson–Bailey model and its modified forms have been analyzed by many researchers (for instance, see Beddington, 1975; Beddington et al., 1975; Gurney and Nisbet, 1998; Lane et al., 1999; Hassell, 2000a).

In this paper, we analyze another time-discrete host–parasite system which is an extension of the Nicholson–Bailey model, introducing the host intraspecific density effect and the harvesting effect. We investigate the condition with which the harvesting of the host results in an eventual increase of its population, analytically proving that such a paradoxical increase could occur even when the harvesting does not directly affect the parasite population at all. We show that the paradox of pest control could be caused essentially by the native interspecific and the intraspecific density effect.

2. Model

In general, parasites attack only one or a few of the host stages (i.e., egg, larva, or pupa) (Godfray, 1994; Murdoch and Briggs, 1996; Takagi, 1999). In our model, we suppose that there is a season for the parasitism in each year. In each year, the parasitism season has a given length T , beginning at time $\tau = 0$ and lasting until $\tau = T$. See Fig. 1.

We harvest a portion ρ ($0 \leq \rho \leq 1$) of the host population at a fixed moment $\tau = \theta T$ ($0 \leq \theta \leq 1$) from the beginning (at $\tau = 0$) of the parasitism season (see Fig. 1). We assume that the harvesting is repeated periodically every year. The harvesting operation in our model may be regarded as the repetitive application of some pesticides, pest-handpicking, or infertile enemies (i.e., *biopesticides*, that is, the short-time biological control, sometimes called “augmentation”).

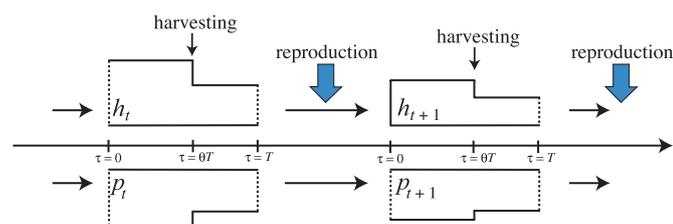


Fig. 1. Scheme of the host–parasite dynamics under a harvesting effect in our model (3). h_t is the host population density and p_t is the parasite population density at the beginning of the t th parasitism season.

For example, see Huffaker et al., 1976; Takagi, 1999 or Hajek et al., 2007).

Let h_t and p_t , respectively, be the host population density and the parasite one at the beginning of the t th parasitism season. Before $\tau = \theta T$ in the parasitism season, the host population undergoes the density effect on h_t . After $\tau = \theta T$, the density effect is on the host population of size $(1 - \rho)h_t$ which has successfully escaped from the harvesting. Making use of the modelling for the Nicholson–Bailey model (1) with a Poisson distribution of successful parasitism probability, we assume that, just after the moment of harvesting, the non-parasitized and the parasitized host population densities are, respectively, given by $(1 - \rho)h_t e^{-a\theta T p_t}$ and $(1 - \rho)h_t(1 - e^{-a\theta T p_t})$, where a represents the parasitism efficiency including the efficiency of *searching* and *catching* the host individual.

In our model, the target of the harvesting is the host population, whereas it may affect also the parasite population. We assume that the parasite population is reduced by a portion f with the harvesting which targets the host. Since the harvesting essentially targets the host, the parasite removal portion f is assumed to be determined by the host removal portion ρ : $f = f(\rho)$, satisfying that $0 \leq f(\rho) \leq 1$, $f(0) = 0$, and $df(\rho)/d\rho \geq 0$. The last assumption of the non-negative ρ -derivative of f means that the stronger harvesting of the host could cause the stronger secondary effect on the parasite. The harvesting reduces the parasite population density p_t to $\{1 - f(\rho)\}p_t$.

Since the rest of the parasitism season has the length $(1 - \theta)T$ after the harvesting, as the Nicholson–Bailey model (1), we can give the non-parasitized host population density by

$$(1 - \rho)h_t e^{-a\theta T p_t} \cdot e^{-a(1-\theta)T(1-f(\rho))p_t},$$

and the parasitized host population density by

$$(1 - \rho)h_t(1 - e^{-a\theta T p_t}) + (1 - \rho)h_t e^{-a\theta T p_t} \times [1 - e^{-a(1-\theta)T(1-f(\rho))p_t}]$$

at the end of the parasitism season. Then, with the reproductive rate λ' of the host and μ of the parasite, we have the following system of the host–parasite population dynamics:

$$\begin{aligned} h_{t+1} &= \lambda'(1 - \rho)h_t e^{-a(1-(1-\theta)f(\rho))T p_t}, \\ p_{t+1} &= \mu(1 - \rho)h_t [1 - e^{-a(1-(1-\theta)f(\rho))T p_t}]. \end{aligned} \quad (2)$$

Next, to incorporate the density effect on the host population into λ' , we assume that the density effect during the juvenile period determines the host's reproductive success. Especially in our model, let us assume that the cumulative density effect during the parasitism season determines it. Making use of the Beverton–Holt type of density effect (Beverton and Holt, 1957), the intensity of density effect before the harvesting is assumed to be proportional to $(1 + b h_t)^{-1}$, and that after the harvesting is to $\{1 + b(1 - \rho)h_t\}^{-1}$, where b is the coefficient for the intraspecific density effect on the net growth rate. We note

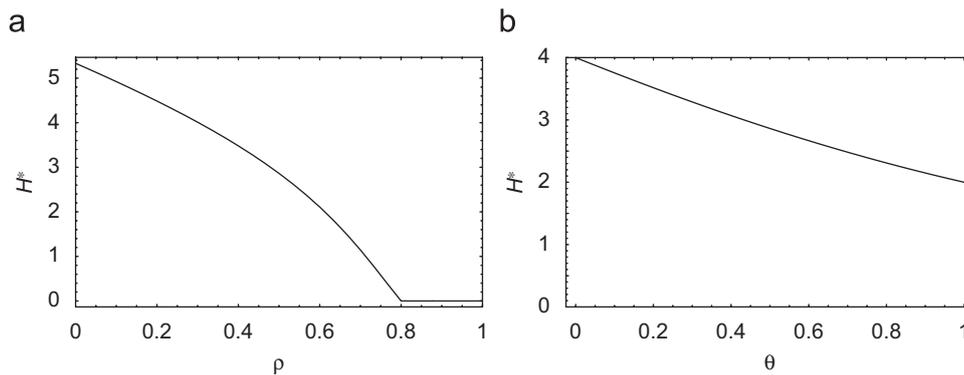


Fig. 2. Parameter dependence of the equilibrium H^* for (4) with $P_t \equiv 0$. (a) $\theta = 0.5$; (b) $\rho = 0.5$. Commonly, $\lambda = 5.0$; $\beta = 0.75$.

that, although the harvesting decreases the host population, it simultaneously weakens the intraspecific density effect for the host population. Our modelling may be regarded as assuming that the parasitized host does not die during the season. In this case, the parasitized host individual contributes to the density effect on the unparasitized host. Certainly we could assume that the density effect on the parasitized host causes the reduction of the parasite reproduction from the parasitized host. However, in our modelling, this is not assumed to occur. In some cases, the alive parasitized host behaves gluttonous with an effect of hormonal substances secreted from the parasite's egg or juvenile. Such a case may be applicable for our model.

The cumulative density effect on the non-parasitized host at the end of parasitism season is assumed to be determined by the proportion θ of the period before the harvesting in the parasitism season, so that we introduce

$$\lambda' = \lambda \left\{ \frac{\theta}{1 + bh_t} + \frac{1 - \theta}{1 + b(1 - \rho)h_t} \right\},$$

where λ is the intrinsic per capita growth rate of the host. Then, from (2), we lastly derive the following host–parasite system with harvesting effect:

$$h_{t+1} = \lambda' \left\{ \frac{\theta}{1 + bh_t} + \frac{1 - \theta}{1 + b(1 - \rho)h_t} \right\} \times (1 - \rho)h_t e^{-a\{1 - (1 - \theta)f(\rho)\}Tp_t},$$

$$p_{t+1} = \mu(1 - \rho)h_t[1 - e^{-a\{1 - (1 - \theta)f(\rho)\}Tp_t}]. \quad (3)$$

In our model, as the Nicholson–Bailey model, we assume that every parasitized host produces a fixed (*mean*) number of parasites in the next generation. In this sense, we may consider that contest competition is assumed among the parasite juveniles multi-parasitized in the same host individual, or alternatively assume mono-parasitism (no superparasitism). On the other hand, the parasite reproduction is assumed to occur after the specific parasitism season (see Fig. 1).

Now making use of the transformation of variables and parameters

$$P_t = aTp_t, \quad H_t = aT\mu h_t, \quad \beta = \frac{b}{aT\mu},$$

we get the corresponding non-dimensionalized system:

$$H_{t+1} = \lambda \left\{ \frac{\theta}{1 + \beta H_t} + \frac{1 - \theta}{1 + \beta(1 - \rho)H_t} \right\} \times (1 - \rho)H_t e^{-\{1 - (1 - \theta)f(\rho)\}P_t},$$

$$P_{t+1} = (1 - \rho)H_t[1 - e^{-\{1 - (1 - \theta)f(\rho)\}P_t}]. \quad (4)$$

For mathematical simplicity without loss of generality, we hereafter analyze this non-dimensionalized system (4).

When the parasite is absent, that is, for (4) with $P_t \equiv 0$, it becomes the Beverton–Holt model (Beverton and Holt, 1957) and gives a variation in generations similar to logistic growth. We have the following unique equilibrium H^* :

$$H^* = \frac{A + \sqrt{A^2 + B}}{2(1 - \rho)\beta}, \quad (5)$$

where $A = (1 - \theta\rho)(1 - \rho)\lambda - 2 + \rho$ and $B = 4(1 - \rho)\{(1 - \rho)\lambda - 1\}$. It exists if and only if $(1 - \rho)\lambda > 1$. If it exists, it is globally stable. If $(1 - \rho)\lambda < 1$, the host population goes extinct. Neither periodic nor chaotic variation occurs. We can easily prove that the harvesting necessarily reduces the equilibrium host population density (Fig. 2).

3. Analysis

3.1. Without harvesting

First, let us consider system (4) without harvesting ($\rho = 0$). In this case, there are at most three equilibria: $(0, 0)$ and

$$\begin{aligned} (\bar{H}, 0) &= \left(\frac{\lambda - 1}{\beta}, 0 \right), \\ (H^*, P^*) &= \left(\frac{\lambda e^{-P^*} - 1}{\beta}, H^*(1 - e^{-P^*}) \right). \end{aligned} \quad (6)$$

The equilibrium $(\bar{H}, 0)$ exists if and only if $\lambda > 1$, and (H^*, P^*) does if and only if $\lambda > 1 + \beta$.

The equilibrium $(\bar{H}, 0)$ is locally stable when $1 < \lambda < 1 + \beta$ and unstable when $\lambda > 1 + \beta$. We numerically analyzed the eigenvalues to investigate the local stability of (H^*, P^*) . As shown in Fig. 3, the equilibrium (H^*, P^*) is locally stable when $1 + \beta < \lambda < \lambda^*(\beta)$, where $\lambda^*(\beta)$ is a function of β . Numerical calculations indicate that the eigenvalue is complex when the equilibrium (H^*, P^*) changes its stability. Hence, from the characteristic equation for the eigenvalue about (H^*, P^*) , we have the following equation of parameters at the stability boundary for (H^*, P^*) :

$$(1 - 2\beta)\lambda - \sqrt{\lambda(\lambda - 4\beta)} - 2\lambda\beta \ln \frac{\lambda + 2 - \sqrt{\lambda(\lambda - 4\beta)}}{2\lambda} = 0. \tag{7}$$

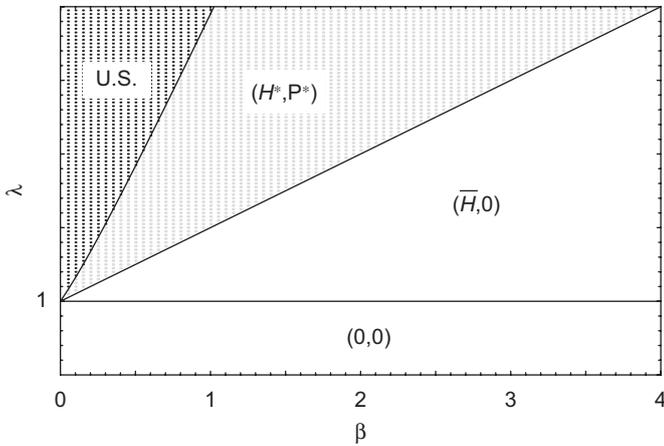


Fig. 3. (β, λ) -Dependence of the local stability of equilibria in the case without harvesting, (4) with $\rho = 0$. For the region “u.s.,” every equilibrium is unstable. Regions of (H^*, P^*) and “u.s.” are numerically obtained.

In fact, Eq. (7) appears to coincide with the numerically obtained stability boundary for (H^*, P^*) (Fig. 3; the boundary curve may seem linear, though it is really nonlinear).

Fig. 4 shows numerically obtained bifurcation structures of the limiting state (mathematically attained as $t \rightarrow \infty$) in terms of λ . For $\lambda > \lambda^*(\beta)$, the limiting state appears chaotic (see also Figs. 5(b) and (c)). However, the numerically obtained Lyapunov exponent is not greater than zero but almost zero for the corresponding value of λ (Fig. 6(a)). This bifurcation to chaos is what is called a *Neimark–Sacker bifurcation* or a *secondary Hopf bifurcation* (for instance, see Seydel, 1994) as indicated by the complex eigenvalue at the stability boundary for the equilibrium (H^*, P^*) (see Fig. 6(c)). Indeed, the numerical calculations as those in Fig. 5(c) indicate that any point (H_t, P_t) for sufficiently large t is asymptotically on a closed curve in the (H, P) phase plane. In this sense, this chaotic variation is sometimes called a *quasi-periodic state*, too. In addition, we can see a periodic behavior for some values (i.e., in some windows) of $\lambda > \lambda^*(\beta)$ (Figs. 4 and 5(d)).

3.2. With harvesting

We focus on how the intensity of harvesting (ρ) and its timing (θ) affect the nature of the limiting state. System (4) has at most three equilibria as in the case without harvesting. As for the equilibrium $(\bar{H}, 0)$, we can find that it exists if and only if $(1 - \rho)\lambda > 1$. From the local stability analysis, $(\bar{H}, 0)$ is locally stable if $1 < (1 - \rho)\lambda < (1 - \rho)\tilde{\lambda}$, where

$$(1 - \rho)\tilde{\lambda} = \frac{\{\beta + 1 - (1 - \theta)f(\rho)\}[\beta + (1 - \rho)\{1 - (1 - \theta)f(\rho)\}]}{\{1 - (1 - \theta)f(\rho)\}[(1 - \theta)\beta + (1 - \rho)\{1 - (1 - \theta)f(\rho)\}]} \tag{8}$$

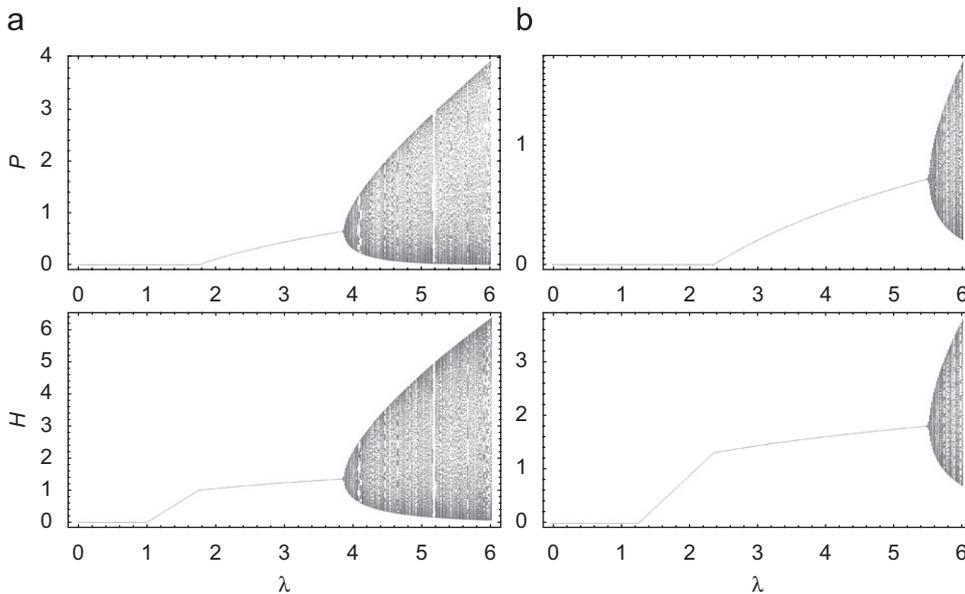


Fig. 4. Bifurcation diagram for the limiting state of system (4) in terms of λ . (a) $\rho = 0$; (b) $\rho = 0.2$; $\theta = 0.5$; $f(\rho) = 0.1$. Commonly $\beta = 0.75$.

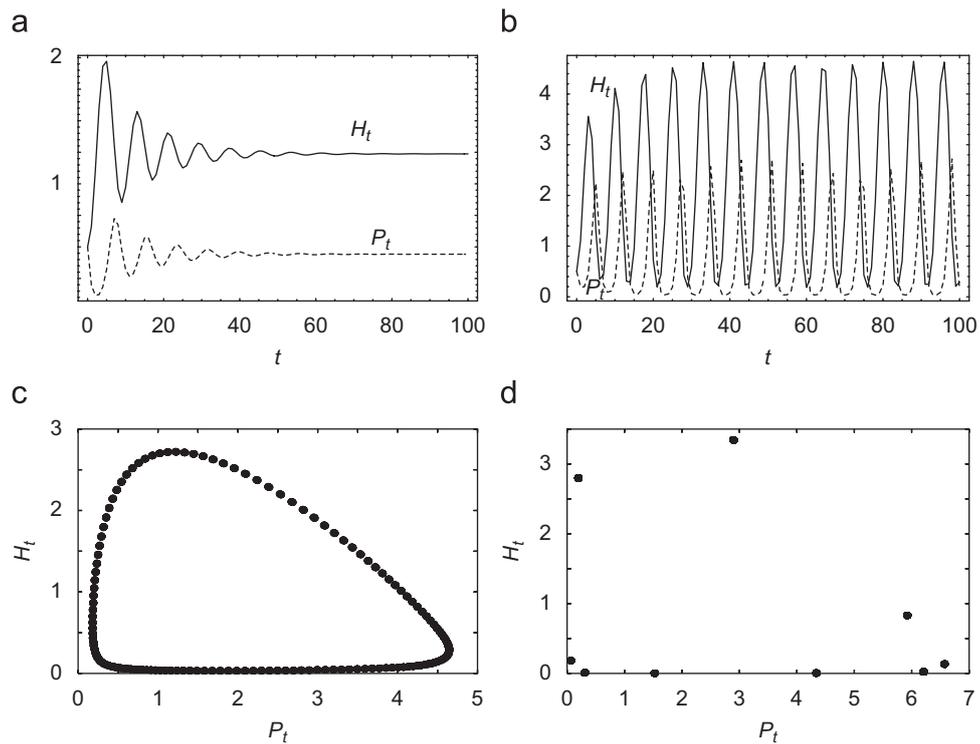


Fig. 5. Temporal variation of host and parasite populations in the case without harvesting ($\rho = 0$). (a) $\lambda = 3.0$; (b,c) $\lambda = 5.0$; (d) $\lambda = 6.12$. Commonly, $\beta = 0.75$; $H_0 = P_0 = 0.5$. In (c) and (d), plots are only for a range of sufficiently large t .

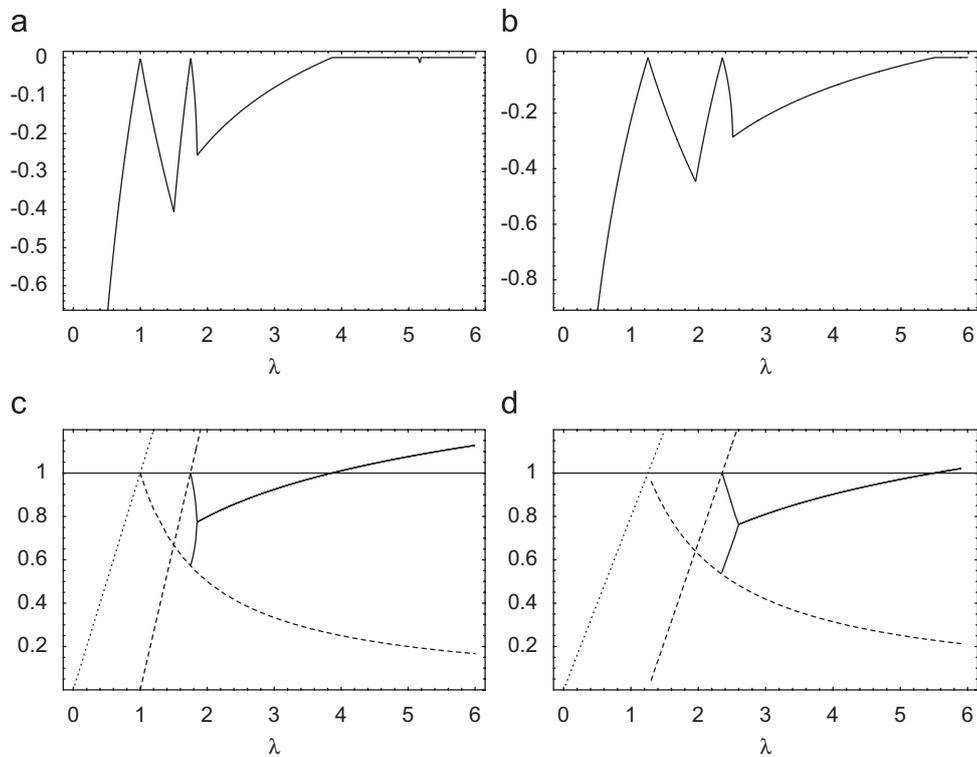


Fig. 6. Numerically obtained λ -dependence of (a,b) the Lyapunov exponent and (c,d) the absolute value of eigenvalues for the equilibria of (4). In (c,d), the solid curve indicates the eigenvalue for (H^*, P^*) . Thick dashed curves are for $(\bar{H}, 0)$, and thin dashed ones for $(0, 0)$. (a,c) $\rho = 0$; (b,d) $\rho = 0.2$; $\theta = 0.5$; $f(\rho) = 0.1$. Commonly $\beta = 0.75$.

We numerically investigate the bifurcation structure, the Lyapunov exponent, and the eigenvalues of the equilibria for (4) as shown in Figs. 4 and 6. We find that the bifurcation structure is qualitatively similar to the case without harvesting (see Fig. 4). The temporal variations in the case with harvesting are qualitatively similar to those in Fig. 5, too. However, the location of bifurcation points are significantly affected by the nature of harvesting. Numerical calculations indicate that, as for the equilibria $(\bar{H}, 0)$ and (H^*, P^*) , harvesting makes the bifurcation point in terms of λ occur at a larger value of λ than in the case without harvesting (Figs. 4 and 6–8).

3.3. Impact of harvesting

As ρ gets larger, $(\bar{H}, 0)$ and (H^*, P^*) , respectively, require a larger value of λ in order to be locally stable (Fig. 7). Moreover, as indicated by Figs. 7 and 8, we can see that the host population density H^* at the coexistence equilibrium increases as ρ gets larger, while the parasite population density P^* decreases even if the parasite is not directly affected at all by the harvesting, that is, even if $f(\rho) = 0$ (also see Fig. 9(a)). In contrast, in the case of chaotic variation, the time-averaged host population density $\langle H \rangle^*$ decreases as ρ gets larger (Fig. 10). Harvesting could suppress the chaotic variation toward the equilibrium state as Figs. 7–10 indicate. The harvesting makes the equilibrium host population density H^* larger (“paradox”) while it makes the parasite population density P^* smaller. These results are independent of the curvature of the function $f(\rho)$ (e.g., concave or convex) as easily seen from Fig. 8.

These features appear in our model commonly for any θ . As indicated by Fig. 7(b), the harvesting timing given by θ certainly affects the emergence of paradox although its θ -dependence is relatively weak, compared to the ρ -dependence. The equilibrium host population density H^* is

slowly increasing in terms of θ when the host coexists with the parasite, that is, at (H^*, P^*) (Fig. 7(b)).

With respect to the emergence of the paradoxical increase of the host population density H^* by the harvesting, we can prove the following theorem (Appendix A).

Theorem. For the coexistence equilibrium (H^*, P^*) , we always have

$$\lim_{\rho \rightarrow 0^+} \frac{\partial H^*}{\partial \rho} > 0 \quad \text{and} \quad \lim_{\rho \rightarrow 0^+} \frac{\partial P^*}{\partial \rho} < 0.$$

This theorem means that the harvesting necessarily makes the equilibrium host population density H^* larger and the coexisting parasite population density P^* smaller, compared to those at the coexistence equilibrium state without harvesting.

4. Comparison to some other models

In comparison to the case of the Beverton–Holt type of density effect in our model (4), Fig. 11 is a numerically obtained bifurcation diagram for the following system with the Ricker (or Moran–Ricker) type of density effect (Moran, 1950; Ricker, 1954):

$$H_{t+1} = \lambda(1 - \rho)\{\theta e^{-\beta H_t} + (1 - \theta)e^{-\beta(1-\rho)H_t}\} \times H_t e^{-(1-(1-\theta)f(\rho))P_t},$$

$$P_{t+1} = (1 - \rho)H_t[1 - e^{-\{1-(1-\theta)f(\rho)\}P_t}]. \tag{9}$$

This model without harvesting (i.e., $\rho = 0$) has been analyzed by many researchers (for example, Beddington et al., 1975). For review, see Hassell (2000b) and Hochberg and Anthony (2000). As seen from Fig. 11, our numerical calculation for (9) with harvesting ($\rho > 0$) shows that the host population density H^* at the coexistence equilibrium increases as ρ gets larger, similar to our model (4).

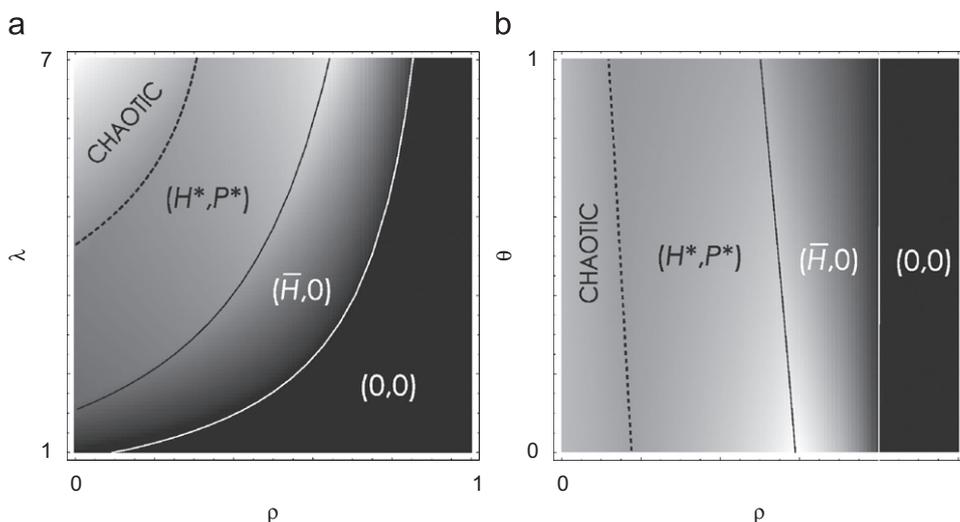


Fig. 7. Parameter dependence of the time-averaged host population density at the limiting state. Numerically obtained. Darker region corresponds to the smaller time-averaged host population density. (a) (ρ, λ) -dependence with $\theta = 0.5$; (b) (ρ, θ) -dependence with $\lambda = 5.0$. Commonly, $\beta = 0.75$; $f(\rho) = \rho/2$.

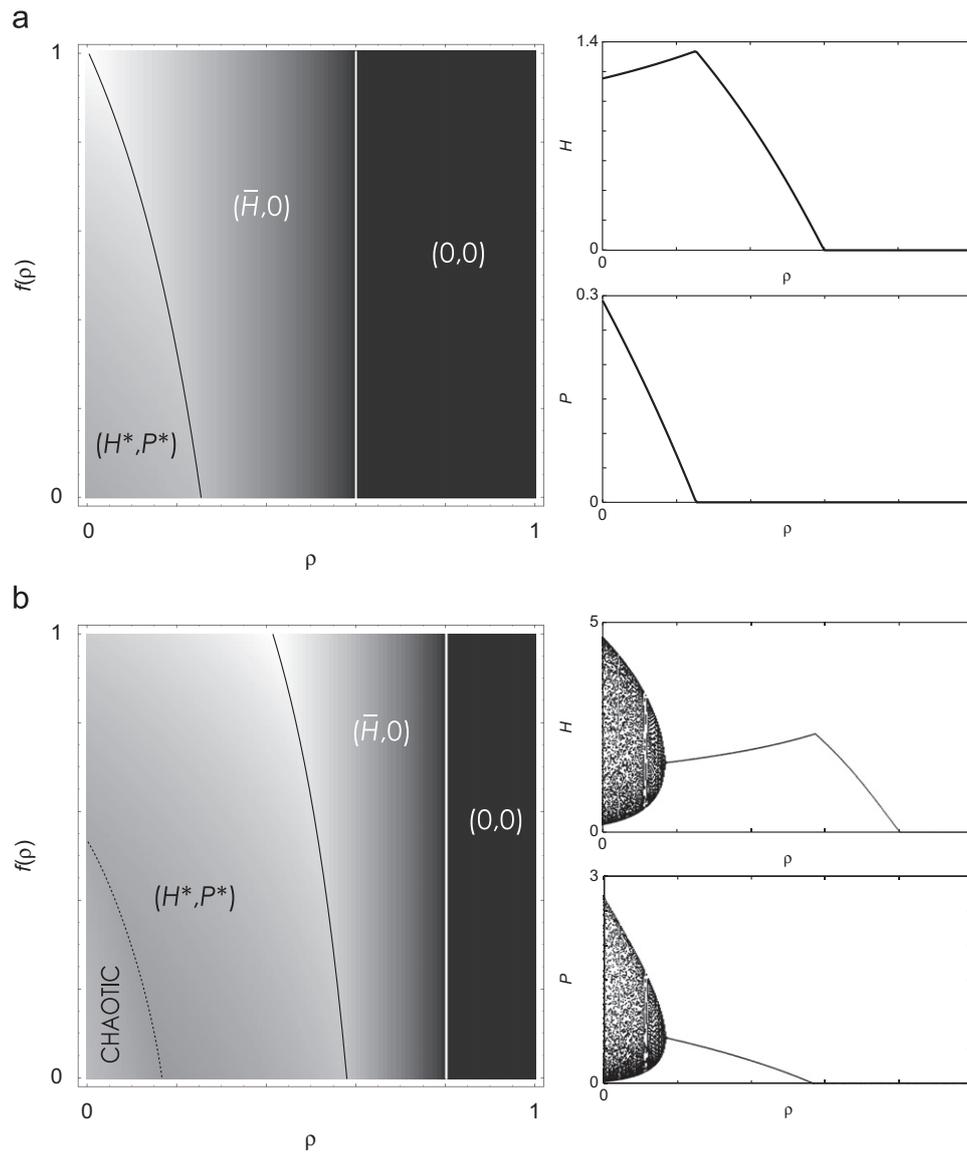


Fig. 8. $(\rho, f(\rho))$ -Dependence of the limiting state. Numerically obtained for pairs of the values ρ and $f(\rho)$. (a) $\lambda = 2.5$; (b) $\lambda = 5.0$. Commonly, $\beta = 0.75$; $\theta = 0.5$. In the density plots, the darker region corresponds to the smaller time-averaged host population density at the limiting state. The attached bifurcation diagram in terms of ρ is in the case when $f(\rho) = 0$. If we draw the curve of a specific function $f(\rho)$ overlapping the density plot, we can see the ρ -dependence with the given function $f(\rho)$.

As another type of the host–parasite model, let us consider the following model:

$$\begin{aligned}
 H_{t+1} &= \lambda \left\{ \frac{\theta}{1 + \beta H_t} + \frac{1 - \theta}{1 + \beta(1 - \rho)H_t} \right\} (1 - \rho)H_t \Pi(P_t), \\
 P_{t+1} &= (1 - \rho)H_t \{1 - \Pi(P_t)\},
 \end{aligned}
 \tag{10}$$

where $\Pi(P_t) = [1 + \{1 - (1 - \theta)f(\rho)\}P_t/k]^{-k}$ with a positive parameter k . This model is derived by substituting the negative binomial distribution for the Poisson distribution in (4). In this case, May et al. (1981) show that, as long as $k < 1$, for any host density effect, parasitism can stabilize the interaction. In this paper, aside from the stabilization role of the negative binomial distribution, let us focus the effect of harvesting on the host population density H^* at

the coexistence equilibrium. We numerically found that, in some cases for this model (10), the equilibrium host population density H^* decreases as ρ gets larger (Figs. 12(a) and (c)). In the case of a sufficiently large parasitism probability with large k , the equilibrium host population density H^* increases as ρ gets larger (Fig. 12(b)). The equilibrium host population density H^* decreases as ρ gets larger with a relatively weak intraspecific density effect on the host (small β) (Fig. 12(c)), whereas it increases in terms of ρ with a sufficiently strong intraspecific density effect (large β) (Fig. 12(b)) or with a sufficiently large probability of parasitism (Fig. 12(d)). Indeed, the probability of parasitism in model (4) is always larger than that in model (10) for any positive value of k .

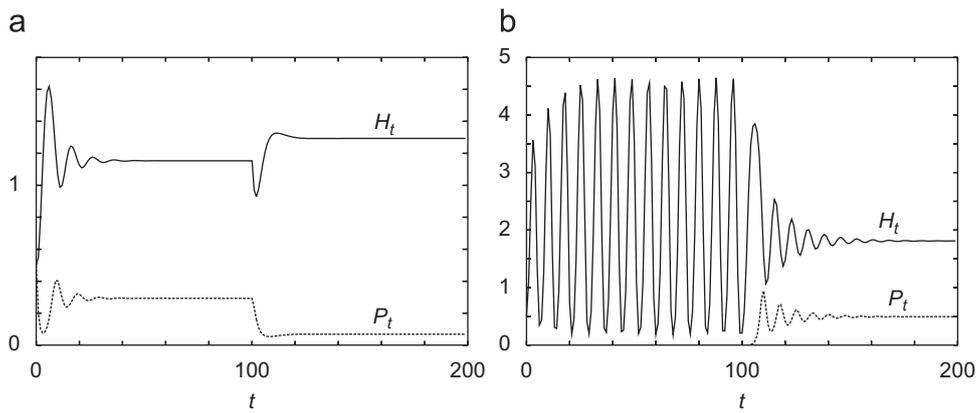


Fig. 9. Temporal variation of host and parasite populations before and after the initiation of harvesting operation. $\beta = 0.75; \theta = 0.5; f(\rho) = 0$. (a) $\lambda = 2.5$. The harvesting starts at $t = 100$ with $\rho = 0.2$. The previous equilibrium state shifts to another with the larger host population and the smaller parasite one. (b) $\lambda = 5.0$. The harvesting starts at $t = 100$ with $\rho = 0.3$. Chaotic (quasi-periodic) variation changes to the convergence toward an equilibrium state after the initiation of harvesting.

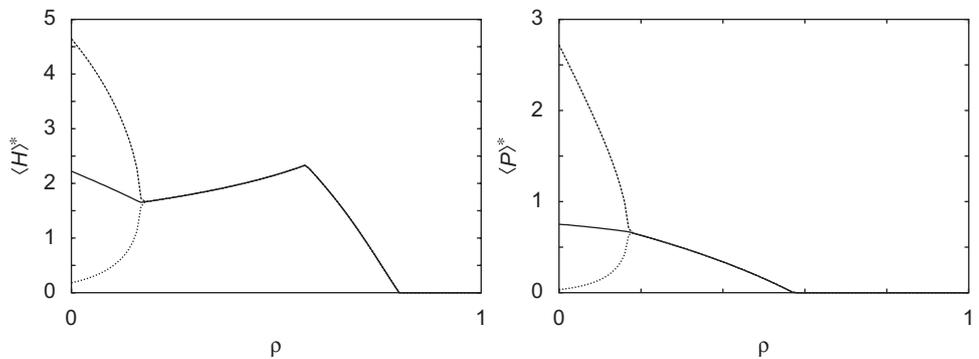


Fig. 10. ρ -Dependence of the time-averaged population density of the host and the parasite at the limiting state. Dashed curves indicates the range of the temporally variable limiting state. $\beta = 0.75; \lambda = 5.0; \theta = 0.5; f(\rho) = 0$.

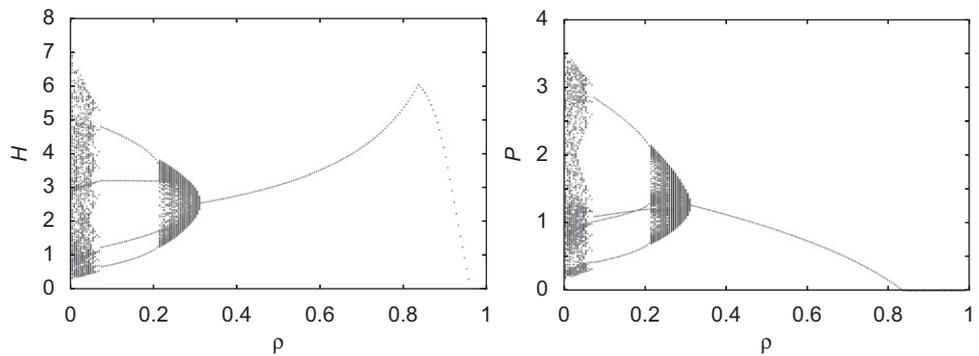


Fig. 11. Bifurcation diagram of the host and the parasite populations in terms of ρ for system (9). Numerically drawn with $\beta = 0.75; \lambda = 20.0; \theta = 0.5; f(\rho) = 0$.

As shown in Figs. 7, 8, 10 and 11, as the equilibrium parasite population density P^* gets smaller with the stronger harvesting (the greater ρ), the equilibrium host population density H^* becomes larger toward the carrying capacity determined by a specific value of ρ , only below which the parasite can coexist with the host. For ρ greater than the specific value, the parasite goes extinct due to the

harvesting while the host survives until another critical value of ρ beyond which the host goes extinct. In contrast, as shown by Fig. 12, this is not always true for the model with a negative binomial distribution for the successful parasitism probability, given by (10). The depression of the equilibrium parasite population size P^* does not necessarily lead to the (paradoxical) increase of the equilibrium

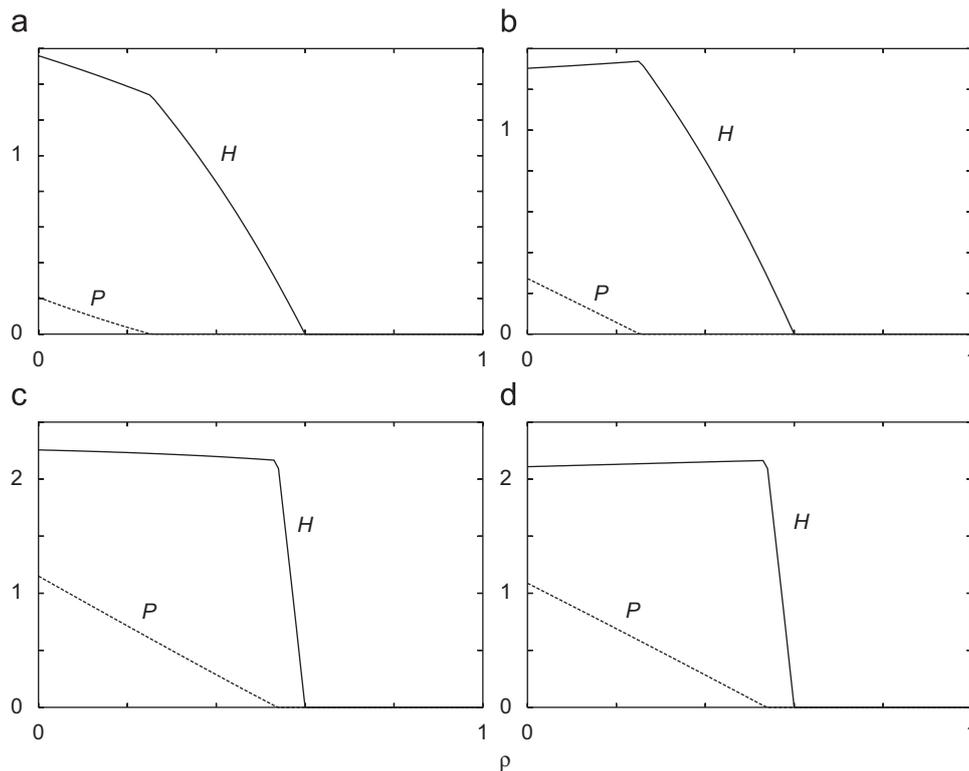


Fig. 12. Bifurcation diagram of the host and the parasite populations in terms of ρ for system (10). (a) $\beta = 0.75; k = 0.2$. (b) $\beta = 0.75; k = 0.8$. (c) $\beta = 0.1; k = 0.8$. (d) $\beta = 0.1; k = 0.95$. Commonly $\lambda = 2.5; \theta = 0.5; f(\rho) = 0$.

host population size H^* . These results suggest that the strong parasitism and the strong host density dependence would be likely to enhance the emergence of the paradox.

5. Conclusion

In our model, in the absence of the parasite, the equilibrium host population density necessarily decreases as the harvesting intensity ρ gets larger. In contrast, at the coexistence equilibrium with the parasite, the harvesting necessarily makes 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 at the moment of 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 (Fig. 13). In our model, the parasite population eventually decreases under the repetitive harvesting operation targeted to the host. If the reduction of the parasite's reproduction rate would be so serious that the parasite population cannot compensate it with parasitizing the surviving host population, the paradox could emerge.

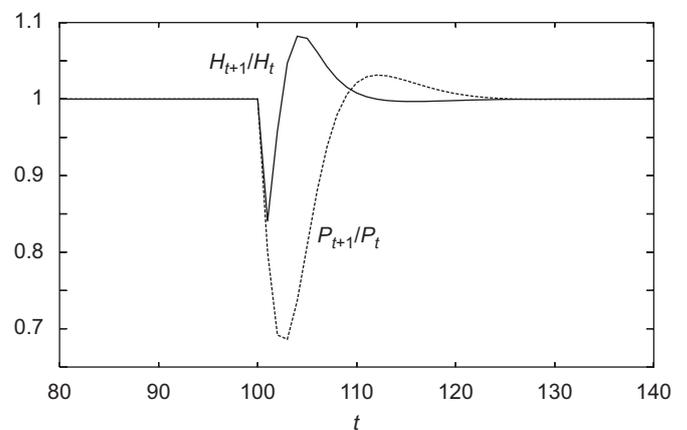


Fig. 13. Temporal variation of the net per capita reproduction rates of host and parasite populations before and after the initiation of harvesting operation for (4). $\lambda = 2.5; \beta = 0.75; \theta = 0.5; f(\rho) = 0$. The harvesting starts at $k = 100$ with $\rho = 0.2$.

As seen for model (10) with the negative binomial distribution of the successful parasitism probability, the host population density decreases by the harvesting when the intraspecific density effect of the host is sufficiently weak. Therefore, one of the essential factors to cause the paradox would be the relaxation of the host's tense intraspecific density effect by the harvesting. Moreover, since the paradox could occur for the sufficiently large parasitism probability for (10), the emergence of the paradox would depend on the intensity of parasitism.

In the case of 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 increase of the host population density.

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 or the pest hormesis. The purely ecological balance in the native population dynamics may do cause it, as Huffaker et al. (1976) emphasized the importance of "balance of nature" and "density-dependence" which regulates the populations in the system involving the pest. For the pest control, the native ecological 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 (Murdoch and Briggs, 1996; Perkins, 1982; Plant and Mangel, 1987; Stern et al., 1959; Takagi, 1999; Tang et al., 2005).

As numerically demonstrated in this paper, the model with a negative binomial distribution for the successful parasitism probability, given by (10), presents an open problem about the consequence of the effect combined the parasitism and the host density dependence: the emergence of paradoxical increase of host equilibrium density by harvesting. As Beddington et al. (1975) and May et al. (1981) discussed, some combined effect leads to stabilize the coexistence equilibrium, which is relied less on the host density dependence in case of the negative binomial model (also see Hassell, 2000b): The negative binomial model can depress the host well below its carrying capacity without making the coexistence equilibrium unstable. Therefore, according to results of our model with the effect of harvesting, the reduction of the parasite's reproduction rate due to the harvesting would play a principal role to cause the paradox, although this is still a conjecture to be investigated. The negative binomial model would be interesting to be analyzed more detail. However, the main purpose of this paper is to show clearly the theoretical possibility of the emergence of paradox only by the native ecological interaction, and we have not entered deeper into the analysis of the negative binomial model. In fact, we have already gotten some mathematical results about the condition for the occurrence of paradox in a more general framework of host-parasite model, including the negative binomial model, and are preparing to present it elsewhere.

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Appendix A. Proof of Theorem

As for the equilibrium (H^*, P^*) of (4), we have the following equations to determine H^* and P^* :

$$\ln \Psi(H^*) = (1 - \rho)\{1 - (1 - \theta)f(\rho)\}H^* \left\{1 - \frac{1}{\Psi(H^*)}\right\},$$

$$P^* = \frac{1}{1 - (1 - \theta)f(\rho)} \ln \Psi(H^*), \tag{A.1}$$

where

$$\Psi(H^*) = \lambda(1 - \rho) \left\{ \frac{\theta}{1 + \beta H^*} + \frac{1 - \theta}{1 + \beta(1 - \rho)H^*} \right\}.$$

From (A.1), we can obtain

$$\lim_{\rho \rightarrow 0^+} \frac{\partial H^*}{\partial \rho} = \frac{1}{\beta} \left[\frac{Q(z) df}{S(z) d\rho} + \frac{R(z)}{S(z)} \right] \tag{A.2}$$

and

$$\lim_{\rho \rightarrow 0^+} \frac{\partial P^*}{\partial \rho} = \frac{V(z)}{U(z)} + \frac{W(z) df}{U(z) d\rho}, \tag{A.3}$$

where $z = [e^{-P^*}]_{\rho=0}$ and

$$Q(z) = \lambda(1 - \theta)z(\lambda z - 1)(z - 1),$$

$$S(z) = 2\lambda z^2 - (\lambda + 1)z - \beta,$$

$$R(z) = (1 - \theta)(\lambda z - 1)U(z) - \lambda z V(z),$$

$$U(z) = z(\lambda z - 1) - \beta,$$

$$V(z) = \lambda z - \beta - 1, \quad W(z) = (1 - \theta)z \frac{(\lambda z - 1)^2}{\beta}.$$

From (A.1), we can easily find that z satisfies the following equation:

$$\psi(z) = (\lambda z - 1)(1 - z) + \beta \ln z = 0. \tag{A.4}$$

The equation $U(x) = 0$ has a unique positive root $\bar{x} < 1$ when $(H^*, P^*)_{\rho=0}$ of (6) exists, that is, when $\lambda > \beta + 1$. Making use of $U(\bar{x}) = 0$, we can find that $\psi(\bar{x})$ is monotonically increasing in terms of λ . Further, we can easily prove that $\psi(\bar{x})|_{\lambda=1+\beta} = 0$ since $\bar{x}|_{\lambda=\beta+1} = 1$. Therefore, $\psi(\bar{x}) > 0$ for $\lambda > 1 + \beta$. Hence, we find that $z < \bar{x} < 1$. This means that $U(z) < 0$. In addition, from (A.4), we can easily find that $V(z) > 0$. Since $W(z)$ is always positive, these results prove that (A.3) and $R(z)$ are negative.

On the other hand, $Q(z)$ is negative because $1/\lambda < z < 1$ as easily seen from (A.4). The equation $S(x) = 0$ has a unique positive root $x^\dagger < 1$ whenever $(H^*, P^*)_{\rho=0}$ exists. We can easily find that $S(z) < 0$ if and only if $z < x^\dagger$. At the same time, from (A.4), we note that $\psi(x) > 0$ for any x such that $z < x < 1$, and that $\psi(x) < 0$ for any $x < z$. Thus, if $\psi(x^\dagger) > 0$,

then $z < x^\dagger < 1$, so that $S(z) < 0$. Making use of $S(x^\dagger) = 0$, we have

$$\frac{\partial \psi(x^\dagger)}{\partial \lambda} = \frac{(\lambda - 1)x^{\dagger 2} - 2\beta x^\dagger + \beta}{4\lambda x^\dagger - \lambda - 1}. \quad (\text{A.5})$$

The numerator of (A.5) is positive for any x^\dagger since $\lambda > \beta + 1$. The denominator of (A.5) is also positive, because $S((\lambda + 1)/4\lambda) < 0$ so that $(\lambda + 1)/(4\lambda) < x^\dagger$. Therefore we have $\partial \psi(x^\dagger)/\partial \lambda > 0$ for $\lambda > \beta + 1$. We can easily prove that $\psi(x^\dagger)|_{\lambda=\beta+1} = \beta \ln x^\dagger|_{\lambda=\beta+1} = 0$. Thus, we now have $\psi(x^\dagger) > 0$ for $\lambda > \beta + 1$. Lastly, we find $z < x^\dagger < 1$. This means $S(z) < 0$. At last, (A.2) is positive for $\lambda > \beta + 1$. These arguments prove the theorem.

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