

# A Paradox in Discrete Single Species Population Dynamics with Harvesting/Thinning

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## Abstract

We analyze a general time-discrete mathematical model of single species population dynamics with the intraspecific density effect and the harvesting/thinning effect. We harvest a portion of the population at a moment in each year. We investigate the condition under which the harvesting/thinning causes an eventual increase of its population at the equilibrium, and show that such a paradoxical increase could occur for the discrete single species population dynamics with a large family of density effect functions. Some typical models are analyzed in detail according to the possibility of the paradox emergence. Our result implies that the contest competition would never cause the paradox, while the scramble competition would be likely to cause it.

*Key words:* resurgence, pest control, density effect, mathematical model

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## 1 Introduction

In this paper, we analyze a general time-discrete mathematical model of single species population dynamics with the intraspecific density effect and the harvesting/thinning effect. The harvesting/thinning is in general aimed to minimize the possibility of a population extinction, to maintain a population stock at productive levels, or to depress a pest density below some critical ‘damage threshold’ [1]. Related to these problems, a variety of mathematical models introduced the harvesting/thinning effect have been considered and analyzed, mainly from the viewpoint of a sustainable management/development of natural resources (for example, see [2,3]).

In agriculture, one of the serious problems has been the pest outbreak. So the pest management has been studied empirically and theoretically (for reviews, see [4–12]). 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 subsequently results in an unexpected increase or 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 about the resurgence have been carried out (for instance, see [13–17]). 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 [18]. 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 [18,19]. Such phenomenon is called the *hormesis* or the *homoligosis* [18,20]. The hormesis would play an important role to cause the resurgence [18].

In previous researches, the harvesting/thinning by various forms of physical control, spraying of pesticides, and biological control was always regarded to necessarily reduce the population size. In this paper, it is implied that the subsequent population sizes would not be always reduced by the harvesting/thinning, and such hypothesis that the harvesting/thinning would always work to reduce the population size as the eventual consequence of its application may be inappropriate in some cases.

In our time-discrete mathematical model of single species population dynamics with the intraspecific density effect and the harvesting/thinning effect, we harvest a portion of the population at a moment in each year. We investigate the condition under which the harvesting/thinning causes an eventual increase of its population at the equilibrium, and show that such a paradoxical increase can occur for the discrete single species population dynamics with a large family of density effect functions. Some typical models are analyzed in detail according to the possibility of the paradox emergence.

Although our model is fundamental and very simple, we can see that the harvesting/thinning would potentially work to increase the equilibrium size of a population targeted by it. This appears to be a *paradox* against the intuition from the direct effect of harvesting/thinning to reduce the population size. In the previous researches, such resurgent phenomena against some harvesting/thinning operation in nature or in agriculture/fishery/forestry have been used to be explained by some specific secondary effect of the harvesting/thinning, as mentioned above. In contrast, our result implies that, even without any of such specific causes, the resurgent phenomenon may emerge only by the native ecological structure in the population dynamics disturbed by the harvesting/thinning operation.

Maximal sustainable yield (MSY) aside, our results imply that an appropriate harvesting/thinning would be useful to increase the (time-averaged) population size as a consequence of the operation, which could enhance the persistence or the sustainability of the targeted population.

## 2 Model

We consider the following time-discrete single species population dynamics:

$$h_{t+1} = \lambda \{ \theta R(h_t) + (1 - \theta) R((1 - \rho)h_t) \} (1 - \rho)h_t, \quad (1)$$

where  $h_t$  is the population size at a fixed moment (i.e., a fixed observation point) of the  $t$  th year. The sufficiently smooth function  $R (\geq 0)$  of the population size introduces the intraspecific density effect on the reproductive rate, satisfying that  $0 < R \leq 1$ . The positive parameter  $\lambda$  means the intrinsic growth rate, and  $\lambda R$  gives the per capita reproductive rate affected by the intraspecific density effect.

We harvest a portion  $\rho$  ( $0 \leq \rho < 1$ ) of the population at a moment given by  $\theta$  ( $0 \leq \theta \leq 1$ ) in a specific season of each year (see Fig. 1). As the exact definition,  $h_t$  gives the population size at the beginning of the specific season in the  $t$  th year. In our model (1), we consider only the case of such a *proportional* harvesting/thinning,  $(1 - \rho)h_t$ , instead of a *constant* harvesting/thinning:  $h_t - H$  ( $H$  is an appropriate positive constant). This means that the assumed harvesting/thinning is performed with a random operation, for example, by a pesticide.

As in Matsuoka and Seno [21], we assume the specific season during which

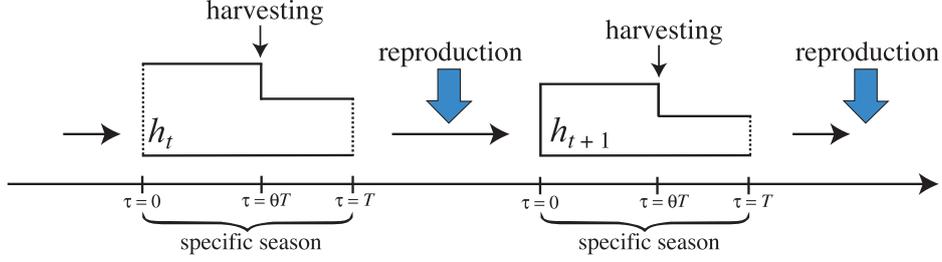


Fig. 1. Scheme of the population dynamics with harvesting/thinning in our model (1).  $h_t$  is the population density at the beginning of the  $t$  th specific season in which the harvesting/thinning is applied.

the individual accumulates the energy for the reproduction. The total amount of the accumulated energy is reflected to the reproductive success. Then we assume that the cumulative density effect during the specific season determines the total amount. As seen in (1), the cumulative density effect is assumed to be additively given by the proportion  $\theta$  of the period before/after the harvesting/thinning in the specific season. The case of  $\theta = 0$  may be regarded to correspond to the harvesting/thinning before the specific season, and the case of  $\theta = 1$  may be to the harvesting/thinning after it.

In this paper, we assume that the density effect function  $R(h)$  is sufficiently smooth, two times continuously differentiable, satisfying that  $R(0) = 1$ ,  $\lim_{h \rightarrow \infty} R(h) = 0$ , and  $R'(h) = dR(h)/dh < 0$  for any  $h > 0$ .

With these assumptions, the per capita reproductive rate  $\lambda R$  is decreasing in terms of the population size, which introduces the intraspecific density effect that can regulate the population growth. When  $\lambda > 1$ , from the assumptions, there is a unique positive value of  $h$ , say  $h_c$ , such that  $\lambda R(h_c) = 1$ . We can easily see that, in the case of no harvesting/thinning ( $\rho = 0$ ), the population approaches a stationary size given by  $h_c$ : The equilibrium  $h = h_c$  is globally stable for any positive initial state  $h_0$ .

In contrast, when  $\lambda < 1$ , the population eventually goes extinct independently of whether the harvesting/thinning is applied or not. This is because the net reproductive rate given by  $h_{t+1}/h_t$  is always less than 1, as easily seen from (1). When  $\lambda = 1$ , in the same reason, the population eventually goes extinct if a harvesting/thinning is applied ( $\rho > 0$ ). Also in the case of no harvesting/thinning ( $\rho = 0$ ) when  $\lambda = 1$ , we can easily prove that the population size is monotonically decreasing in generation, and that the extinction necessarily occurs. Therefore, from the biological interest, we hereafter consider our model (1) with the assumption  $\lambda > 1$ .

### 3 Analysis

#### 3.1 Existence and stability of non-trivial equilibrium

In this section, we consider the existence of the non-trivial equilibrium  $h = h^* > 0$  when a harvesting/thinning is applied with  $\rho > 0$ . The equilibrium population size  $h^*$  satisfies the following equation:

$$\lambda \{ \theta R(h^*) + (1 - \theta) R((1 - \rho)h^*) \} = \frac{1}{1 - \rho}. \quad (2)$$

From the assumptions,  $\lambda > 1$  and the function  $R(h)$  is monotonically decreasing toward zero in terms of  $h > 0$ , and so is the function  $\theta R(h) + (1 - \theta) R((1 - \rho)h)$  of  $h$ . Since the left side of (2) is necessarily less than  $\lambda$  for  $h^* > 0$ , the equation (2) has a unique positive root only when  $\lambda(1 - \rho) > 1$ , that is, only when  $\rho < 1 - 1/\lambda$ . If  $\rho \geq 1 - 1/\lambda$ , it is clear that the equation (2) cannot have any positive root for  $h^*$ , because the left side is less than  $1/(1 - \rho)$  for any  $h > 0$  in this case. In the case of  $\rho \geq 1 - 1/\lambda$ , the population size is monotonically

decreasing in generation and necessarily goes extinct. From these arguments, we now have the following result:

**Result:** The equilibrium  $h = h^* > 0$  uniquely exists if and only if  $\rho < 1 - 1/\lambda$ .

Making use of the standard local stability analysis for the equilibrium  $h = h^* > 0$ , we can get the following result:

**Result:** The equilibrium  $h = h^* > 0$  is asymptotically stable if

$$\left. \frac{d}{dh} \left[ h^2 \{ \theta R(h) + (1 - \theta) R((1 - \rho)h) \} \right] \right|_{h=h^*} > 0.$$

It is unstable if the inequality is reversed.

We remark that, when no harvesting/thinning is applied (i.e.,  $\rho = 0$ ), we have  $h^* = h_c$ . Hence, from the above result, we find that, in the case of  $\rho = 0$ , the equilibrium  $h = h_c$  is asymptotically stable if  $\lambda |R'(h_c)| h_c < 2$ , while it is unstable if this inequality is reversed.

### 3.2 Increase of the equilibrium population size by harvesting/thinning

In this section, we consider the  $\rho$ -dependence of the population size  $h^*$  at the non-trivial equilibrium. From the direct  $\rho$ -derivative for (2), we have the following equation:

$$\frac{\partial h^*}{\partial \rho} = \frac{1}{(1 - \rho)\Lambda} \left[ \theta R(h) + (1 - \theta) \frac{\partial}{\partial h} \{ R((1 - \rho)h) h \} \right]_{h=h^*}, \quad (3)$$

where  $\Lambda = \theta R'(h^*) + (1 - \theta)(1 - \rho)R'((1 - \rho)h^*) < 0$  because  $R' < 0$ . Therefore we obtain the following result:

**Result:** To increase the harvesting/thinning rate causes the increase of the equilibrium population size only if the following condition is satisfied:

$$\theta R(h^*) + (1 - \theta) \left. \frac{d}{dh} \{R(h)h\} \right|_{h=(1-\rho)h^*} \leq 0. \quad (4)$$

This is the condition for the emergence of such a paradox that the reduction of population by the harvesting/thinning consequently causes its eventual increase. We can immediately obtain the following important corollary from (4):

**Result:** The paradoxical increase occurs only if

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

Therefore, in order of the paradox emergence, the function  $R(h)h$  which gives what is sometimes called the *reproduction curve* in population ecology or the *return map* in the dynamical system theory necessarily has a range of monotonically decreasing. Further, as a conventional theoretical assumption to consider the population dynamics, if the population is closed, that is, if any immigration or emigration is negligible in terms of the population size change, then  $R(h)h \rightarrow 0$  as  $h \rightarrow 0$ . In such a case, the above necessary condition for the paradox emergence indicates a *humped shape* of the reproduction curve:

**Result:** The humped reproduction curve is necessary to cause the paradox for the closed population dynamics.

Therefore, the population under a *scramble competition* [22] is likely to cause the paradox, because the humped reproduction curve due to the intraspecific density effect defines the scramble competition (As for the concept of ‘scramble’ and the ‘contest’ competition, for example, see [23]).

From (4), as a sufficient condition for the paradox emergence, we can find the following:

**Result:** If the function  $R$  satisfies that

$$\frac{d}{dh} \{R(h)h\} \geq 0 \text{ for any } h > 0,$$

then the equilibrium population size  $h^*$  is always monotonically decreasing in term of  $\rho$ , so that the paradoxical increase never occurs.

Therefore, it is implied that the paradoxical increase could occur only in the case when the reproductive rate is sufficiently sensitive to the intraspecific density effect and it steeply decreases as the population size gets sufficiently large at least in a range of population size. The population under a *contest competition* [22] never causes the paradox, because the reproduction curve due to the contest competition is monotonically increasing (with an upper bound) in terms of the population size.

In addition, from (4), we can find the following result, too:

**Result:** For sufficiently large  $\theta$  ( $\leq 1$ ), the paradoxical increase of the population size never occurs and the harvesting/thinning makes the equilibrium population size necessarily decrease.

This is because the condition (4) does not hold when  $\theta = 1$ . From this result, the harvesting/thinning in the later period of the specific season necessarily decreases the equilibrium population size, compared to that without the harvesting/thinning:

**Result:** The paradox emergence requires a sufficiently small  $\theta$ .

These arguments should be applied only for the case that the non-trivial equilibrium exists stable, because our discussion is about the harvesting/thinning effect on the population size at the equilibrium. In the subsequent section, we consider some cases of concrete function  $R$ , in which we will make more detail analysis for each case, combining the condition for the stability condition with that for the paradox emergence.

### 3.3 Application for some typical cases

#### *Beverton-Holt type function: logistic growth case*

Next, let us consider the following rational function  $R$ :

$$R(h) = \frac{1}{1 + bh}, \quad (5)$$

where  $b$  is a positive constant. This case corresponds to what is frequently called the Beverton-Holt model [24–26]. This model has a monotonically increasing reproduction curve, which corresponds to the contest competition [22]. Whenever the non-trivial equilibrium  $h = h^* > 0$  exists for  $\lambda(1 - \rho) > 1$ , it is globally stable such that the population size asymptotically and monotonically approaches  $h^*$  from any positive initial value  $h_0$ . This is the logistic growth with the carrying capacity  $h^*$ .

In this case, we can easily find that the condition for the paradox emergence (4) is *never* satisfied for any  $h^* > 0$ . The paradoxical increase never occurs in this case: The harvesting/thinning eventually makes the equilibrium population size smaller than that before the harvesting/thinning is applied.

*Exponential function: Ricker model case*

In this section, we consider the exponential function  $R$ ,

$$R(h) = e^{-\beta h}, \tag{6}$$

where  $\beta$  is a positive constant. This gives what is called the Ricker model or the Ricker-Moran model [27–30]. This model has a humped reproduction curve corresponding to the scramble competition [22].

In the case of  $\rho = 0$ , we can easily find that the paradoxical increase can occur if  $\theta < 1/2$  and  $e^{1/(1-\theta)} < \lambda < e^2$ : For  $\rho = 0$ , the non-trivial equilibrium  $h = h^* > 0$  exists globally stable if and only if  $1 < \lambda < e^2$ . From our results about the general model, we can find that, if and only if  $\lambda > e^{1/(1-\theta)}$ , the paradoxical increase of  $h = h^* > 0$  occurs as  $\rho$  gets larger near  $\rho = 0$ . That is, if we apply a weak harvesting/thinning for the population at the equilibrium when the harvesting/thinning has not been applied yet, the harvesting/thinning with  $\theta < 1/2$  and  $e^{1/(1-\theta)} < \lambda < e^2$  results in the paradox emergence.

In the similar way, we can easily find that, for  $\theta = 0$ , the paradoxical increase occurs if and only if  $1 - e^2/\lambda < \rho < 1 - e/\lambda$  while the equilibrium exists globally stable for  $1 - e^2/\lambda < \rho < 1 - 1/\lambda$ . In contrast, for  $\theta = 1$ , though the equilibrium exists globally stable for  $1 - e^2/\lambda < \rho < 1 - 1/\lambda$  (the same condition as that in the case of  $\theta = 0$ ), the paradoxical increase *never* occurs. See Fig. 2.

As for the general case of  $\rho > 0$  and  $0 < \theta < 1$ , we can numerically investigate the time-averaged population size in the sufficiently later generations as shown in Fig. 3. As in the case of the piecewise linear  $R$ , when the paradoxical

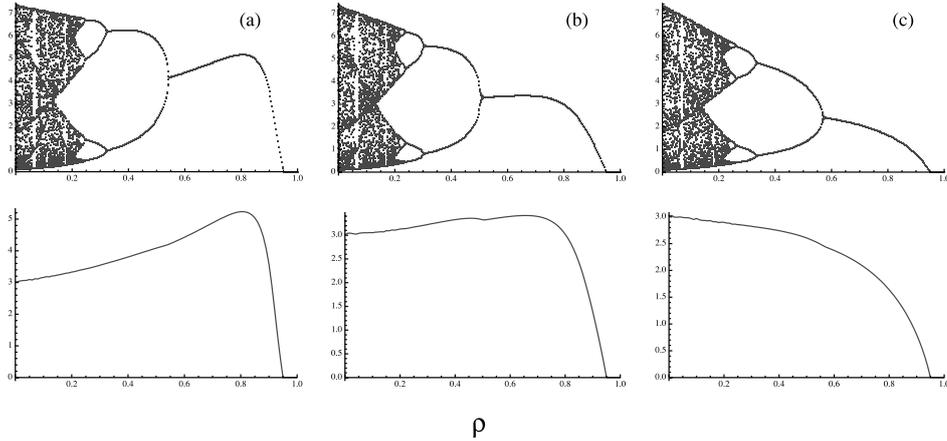


Fig. 2. Bifurcation diagrams and the time-averaged values in terms of  $\rho$  for the Ricker model case with the exponential  $R$  given by (6). Numerically drawn. (a)  $\theta = 0.3$ ; (b)  $\theta = 0.6$ ; (c)  $\theta = 0.9$ . Commonly  $\beta = 1.0$  and  $\lambda = 20.0$ . In each case, the upper is the bifurcation diagram and the lower the time-averaged value.

increase occurs at the equilibrium, there is such a specific value of  $\rho$  that the harvesting/thinning enlarges the equilibrium population size by the largest amount.

However, differently from the case of the piecewise linear  $R$ , even when the population size has a chaotic or periodic variation, the time-averaged population size does not always tend to become larger as the harvesting/thinning gets stronger (the larger  $\rho$ ). Roughly speaking from the numerical calculations, under the condition that the paradoxical increase occurs by the harvesting/thinning applied in the earlier period of the specific season (the smaller  $\theta$ ), the relatively weak harvesting/thinning could not reduce the time-averaged size but eventually increase it, so that a sufficiently strong harvesting/thinning is required in order to reduce the population size to the level less than that before the harvesting/thinning is applied.

Under the condition that the paradoxical increase does not occur by the

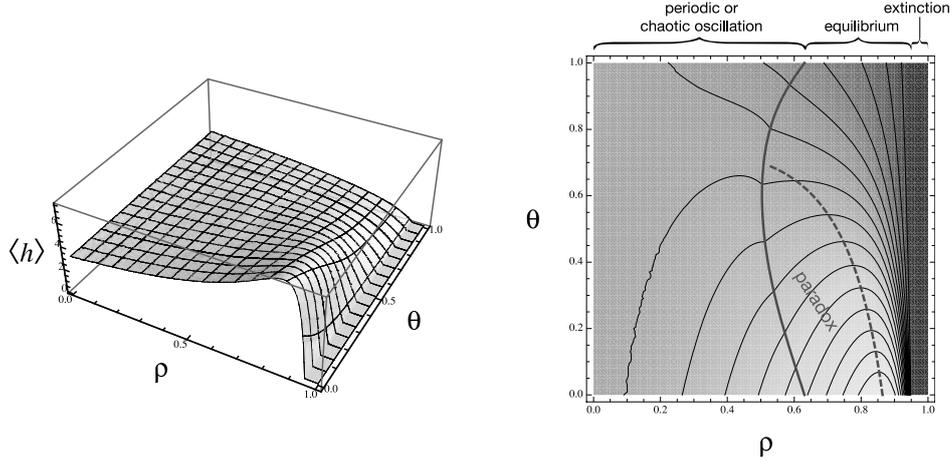


Fig. 3.  $(\rho, \theta)$ -dependence of the time-averaged population size  $\langle h \rangle$  in the sufficiently later generations for the Ricker model case with the exponential  $R$  given by (6). Numerically drawn with  $\beta = 1.0$  and  $\lambda = 20.0$ . In the density plot, the lighter region indicates the larger time-averaged population size  $\langle h \rangle$ . Some isograms are numerically drawn by thin curves, too. In the region between the solid and dotted curves, the paradoxical increase of the equilibrium population size in terms of  $\rho$  occurs.

harvesting/thinning applied in the later period of the specific season (the larger  $\theta$ ), the harvesting/thinning could reduce the (time-averaged) population size as the result.

### *Power function*

In this section, we consider the following power function  $R$ :

$$R(h) = h^{-\gamma}, \quad (7)$$

where  $\gamma$  is a positive constant different from 1. Since the right hand of (1) is a constant independent of  $h_t$  if  $\gamma = 1$  in (7), we exclude this singular case. This is the density effect studied by [31] (also see [32]). Although this density effect function  $R$  does not satisfy the assumption  $R(0) = 1$  for our arguments in

this paper, our results are applicable as long as the equilibrium is considered. This is because the assumption  $R(0) = 1$  is relevant only to the existence of equilibrium  $h = h^*$ , and further, in this case, the following unique non-trivial equilibrium  $h = h^* > 0$  always exists:

$$h^* = \left[ \lambda \left\{ \theta(1 - \rho) + (1 - \theta)(1 - \rho)^{1-\gamma} \right\} \right]^{1/\gamma}.$$

This equilibrium is asymptotically and globally stable for  $\gamma < 2$ , and unstable for  $\gamma \geq 2$ . When it is unstable, the population size shows an exciting oscillation and positively diverges. Since the stability is determined only by the parameter  $\gamma$  and independent of the harvesting/thinning, this could be regarded as one of specific cases about the density effect function for our model framework.

From (4) and the expression of the non-trivial equilibrium  $h^*$  given above, we can find that the paradoxical increase *never* occurs if  $\gamma < 1$ . In contrast, if  $\gamma > 1$  (and  $\gamma < 2$  for the stable existence of  $h = h^* > 0$ ), then

$$\begin{cases} \frac{\partial h^*}{\partial \rho} \leq 0 \text{ for } \rho \leq \rho_c; \\ \frac{\partial h^*}{\partial \rho} > 0 \text{ for } \rho > \rho_c, \end{cases}$$

where

$$\rho_c = 1 - \left\{ \frac{1 - \theta}{\theta} (\gamma - 1) \right\}^{1/\gamma}.$$

Further from this result, we can easily find that the paradoxical increase *always* occurs if  $\gamma \geq 1/(1 - \theta)$  and  $\theta < 1/2$  whenever the non-trivial equilibrium exists asymptotically stable. When  $1 < \gamma < 1/(1 - \theta)$ , the paradoxical increase occurs if and only if  $\rho > \rho_c$  (see Fig. 4). With the same arguments, we can find that,

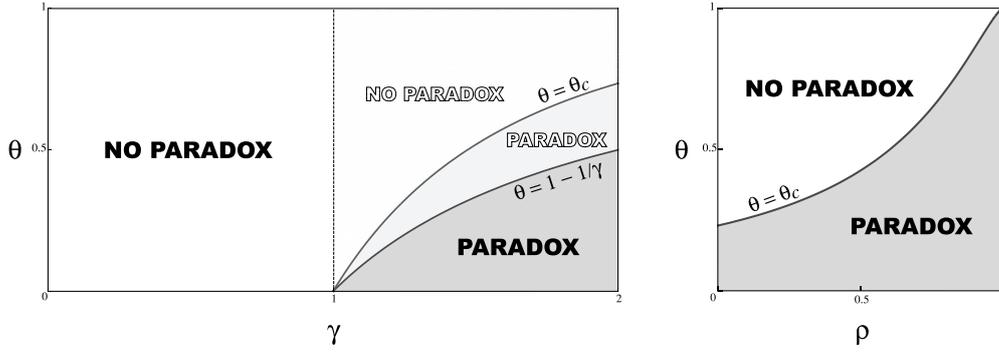


Fig. 4.  $(\gamma, \theta)$ - and  $(\rho, \theta)$ -dependence of the paradox emergence for the model with the power function  $R$  given by (7). Numerically drawn respectively with  $\rho = 0.4$  and  $\gamma = 1.3$ . See the text for the detail.

for given  $\rho$  and  $\gamma > 1$ , the paradox emerges if  $\theta \leq \theta_c$  where

$$\theta_c = \frac{\gamma - 1}{\gamma - 1 + (1 - \rho)\gamma}.$$

Otherwise, it does not emerge (Fig. 4).

We can conclude that, in this case, the stronger density effect (the larger  $\gamma$ ) and the earlier harvesting/thinning (the smaller  $\theta$ ) make the paradoxical increase more likely to occur, whenever the non-trivial equilibrium exists asymptotically stable.

*Piecewise linear function: logistic map case*

At first, let us consider the following piecewise linear function  $R$ :

$$R(h) = \begin{cases} 1 - \frac{h}{h_e} & \text{for } 0 \leq h < h_e; \\ 0 & \text{for } h \geq h_e, \end{cases} \quad (8)$$

where  $h_e$  is a positive constant beyond which every individual cannot succeed in its reproduction. This case corresponds the scramble competition [22]. This function does not satisfy all our assumptions for the function  $R$  because it is not differentiable at  $h = h_e$ . Now we focus the value of  $h$  only in the range  $[0, h_e)$  where every assumption is satisfied, because any positive  $h^*$  is necessarily in  $[0, h_e)$ . As long as considered (8) only in  $[0, h_e)$ , the population dynamics (1) with (8) satisfies all our assumptions.

The population dynamics (1) with (8) essentially corresponds to what is now called a logistic map, which is one of the most famous discrete population dynamics models. It has been providing a variety of discussions about its applicability for the real population dynamics, because it has a nature of period-doubling bifurcation toward chaos [27,33–35] (see Fig. 5).

Cooke and Nusse [36] and Cook *et al.* [37] mathematically considered the qualitative nature of the dynamics described by the similar discrete model concerning the harvesting/thinning effect (only in the case of  $\theta = 0$  of our model (1)), in which the harvesting/thinning was introduced by a constant subtraction of population:  $h_t - H$  ( $H$  is an appropriate positive constant) instead of  $(1 - \rho)h_t$  in our model (1). However, no discussion about our present subject of the paradox emergence has been done.

From (2) with (8), we can explicitly obtain the non-trivial equilibrium population size:

$$h^* = \frac{1 - 1/\{\lambda(1 - \rho)\}}{\theta + (1 - \theta)(1 - \rho)} \cdot h_e. \quad (9)$$

This equilibrium exists if and only if

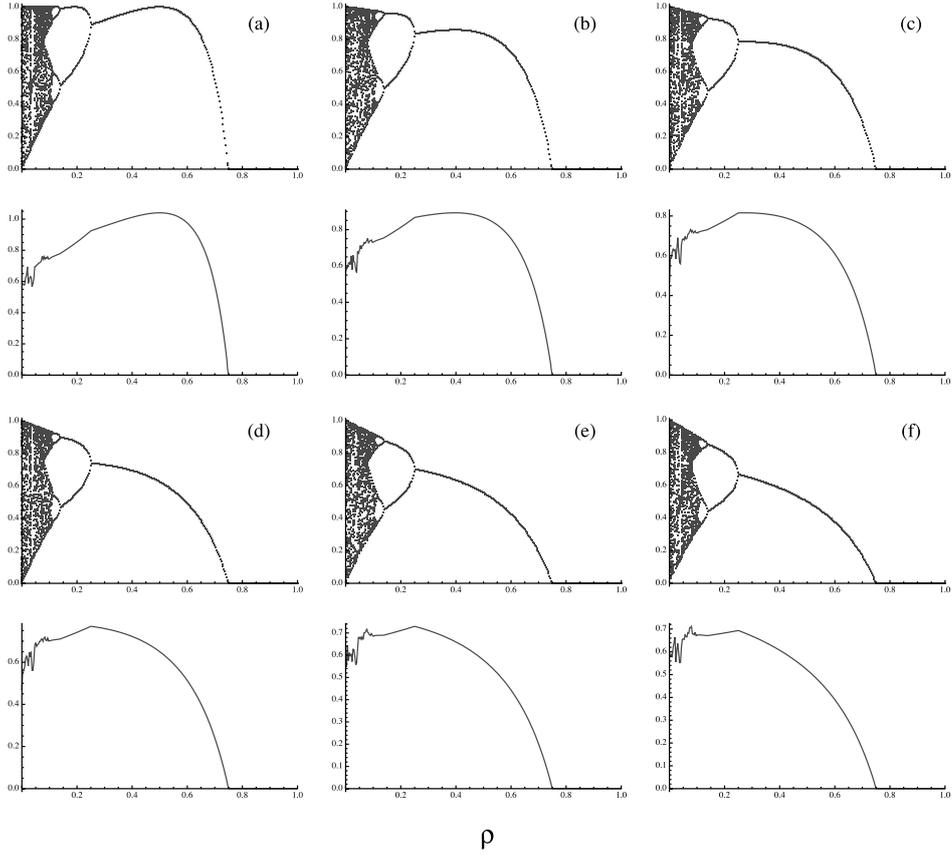


Fig. 5. Bifurcation diagrams and the time-averaged values in terms of  $\rho$  for the logistic map case with the piecewise linear  $R$  given by (8). Numerically drawn. (a)  $\theta = 0.0$ ; (b)  $\theta = 0.2$ ; (c)  $\theta = 0.4$ ; (d)  $\theta = 0.6$ ; (e)  $\theta = 0.8$ ; (f)  $\theta = 1.0$ . Commonly  $h_e = 1.0$  and  $\lambda = 4.0$ . In each case, the upper is the bifurcation diagram and the lower the time-averaged value.

$$1 < \lambda(1 - \rho) < \frac{1}{(1 - \theta)\rho}.$$

The condition for the asymptotical stability is given by

$$\lambda(1 - \rho) < 3,$$

while the condition for the paradox emergence is now obtained as

$$\lambda(1 - \rho) > 2 + \frac{\theta}{(1 - \theta)(1 - \rho)}.$$

From these conditions, we find that the paradoxical increase occurs at the equilibrium state if and only if the following condition is satisfied:

$$2 + \frac{\theta}{(1-\theta)(1-\rho)} < \lambda(1-\rho) < \min\left\{3, \frac{1}{(1-\theta)\rho}\right\}. \quad (10)$$

From this condition, we remark that the paradox emerges only if

$$\rho < \min\left\{\frac{1}{2}, \frac{1-2\theta}{1-\theta}\right\}. \quad (11)$$

Simultaneously we have the other necessary condition that  $\theta < 1/2$ .

It is clear that the paradoxical increase *never* occurs for  $\theta$  sufficiently near 1. In the case of  $\theta = 0$ , it occurs when  $2 < \lambda(1-\rho) < \min\{3, 1/\rho\}$  and  $\rho < 1/2$ . In Fig. 5, we show numerical examples of the paradoxical increase of population size by harvesting/thinning. It is interesting that the time-averaged population size through a sufficiently large number of generations is increased by harvesting/thinning even when the population size has a periodic or chaotic variation as its limiting behaviour.

These results are illustrated by Fig. 6 numerically drawn with  $h_e = 1.0$  and  $\lambda = 4.0$ . We find that, when the paradoxical increase occurs at the equilibrium, there is such a specific value of  $\rho$  that the harvesting/thinning enlarges the equilibrium population size by the largest amount.

Moreover, roughly speaking from the numerical calculations, as long as the population size has a chaotic or periodic variation, the time-averaged population size tends to become larger as the harvesting/thinning gets stronger (the larger  $\rho$ ). See Figs. 5 and 6. Therefore, if the population size has a chaotic or periodic variation, the relatively weak harvesting/thinning could not reduce the time-averaged size but eventually increase it.

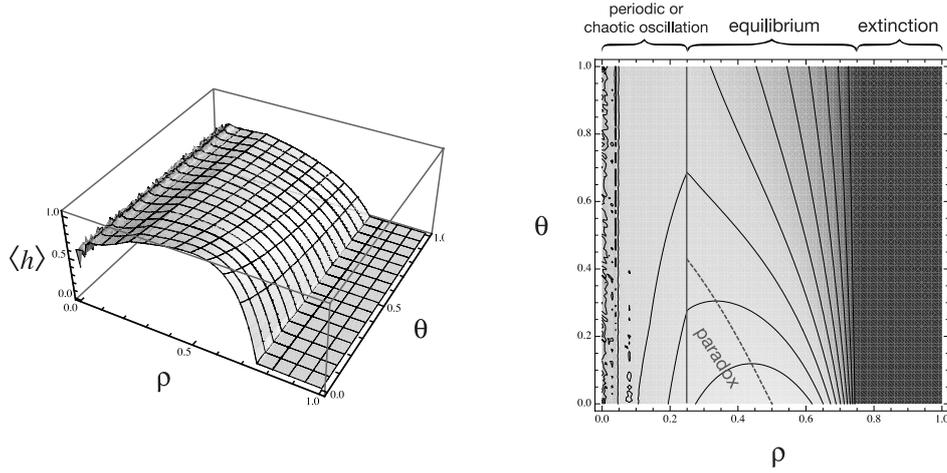


Fig. 6.  $(\rho, \theta)$ -dependence of the time-averaged population size  $\langle h \rangle$  in the sufficiently later generations for the logistic map case with the piecewise linear  $R$  given by (8). Numerically drawn with  $h_e = 1.0$  and  $\lambda = 4.0$ . In the density plot, the lighter region indicates the larger time-averaged population size  $\langle h \rangle$ . Some isograms are numerically drawn by thin curves, too. In the region under the dotted curve, the paradoxical increase of the equilibrium population size in terms of  $\rho$  occurs.

Consequently, a sufficiently strong harvesting/thinning is required in order to reduce the population size to the level lower than that before the harvesting/thinning is applied. Otherwise, the population size could paradoxically increase by the harvesting/thinning.

#### 4 Conclusion

As shown in our analysis for some concrete models, according to the system in which the paradox could emerge, we have a critical harvesting/thinning ratio  $\rho$  that enlarges the equilibrium population size by the largest amount. With the harvesting/thinning with  $\rho$  greater than it, the equilibrium population size could be lowered, and with  $\rho$  greater than another greater critical value, the population goes extinct as intuitively expected. This result demonstrates such

a possibility of the harvesting/thinning operation that it could contribute to enhance the population persistence if designed well in its strength and timing.

In our model, the paradox is more likely to emerge by the harvesting/thinning in the earlier period of the specific season during which the reproductive success in the adulthood is significantly determined because of the importance of the net energy gain for the maturation of fecundity. This means that the earlier reduction of the population density could work to sufficiently moderate the density effect on the competition for the energy gain, and subsequently to increase the per capita net energy gain at the end of the specific season. The increased per capita net energy gain is reflected to the overcompensated total reproduction in the population which eventually leads to the overcompensated population size in the next generation. On the other hand, the harvesting/thinning in the later period of the specific season never causes the paradox. Too later harvesting/thinning could work to moderate the density effect little and could be reflected to a weak enhancement in the total reproduction, so that the population reduction by harvesting/thinning the adult population leads to the smaller population size in the next generation. Therefore, the harvesting/thinning aimed to the targeted population has to be planned for the earlier stage of life history (e.g., egg or seed), while that aimed to depress the targeted population has to be done for the later stage (e.g., juvenile, pupa, or adult).

Moreover, in order of the paradox emergence, the density dependence has to be sufficiently sensitive to the increase in the population density. As implied by the result for the model with the power density effect function (7), the sensitivity would be required to be stronger than the inverse of population density ( $\gamma > 1$  for (7)). As a consequence, the scramble competition would

be likely to cause the paradoxical increase in the equilibrium (or the time-averaged) population size by a harvesting/thinning.

Consequently, only for the targeted species which has a sufficiently sensitive density dependence, the paradox could be caused by the harvesting/thinning operated in the earlier stage of life history and with an appropriately intermediate strength. Our result suggests that a large family of density effect functions, that is, a large family of reproduction curves could cause the paradoxical increase in the equilibrium (or the time-averaged) population size by a harvesting/thinning.

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