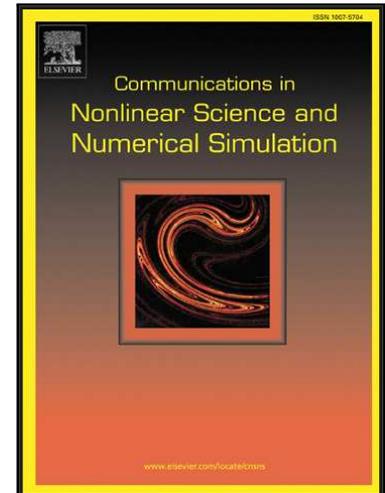


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## Highlights

- We developed a discrete pest growth model with evolution of pesticide resistance.
- Two threshold conditions for extinction of pest population have been provided.
- The optimal pesticide switching times and related key factors have been discussed.
- The effects of dynamic complexity of pest population on its control were studied.

ACCEPTED MANUSCRIPT

# Beverton-Holt discrete pest management models with pulsed chemical control and evolution of pesticide resistance

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**Abstract:** Pest resistance to pesticides is usually managed by switching between different types of pesticides. The optimal switching time, which depends on the dynamics of the pest population and on the evolution of the pesticide resistance, is critical. Here we address how the dynamic complexity of the pest population, the development of resistance and the spraying frequency of pulsed chemical control affect optimal switching strategies given different control aims. To do this, we developed novel discrete pest population growth models with both impulsive chemical control and the evolution of pesticide resistance. Strong and weak threshold conditions which guarantee the extinction of the pest population, based on the threshold values of the analytical formula for the optimal switching time, were derived. Further, we addressed switching strategies in the light of chosen economic injury levels. Moreover, the effects of the complex dynamical behaviour of the pest population on the pesticide switching times were also studied. The pesticide application period, the evolution of pesticide resistance and the dynamic complexity of the pest population may result in complex outbreak patterns, with consequent effects on the pesticide switching strategies.

**Keywords:** Discrete model; Pest resistance; Pesticide switching; Pesticide application period; Threshold condition; Dynamic complexity

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## 1 Introduction

Agricultural pests are usually controlled with pesticides, a preferred method because of its efficiency. However, because of the long-term use of pesticides more than 500 species of targeted pests have developed resistance to them since 1945 [1, 2, 3]. Consequently, farmers' crop losses to pests are increasing, even though more pesticides are being used. For example, in the USA, farmers lost 7% of their crops to pest damage in the 1940s, but the percentage lost had increased to 13% by the 1980s [4].

Therefore, how to reduce or delay pest resistance to pesticides and how to use pesticides reasonably are important questions. Based on the frequency and dosage of pesticide spraying and the genetics of pest resistance, many proposals have been suggested to deal with the problem including rotation or switching between different kinds of pesticides [5], adopting an integrated pest management (IPM) strategy [6, 7, 8, 9, 10] and using other control techniques without pesticides such as leaving untreated refuges where susceptible pests can survive [5].

The forecasting of a pests population density, which can be estimated by mathematical modelling of growth trends, is an important step in the design of a pest control strategy. For example, if the density of a pest population with overlapping generations is very large, it can be treated as continuous growth. Therefore, many pest population growth trends and studies of pest control strategies have been modelled using continuous mathematical models [11, 12, 13, 14, 15, 16, 17].

Recently, we also modelled pest resistance with a continuous mathematical model and studied the optimal time for switching pesticides under three different switching strategies [18]. Moreover, we introduced the development of pesticide resistance into pest-natural enemy interaction models in which the optimal numbers of natural enemies to be released were studied in relation to the development of pest resistance [19, 20].

In the real world, the growth of most pest populations is not continuous, especially for those with non-overlapping generations, so they cannot be assumed to have continuous growth. Thus, for such pest populations and for the genetics of pest resistance, discrete mathematical models are more realistic.

Given the above, questions that arise are (1) how to model the evolution of pest resistance to a pesticide when the pest population growth is discontinuous? (2) How best to switch pesticides when aiming to eradicate a pest population? And(3)in which pest generation will pesticide switching be optimal?

To address the above questions, we developed novel discrete pest population models with impulsive chemical control and the evolution of pest resistance to pesticides. The main purpose was to address how the dynamic complexity of a pest population, develop-

37 ment of pesticide resistance and pulsed chemical control and its spraying frequency affect  
 38 optimal switching strategies, given different control aims. We have derived strong and  
 39 weak threshold conditions which guarantee the extinction of the pest population, as well  
 40 as an analytical formula for the optimal switching time. Further, we addressed switching  
 41 strategies for a given economic injury level (EIL). Moreover, the effects of the complex  
 42 dynamical behaviour of the pest population on the pesticide switching times were stud-  
 43 ied. In particular, the effects of the complex dynamics of the pest population and the  
 44 pesticide application period on the pesticides' switching frequency are discussed in more  
 45 detail. The main results indicated that the pesticide application period, the evolution  
 46 of pesticide resistance and the dynamic complexity of the pest population may result in  
 47 complex outbreak patterns, and consequently can significantly affect pesticide switching  
 48 strategies.

## 49 **2 Model formulation**

50 In this section, we introduce a simple discrete pest population model with a Beverton-  
 51 Holt growth function, in which the evolution of pest resistance is considered. In particular,  
 52 the effects of both the frequency of pesticide applications and their cumulative number on  
 53 the evolution of pest resistance are investigated.

### 54 **2.1 Simple pest growth model with pesticide resistance**

Throughout this study, the pest population is assumed to follow the classic Beverton-  
 Holt model [21, 22, 23, 24, 25, 26], i.e. we have

$$P_{t+1} = \frac{aP_t}{1 + bP_t},$$

55 where  $P_t$  denotes the pest population size at generation  $t$ ,  $a$  is the intrinsic growth rate,  
 56  $b = (a - 1)/K$ , and  $K$  is the carrying capacity. The dynamical behaviour of the above  
 57 model is completely determined by the parameter  $a$ , i.e.  $a \leq 1$  means that the pest  
 58 population will die out eventually, and  $a > 1$  indicates that all solutions of the model  
 59 with positive initial conditions will tend to its unique positive equilibrium  $K$  globally.  
 60 As mentioned in the introduction, the main purpose of this study is to address how the  
 61 evolution of pesticide resistance affects the success or failure of pest control when chemical  
 62 control is applied. Thus, we assume  $a > 1$  throughout this paper.

63 In the following, we divide the total pest population at generation  $t$  into two parts.  
 64 Susceptible pests, very sensitive to the pesticide, are denoted by  $P_t^S$ , accounting for a  
 65 proportion  $\omega_t$  of the total pest population, and resistant pests, denoted by  $P_t^R$ , accounting

66 for  $1 - \omega_t$  of the total pest population. This indicates that  $P_t^S = \omega_t P_t$  and  $P_t^R = (1 -$   
 67  $\omega_t)P_t$ . Thus,  $\omega_t$  may be thought of as the effectiveness of the pesticide at generation  $t$ .  
 68 With increasing pest generations, the pest's resistance to the pesticide develops, and the  
 69 effectiveness of the pesticide decreases, indicating that  $\omega_t$  is a decreasing function of  $t$ .  
 70 Therefore, the evolution of pest resistance can be described by the variable  $\omega_t$ . Further,  
 71 we assume that the death rates due to pesticide applications of the susceptible pests and  
 72 the resistant pests are  $d_1$  ( $0 < d_1 < 1$ ) and  $d_2$  ( $0 \leq d_2 < 1$ ), respectively. Based on these  
 73 assumptions, we have the following discrete pest growth model with pesticide resistance

$$\begin{cases} P_{t+1}^S &= \frac{(1-d_1)\omega_t a P_t}{1+bP_t}, \\ P_{t+1}^R &= \frac{(1-d_2)(1-\omega_t) a P_t}{1+bP_t}. \end{cases} \quad (1)$$

74 Since  $P_{t+1} = P_{t+1}^S + P_{t+1}^R$ , the evolution of the total pest population is given by

$$P_{t+1} = \frac{[(1-d_1)\omega_t + (1-d_2)(1-\omega_t)] a P_t}{1+bP_t}. \quad (2)$$

75 It follows from  $\omega_t = P_t^S / P_t$  that the evolution of the pest's resistance can be modelled as  
 76 follows:

$$\begin{aligned} \omega_{t+1} &= \frac{P_{t+1}^S}{P_{t+1}} \\ &= \frac{(1-d_1)\omega_t}{(1-d_1)\omega_t + (1-d_2)(1-\omega_t)}. \end{aligned} \quad (3)$$

77 Therefore, model (1) can be written as

$$\begin{cases} P_{t+1} &= \frac{[(1-d_1)\omega_t + (1-d_2)(1-\omega_t)] a P_t}{1+bP_t}, \\ \omega_{t+1} &= \frac{(1-d_1)\omega_t}{(1-d_1)\omega_t + (1-d_2)(1-\omega_t)}. \end{cases} \quad (4)$$

78 It follows from  $0 < d_1 < 1$  and  $0 \leq d_2 < 1$  that  $0 < \omega_t < 1$  ( $t = 1, 2, \dots$ ) holds true  
 79 provided that  $0 < \omega_0 < 1$ .

80 In reality, farmers usually spray pesticide within a quite short period, and the effect  
 81 of the pesticide on the pest is instantaneous, so its population density can be reduced  
 82 instantaneously once the pesticide is applied. To depict this realistic control measure, we  
 83 employ an impulsive difference equation based on model (4). Thus, we assume that the  
 84 pesticides are applied periodically at every  $q$ th generation, then the number of pests killed  
 85 at the  $qk$ th generation is  $(\omega_{qk}d_1 + (1 - \omega_{qk})d_2)P_{qk}$ ,  $k = 1, 2, \dots$ . Therefore, we have the  
 86 following impulsive difference equation

$$\begin{cases} P_{t+1} = \frac{aP_t}{1+bP_t}, \quad t = 0, 1, 2, \dots, \\ P_{qk+} = (1 - \omega_{qk}d_1 - (1 - \omega_{qk})d_2)P_{qk}, \quad k = 1, 2, \dots, \\ \omega_{t+1} = \frac{(1-d_1)\omega_t}{(1-d_1)\omega_t + (1-d_2)(1-\omega_t)}, \end{cases} \quad (5)$$

87 where  $P_{qk+}$  represents the number of pests after a single pesticide application at generation  
 88  $qk$ , and the initial value  $P_{0+} = P_0 > 0$ . That is to say the initial density of the pest  
 89 population in model (5) is chosen as the density of pests after the first pesticide spraying.

90 However, for simplicity, we assume that the resistant pests have near-complete resis-  
 91 tance to the pesticide, which means that  $d_2 \approx 0$  [27], so system (5) becomes

$$\begin{cases} P_{t+1} = \frac{aP_t}{1+bP_t}, & t = 0, 1, 2, \dots, \\ P_{qk+} = (1 - \omega_{qk}d_1)P_{qk}, & k = 1, 2, \dots, \\ \omega_{t+1} = \frac{(1-d_1)\omega_t}{1-d_1\omega_t}. \end{cases} \quad (6)$$

92 Model (6) indicates that, obviously, the killing efficacy of the pesticide decreases as the  
 93 resistance develops.

## 94 2.2 The effect of the frequency of pesticide applications on the evolution 95 of pest resistance

96 The third equation of model (6) describes how the proportion of susceptible pests in  
 97 the population develops with increasing pest generations, and thus the evolution of pest  
 98 resistance with increasing time, so we call it the evolution of pest resistance equation. In  
 99 reality, the frequency of pesticide applications, the pesticide application period and the  
 100 dosage of the applications are also factors contributing to the pest resistance. Therefore, in  
 101 order to understand the system in more detail, all of these factors should also be involved  
 102 in this equation. Although achieving this was challenging, we employed the following  
 103 simple method to tackle the task.

104 By using the general Beverton-Holt equation we extend the third equation of model (6)  
 105 as follows:

$$\omega_{t+1} = \frac{(1-d_1)\omega_t}{1-d_1\omega_t^{r_k}}, \quad qk \leq t < (k+1)q, \quad (7)$$

106 here at each  $qk$ th ( $k = 1, 2, \dots$ ) generation one pulse of pesticide is applied, and the  
 107 dynamic parameter  $r_k$ , which depends on the total number of pesticide applications, was  
 108 introduced to represent the effects of their period and dosage on the evolution of pest  
 109 resistance. So  $r_k$  should be a function of the interval of  $q$  generations between the  $k$ th and  
 110  $(k+1)$ th pesticide applications, the number of pesticide applications  $k$  and the dosage  $D_k$   
 111 of the  $k$ th pesticide application for all  $k = 1, 2, \dots$ . We know that the values of  $d_1$  and  
 112  $d_2$  strictly depend on the pesticide dosage  $D_k$ . For simplicity, we assume that the same  
 113 dosage of pesticide is applied at each control event, and so, without loss of generality,  
 114 we let  $D_k = 1$  and  $d_1, d_2$  represent the death rates of the pest after one unit of sprayed  
 115 pesticide. Thus the simplest formula for  $r_k$  could be defined as  $r_k = \frac{k+1}{q}$ , i.e.  $r_0 = 1/q$   
 116 for  $t = 1, 2, \dots, q-1$ ;  $r_1 = 2/q$  for  $t = q, q+1, \dots, 2q-1$ ;  $\dots$ ;  $r_k = (k+1)/q$  for  
 117  $t = kq, kq+1, \dots, (k+1)q-1$ . In order to show how the spraying period and the number  
 118 of pesticide applications or frequency of pesticide applications affect the development of

119 resistance, the evolution of  $\omega_t$  with four different  $r_k$  are shown in Fig.1, from which we can  
 120 see that the smaller spraying period, the faster the evolution of pest resistance. This is  
 121 because the smaller the spraying period the greater the number of pesticide applications,  
 122 and thus faster decreases of the pest's sensitivity to the pesticide and accelerated evolution  
 123 of pest resistance.

124 By induction, we can get the recursion formula for  $\omega_t$  of equation (7) as follows:

$$\omega_t = \frac{A^t \omega_0}{M_t}, \quad t = 1, 2, \dots, \quad (8)$$

125 where  $A = 1 - d_1$ ,  $M_t = M_{t-1} (1 - A^{(t-1)r_k} Q_k M_{t-1}^{-r_k})$ ,  $Q_k = d_1 \omega_0^{r_k}$  for  $t = kq, kq +$   
 126  $1, \dots, (k+1)q - 1$ , and  $M_0 = 1$ .

127 In particular, if  $r_k = 1$ , i.e. the evolution of  $\omega_t$  satisfies the third equation of model (4),  
 128 then

$$\omega_t = \frac{A^t \omega_0}{1 - (1 - A^t) \omega_0}, \quad t \geq 0. \quad (9)$$

### 129 3 Pest extinction resulting from control and the optimal 130 time to switch pesticides

131 One of the main purposes of this paper is to investigate how to spray pesticides and  
 132 manage the evolution of pest resistance such that the pest population will be eradicated  
 133 eventually or be maintained at a density below a given value (i.e. EIL). In order to address  
 134 this topic, we introduce two methods, and for each method we investigate the threshold  
 135 condition which guarantees the extinction of the pest population and discuss the optimal  
 136 pest generation when pesticides should be switched.

#### 137 3.1 Switching pesticides with a strong threshold condition

138 *Strong threshold condition for pest extinction:* Considering the effects of pest control on  
 139 the evolution of pest resistance, model (6) becomes the following periodic control model:

$$\begin{cases} P_{t+1} = \frac{aP_t}{1+bP_t}, \quad t = 0, 1, 2, \dots, \\ P_{qk+} = (1 - \omega_{qk} d_1) P_{qk}, \quad k = 1, 2, \dots, \\ \omega_{t+1} = \frac{(1-d_1)\omega_t}{1-d_1\omega_t^{r_k}}. \end{cases} \quad (10)$$

140 where  $q$  is the period of pesticide applications and  $r_k = (k+1)/q$ ,  $P_{0+} = P_0$ .

141 Note that the pest resistance equation in model (10) (i.e. the third equation) is inde-  
 142 pendent of the pest population growth equation (i.e. the first equation), thus  $\omega_t$  can be  
 143 studied independently using the formula for it given by (8).

144 Solving the first equation of model (10) in pulse interval  $kq < t \leq (k+1)q$ ,  $k =$   
 145  $0, 1, 2, \dots$ , yields

$$P_t = \frac{a^{t-qk} P_{qk+}}{1 + b \left( \sum_{i=0}^{t-qk-1} a^i \right) P_{qk+}}, \quad (11)$$

146 which means that

$$\begin{aligned} P_{(k+1)q} &= \frac{a^q P_{kq+}}{1 + b P_{kq+} \left( \sum_{i=0}^{q-1} a^i \right)} \\ &= \frac{(1 - \omega_{kq} d_1) a^q P_{kq}}{1 + b(1 - \omega_{kq} d_1) P_{kq} \left( \sum_{i=0}^{q-1} a^i \right)}. \end{aligned} \quad (12)$$

147 Denote  $Y_k = P_{qk}$ , then we have the following difference equation

$$Y_{k+1} = \frac{(1 - \omega_{kq} d_1) a^q Y_k}{1 + b(1 - \omega_{kq} d_1) \left( \sum_{i=0}^{q-1} a^i \right) Y_k}, \quad (13)$$

148 which is a non-autonomous Beverton-Holt difference equation, and  $Y_k$  depends on  $\omega_{kq}$  or  
 149 the third equation of model (10). For recent studies of non-autonomous Beverton-Holt  
 150 difference equations with or without impulsive effects see [24, 25, 26, 28].

151 In this study, the stability of the zero solution of equation (13) is our main interest,  
 152 given the practical problem of eradicating the pest population. It follows from equation  
 153 (13) that the inequality

$$Y_{k+1} < (1 - \omega_{kq} d_1) a^q Y_k$$

154 holds true for all  $k = 1, 2, \dots$ . Thus, we can define the dynamic threshold value  $R_0(n, T)$   
 155 as follows:

$$R_0(k, q) \doteq (1 - \omega_{kq} d_1) a^q \quad (14)$$

156 where  $\omega_{kq}$  can be calculated by (8). Therefore, if  $R_0(k, q) < 1$  for all  $k = 1, 2, \dots$  (called a  
 157 strong threshold condition for pest eradication), then the zero solution of equation (13) is  
 158 globally asymptotically stable. This indicates that the pest population will be eradicated  
 159 if the threshold value  $R_0(k, q) < 1$  for all  $k = 1, 2, \dots$ . The key factors including the  
 160 evolution of pesticide resistance (i.e.  $\omega_{kq}$ ), the instantaneous killing rate (i.e.  $d_1$ ), the  
 161 intrinsic growth rate (i.e.  $a$ ) and the period of pesticide application (i.e.  $q$ ) are all involved  
 162 in the formula for the threshold value, which is very dynamic. We will address the effect  
 163 of the period of pesticide applications on the threshold value  $R_0(k, q)$  in more detail later.

164 In particular, if  $r_k = 1$  for  $k = 1, 2, \dots$  (i.e.  $\omega(t)$  satisfies equation (4)), then

$$R_0(k, q) = \left( 1 - \frac{d_1 A^{kq} \omega_0}{1 - (1 - A^{kq}) \omega_0} \right) a^q \doteq R_0^1(k, q). \quad (15)$$

165 Fig.2 describes the effects of the spraying time  $k$  and the spraying period  $q$  on the  
 166 threshold value  $R_0(k, q)$ , from which we can see that  $R_0(k, q)$  is an increasing function  
 167 with respect to  $k$ , and that it will reach and exceed 1 after several pesticide applications.  
 168 These results confirm that the pesticide is effective at the initial stage. However, with the  
 169 development of pesticide resistance, there will be an outbreak of the pest population after  
 170 a certain number of pesticide sprays. Fig.2 also indicates that  $R_0(k, q)$  is an increasing  
 171 function with respect to period  $q$ , and the longer the spraying period, the fewer the number  
 172 of times that the pesticide applications remain efficient due to the evolution of the pesticide  
 173 resistance.

174 In Fig.3 we have plotted the solutions of model (10) for different  $q$  values to show how  
 175 fast the solutions reach or exceed the given EIL and to show the effects of the pesticide  
 176 application period on the density of the pest population. From Fig.3 we can see that  
 177 the density of the pest population is decreasing at the first few pesticide applications,  
 178 but it increases, even reaching or exceeding the EIL quickly, as the number of pesticide  
 179 applications increase. This is because of the strengthening of the pest's resistance to the  
 180 pesticide and the decreasing efficacy of the pesticide.

181 Fig.3 also shows that the longer the period of pesticide applications  $q$  (i.e. low frequency  
 182 of pesticide applications), the higher the probability that there will be a pest outbreak.  
 183 However, the smaller the period of pesticide applications  $q$  (i.e. higher frequency of pes-  
 184 ticide applications), the faster the development of pest resistance, and the easier it is for  
 185 the pest to reach outbreak levels. Therefore, the question is how to control pest resistance  
 186 (i.e. what is the optimal generation of the pest after the start of control operations when  
 187 a switch to a new type of pesticide is best) such that the pest population will die out or its  
 188 density will fall below the *EIL*? We will address this question in the following subsection.

189 *Justifications and the optimal time to switch pesticides:* As mentioned in the introduc-  
 190 tion, pest control will fail if the pest has developed resistance to some pesticides and  
 191 people repeatedly use those pesticides. If so, the density of the pest population will grow  
 192 quickly (as shown in Fig.3), and even result in pest outbreaks or resurgence. Therefore, in  
 193 order to control pests successfully, people usually switch from using one type of pesticide  
 194 to spraying another type of pesticide to avoid or decrease the development of resistance.  
 195 Thus, in order to optimally use the same type of pesticides, it is important to choose the  
 196 optimal switching time with the aim of controlling the pest population economically and  
 197 effectively. In the following, we will provide a method based on our model (10) to de-  
 198 termine the optimal time for switching pesticides according to a threshold condition. We  
 199 assumed that for each new type of pesticide, the evolution of pest resistance to it follows  
 200 the same trend (i.e.  $\omega$  follows the same equation) and has the same initial condition  $\omega_0$ .

From Fig.2, we can see that  $R_0(k, q)$  is increasing with respect to  $k$  and it will exceed 1 after several pesticide applications. According to the definition of  $R_0(k, q)$ , if the aim of pest control is to eradicate the pest population, the threshold value  $R_0(k, q)$  should be below one for all  $k = 1, 2, \dots$ , i.e. the strong threshold condition should be satisfied. To maintain the threshold value  $R_0(k, q)$  below one, we must switch to using another kind of pesticide before the threshold value  $R_0(k, q)$  reaches one. Therefore, the optimal pesticide switching tactics should be implemented at the last spraying time before  $R_0(k, q)$  reaches one. Without loss of generality, we assume that the threshold value  $R_0(k, q)$  will increase and exceed one unit after  $k_1^{(1)}$  sprays of the same kind of pesticide, i.e.

$$k_1^{(1)} = \max\{k : R_0(k, q) \leq 1\}, \quad (16)$$

thus the optimal switching time is  $k_1^{(1)}q$ .

In order to determine  $k_1^{(1)}$  analytically, we let  $R_0(k, q) = 1$ , then

$$\omega_{kq} = \frac{1 - a^{-q}}{d_1},$$

where  $\omega_{kq}$  is given by (8) and  $(1 - a^{-q})/d_1 \leq \omega_0$ . Therefore,

$$k_1^{(1)} = \left\lceil \left\{ k : \omega_{kq} = \frac{1 - a^{-q}}{d_1} \right\} \right\rceil,$$

and  $\lceil x \rceil$  is defined as the greatest integer no larger than  $x$ .

In particular,  $R_0(k, q) = R_0^1(k, q)$  for  $r_k = 1$ . In this special case, letting  $R_0^1(k, q) = 1$  and solving this equation with respect to  $k$ , we can obtain the optimal switching time  $k_1^{(1)}q$ , where

$$k_1^{(1)} = \left\lceil \frac{1}{q} \log_A \left( \frac{(1 - a^{-q})(1 - \omega_0)}{\omega_0(d_1 - (1 - a^{-q}))} \right) \right\rceil.$$

Thus, according to the above pesticide switching strategy, the pest population will be eradicated completely after several pesticide switches. In order to understand this strategy intuitively, we plotted some numerical simulations in Fig.4 (a), from which we can see that the pest population will be eliminated eventually, with  $k_1^{(1)} = 2$ . This indicates that farmers should switch to another type of pesticide after three pesticide sprays of one type of pesticide (here we assume that the first pesticide spraying is at time  $t = 0$ ) to eliminate the pest population quickly.

### 3.2 Switching pesticides with a weak threshold condition

Note that if the strong threshold condition for pest eradication is satisfied, then we have

$$P_q > P_{2q} > P_{3q} > \cdots > P_{nq} > \cdots,$$

226 and  $P_{nq} \rightarrow 0$  when  $n$  is large enough. This switching method could result in more severe  
 227 environmental pollution due to the speed of switching between pesticides. Therefore, the  
 228 question is how to reduce the switching frequency such that the pest population can still  
 229 be eradicated or maintained at a density below the given EIL? To realize this purpose, we  
 230 propose the following weak threshold condition for pest extinction.

231 *Weak threshold condition for pest extinction:* We assume that after  $n_i$  times of spraying  
 232 with the  $i$ th pesticide, farmers should switch to using the  $(i + 1)$ th pesticide, that is the  
 233  $i$ th pesticide can be used  $n_i$  times at most. For example, the first type of pesticide is  
 234 sprayed at the beginning, at pest generation  $q$ , generation  $2q$ ,  $\cdots$ , generation  $(n_1 - 1)q$ ,  
 235 and the second type of pesticide is applied at generation  $n_1q$ , generation  $(n_1 + 1)q$ ,  
 236  $\cdots$ , generation  $(n_1 + n_2 - 1)q$ ,  $\cdots$ . Thus, all pesticides are switched at generation  $n_1q$ ,  
 237 generation  $(n_1 + n_2)q$ , generation  $(n_1 + n_2 + n_3)q$ , and so on.

Denoting

$$P_{kq}^{(m)} = P_{(\sum_{i=1}^m n_i + k)q}, \quad k = 0, 1, \cdots, n_i,$$

238 which is the density of the pest population at the  $k + 1$ th pesticide spray and after  $m + 1$   
 239 pesticide switches. Specifically,  $P_0^{(m)} = P_{(\sum_{i=1}^m n_i)q}$ .

240 From (12), we have

$$\begin{aligned} P_q^{(m)} &= \frac{a^q P_{0^+}^{(m)}}{1 + b \left( \sum_{i=0}^{q-1} a^i \right) P_{0^+}^{(m)}} \\ &= \frac{a^q (1 - d_1 \omega_0^{(m)}) P_0^{(m)}}{1 + b \left( \sum_{i=0}^{q-1} a^i \right) (1 - d_1 \omega_0^{(m)}) P_0^{(m)}}, \end{aligned} \quad (17)$$

thus,

$$P_{q^+}^{(m)} = \frac{a^q (1 - d_1 \omega_0^{(m)}) (1 - d_1 \omega_q^{(m)}) P_0^{(m)}}{1 + b \left( \sum_{i=0}^{q-1} a^i \right) (1 - d_1 \omega_0^{(m)}) P_0^{(m)}},$$

and

$$\begin{aligned} P_{2q}^{(m)} &= \frac{a^q P_{q^+}^{(m)}}{1 + b \left( \sum_{i=0}^{q-1} a^i \right) P_{q^+}^{(m)}} \\ &= \frac{a^{2q} (1 - d_1 \omega_0^{(m)}) (1 - d_1 \omega_q^{(m)}) P_0^{(m)}}{1 + b \left( \sum_{i=0}^{q-1} a^i \right) (1 - d_1 \omega_0^{(m)}) P_0^{(m)} + b \left( \sum_{i=0}^{q-1} a^i \right) a^q (1 - d_1 \omega_0^{(m)}) (1 - d_1 \omega_q^{(m)}) P_0^{(m)}}, \\ P_{2q^+}^{(m)} &= \frac{a^{2q} (1 - d_1 \omega_0^{(m)}) (1 - d_1 \omega_q^{(m)}) (1 - d_1 \omega_{2q}^{(m)}) P_0^{(m)}}{1 + b \left( \sum_{i=0}^{q-1} a^i \right) (1 - d_1 \omega_0^{(m)}) P_0^{(m)} + b \left( \sum_{i=0}^{q-1} a^i \right) a^q (1 - d_1 \omega_0^{(m)}) (1 - d_1 \omega_q^{(m)}) P_0^{(m)}}, \end{aligned}$$

$$\begin{aligned}
P_{3q}^{(m)} &= \frac{a^q P_{2q^+}^{(m)}}{1+b \left( \sum_{i=0}^{q-1} a^i \right) P_{q^+}^{(m)}} \\
&= \frac{a^{3q} \prod_{i=0}^2 (1-d_1 \omega_{iq}^{(m)}) P_0^{(m)}}{1+b \left( \sum_{i=0}^{q-1} a^i \right) P_0^{(m)} \left( \sum_{k=0}^2 \prod_{j=0}^k (1-d_1 \omega_{jq}^{(m)}) a^{iq} \right)},
\end{aligned}$$

241 where  $\omega_{iq}^{(m)}$  is the proportion of susceptible pests in the population at generation  $iq$  with  
242 the  $(m+1)$ th pesticide. By induction, we have

$$P_{n_{m+1}q}^{(m)} = \frac{a^{n_{m+1}q} \prod_{i=0}^{n_{m+1}-1} (1-d_1 \omega_{iq}^{(m)}) P_0^{(m)}}{1+b \left( \sum_{i=0}^{q-1} a^i \right) P_0^{(m)} \left( \sum_{k=0}^{n_{m+1}-1} \prod_{j=0}^k (1-d_1 \omega_{jq}^{(m)}) a^{iq} \right)}. \quad (18)$$

243 Due to  $P_0^{(m+1)} = P_{n_{m+1}q}^{(m)}$ , therefore, we have the following equation

$$P_0^{(m+1)} = \frac{a^{n_{m+1}q} \prod_{i=0}^{n_{m+1}-1} (1-d_1 \omega_{iq}^{(m)}) P_0^{(m)}}{1+b \left( \sum_{i=0}^{q-1} a^i \right) P_0^{(m)} \left( \sum_{k=0}^{n_{m+1}-1} \prod_{j=0}^k (1-d_1 \omega_{jq}^{(m)}) a^{iq} \right)}, \quad (19)$$

244 this is the well-known Beverton-Holt model, which has a zero equilibrium  $P_1^* = 0$ . It is  
245 stable provided that

$$R_0^i \doteq a^{n_i q} \prod_{j=0}^{n_i-1} (1-d_1 \omega_{jq}^{(i-1)}) < 1, \text{ for all } i = 1, 2, \dots. \quad (20)$$

246 Therefore, the pest population will be eradicated if condition (20) holds true. We define  
247 the above condition as the weak threshold condition for pest eradication in this paper.

248 Specially, if the pest has the same resistance to a different pesticide, then  $n_i = n_{i+1} \doteq \tilde{n}$   
249 and  $\omega_{jq}^{(i-1)} = \omega_{jq}^{(i)} = \omega_{jq}$  for all  $i = 1, 2, \dots$ . Thus,

$$R_0^i = a^{\tilde{n}q} \prod_{j=0}^{\tilde{n}-1} (1-d_1 \omega_{jq}) \doteq \tilde{R}_0(\tilde{n}, q, d_1). \quad (21)$$

250 Note that

$$\tilde{R}_0(\tilde{n}, q, d_1) = a^q (1-d_1 \omega_0) \cdot a^q (1-d_1 \omega_q) \cdots a^q (1-d_1 \omega_{(\tilde{n}-1)q}) = \prod_{j=0}^{\tilde{n}-1} W_j, \quad (22)$$

251 where  $W_j = a^q (1-d_1 \omega_{jq})$ , and  $W_j$  is increasing with respect to  $j$ .

252 *Justifications and the optimal time to switch pesticides:* We want to know how many  
253 times each pesticide can be sprayed or what is the optimal time for switching pesticides  
254 which can eradicate the pest population after some pesticide switches. As before, in

255 order to eradicate the pest population we should maintain  $R_0^i < 1$  for all  $n_i$ ,  $i \in \mathcal{N}$ .  
 256 This indicates that farmers should switch pesticides once  $R_0^i$  goes to one. Because of the  
 257 complexity of  $R_0^i$ , we only focus on the special case, i.e.  $\tilde{R}_0$ . We assume that the threshold  
 258 value  $\tilde{R}_0(\tilde{n}, q, d_1)$  will exceed one after  $k_2^{(2)}$  pesticide applications. From (21), we can see  
 259 that  $\tilde{R}_0(\tilde{n}, q, d_1)$  is an increasing function with respect to  $\tilde{n}$ , so

$$k_2^{(2)} = \max\{\tilde{n} : \tilde{R}_0(\tilde{n}, q, d_1) \leq 1\}, \quad (23)$$

260 i.e.

$$k_2^{(2)} = \left\lceil \{\tilde{n} : \tilde{R}_0(\tilde{n}, q, d_1) = 1\} \right\rceil. \quad (24)$$

261 It follows from expressions (14) and (22) that  $R_0(k, q) < 1$  implies  $W_k < 1$ , which  
 262 indicates  $W_i < 1$  for all  $i \leq k$ , and then  $\prod_{j=0}^k W_j < 1$ . Therefore,  $\tilde{R}_0(k, q, d_1) < 1$ , which  
 263 means that the condition  $R_0(k, q) < 1$  is stronger than the condition  $\tilde{R}_0(k, q, d_1) < 1$ .  
 264 These results confirm that  $k_2^{(2)} \geq k_1^{(1)}$ , i.e. the same type of pesticide can be used more  
 265 times under the weak threshold condition for pest eradication than under the strong  
 266 threshold condition.

267 Fig.4 (b) gives numerical simulations with the weak threshold condition for pest eradica-  
 268 tion. From Fig.4 (b) we can see that the pest population dies out eventually with  $k_2^{(2)} = 3$   
 269 in the case of  $\tilde{R}_0(\tilde{n}, q, d_1) < 1$ . However, if  $\tilde{R}_0(\tilde{n}, q, d_1) > 1$ , then the pest population  
 270 will oscillate periodically under the weak threshold condition (see Fig.5 (a)) and finally  
 271 its density could exceed the given EIL.

## 272 4 Pest control with EIL as a guide

273 Considering the importance of reducing pollution and the cost to farmers of pest control  
 274 measures, farmers usually implement them such that the density of the pest population  
 275 cannot exceed the EIL. It follows from Fig.3 that if we only repeat using one kind of  
 276 pesticide to control the pest, then the resistance of the pest to the pesticide is developed  
 277 and the efficiency of the pesticide declines. Thus, the density of the pest population  
 278 increases quickly and eventually exceeds the given EIL. Therefore, in order to control the  
 279 density of the pest below the EIL, farmers usually switch to another type of pesticide  
 280 before the EIL is exceeded. Therefore, we want to know what is the optimal switching  
 281 time or what is the optimal frequency of one type of pesticide applications for a given  
 282 EIL?

283 In this section, we assume that after  $k$  pesticide applications, farmers should switch  
 284 to another type of pesticide. This indicates that  $P_{kq} \leq EIL$  and there exists a positive  
 285 integer  $m$  ( $0 \leq m \leq q$ ) such that  $P_{kq+m} \geq EIL$ .

286 From (12), we have

$$P_{(k+1)q} = \frac{A_k P_{kq}}{1 + B_k P_{kq}} > EIL, \quad (25)$$

287 where  $A_k = a^q(1 - d_1 \omega_{kq})$  and  $B_k = bA_k(\sum_{i=0}^{q-1} a^{i-q})$ . According to (25), we can get

$$(A_k - B_k EIL)P_{kq} > EIL. \quad (26)$$

It follows from  $P_{kq} \leq EIL$  that

$$A_k - B_k EIL = A_k \left( 1 - bEIL \sum_{i=0}^{q-1} a^{i-q} \right) > 1,$$

or

$$A_k > \frac{1}{1 - bEIL \sum_{i=0}^{q-1} a^{i-q}} > 0.$$

288 This indicates that  $q$  should be satisfied

$$b \sum_{i=0}^{q-1} a^{i-q} = b \sum_{i=0}^{q-1} \frac{1}{a^i} < \frac{1}{EIL}. \quad (27)$$

289 From (26), we have

$$P_{kq} A_k \left( 1 - bEIL \sum_{i=0}^{q-1} a^{i-q} \right) > EIL, \quad (28)$$

thus

$$P_{kq} A_k > \frac{EIL}{1 - bEIL \sum_{i=0}^{q-1} a^{i-q}}.$$

290 Since  $P_{kq} A_k$  is an increasing function with respect to  $k$ , we have

$$k = \left\lceil \left\lfloor \left\{ \left[ P_{lq} A_l = \frac{EIL}{1 - bEIL \sum_{i=0}^{q-1} a^{i-q}} \right] \right\} \right\rfloor \right\rceil + 1. \quad (29)$$

291 Fig.5 (b) gives the numerical simulation under this tactic of switching pesticides, from  
 292 which we can see that pest control will tend towards periodic control after a certain  
 293 number of pesticide switches. In reality, pest control can also tend towards periodic  
 294 control under the weak threshold condition provided that the control period  $q$  is long  
 295 enough (i.e.  $\tilde{R}_0(\tilde{n}, q, d_1) > 1$ ) (see Fig.5 (a)). However, under the weak threshold condition  
 296 with  $\tilde{R}_0(\tilde{n}, q, d_1) > 1$ , unless the switching frequency is more than with the EIL guided  
 297 switching strategy, the density of the pest population will exceed the EIL.

## 298 5 The effects of dynamic complexity of the pest population 299 on the control measures

300 In the previous section, we assumed that the pest population followed the classic  
 301 Beverton-Holt difference equation, which means that the pest population either tends to

302 zero or to the unique positive equilibrium if no control tactics are involved. The question  
 303 now is how do the complex dynamics of the pest population affect the pest control? Also,  
 304 of particular interest is how does this complexity affect the pesticide switching frequency  
 305 and the optimal switching time under different switching justifications?

306 To address the above questions, we extended model (6) by employing the general  
 307 Beverton-Holt function to describe the growth of the pest population, i.e. we have

$$\begin{cases} P_{t+1} = \frac{aP_t}{1+bP_t^m}, t = 0, 1, 2, \dots, \\ P_{qk+} = (1 - \omega_{qk}d_1)P_{qk}, k = 1, 2, \dots, \\ \omega_{t+1} = \frac{(1-d_1)\omega_t}{1-d_1\omega_t^k}. \end{cases} \quad (30)$$

308 where  $m$  is a positive integer.

309 Although we can investigate model (30) by employing the same methods as those for  
 310 model (10), it is very difficult to provide the threshold conditions related to the different  
 311 pesticide switching strategies. So we turn to numerical methods aiming to show how the  
 312 dynamic complexity of the pest population affects the pesticide switching strategies and  
 313 then how it affects the pest control. To address those questions, we first apply bifurcation  
 314 analyses, as shown in Fig.6.

315 With  $m$  as a bifurcation parameter, bifurcation diagrams of system (30) without a  
 316 pesticide switching strategy are plotted in Fig.6 (a) and with the switching strategy under  
 317 the weak threshold condition in Fig.6 (b). The results indicate that system (30) may  
 318 exhibit complex dynamical behaviour such as period doubling bifurcations and multiple  
 319 attractors co-existing for a wide range of parameters.

320 In order to analyze the effects of the dynamic complexity of the pest population with  
 321 the weak threshold condition guiding the pesticide switching strategy, we depict the pest  
 322 population growth trends of models (6) and (30) with different control period  $q$  in Fig.7.  
 323 From Fig.7 (a) and (c), we can see that one type of pesticide should be switched to  
 324 another after two sprays in models (6) and (30) with control period  $q = 2$  and the pest  
 325 population can be eradicated after several pesticide switches. Comparing Fig.7 (a) and  
 326 (c) we conclude that the density of the pest population decreases more quickly in model  
 327 (30) than that in model (6). Increasing the period  $q$  from 2 to 3, it follows from Fig.7  
 328 (d) that the pest population oscillates periodically, and the switching frequency is two  
 329 in model (6), and from Fig.7 (b) we can see that the pesticide switching trends become  
 330 more complex, and the density of the pest population oscillates periodically with a related  
 331 large amplitude in model (30) which could more easily exceed the given EIL. Thus, the  
 332 dynamic complexity of the pest population may result in complex outbreak patterns, and  
 333 consequently can significantly affect the pesticide switching strategies.

334 When choosing the EIL as the guide for the pesticide switching strategy, we focused on  
 335 how the parameter  $m$  affects the EIL switching strategy. To address this question, we let  
 336  $m$  vary and fixed all other parameters in model (30), as shown in Fig.8. The main results  
 337 indicate that for different values of parameter  $m$ , the pesticide switching frequencies are  
 338 quite different: the larger the  $m$  value, the more frequent the need for switching, as shown  
 339 in Fig.8 (a-c). In particular, each type of pesticide can be applied for about three periods  
 340 ( $3q$  here), and then switching should occur in the middle of the third pest control period  
 341 for  $m = 1$  (Fig.8(a)). If we increase  $m$  from 1 to 2, then control with each type of pesticide  
 342 can be implemented for about two periods ( $2q$  here), and then the switching should occur  
 343 in the middle of the second control period (Fig.8(b)). Farmers should switch pesticide  
 344 within one period  $q$  once  $m = 3$ , as shown in Fig.8(c). However, if we increase  $m$  to  
 345 4 as in Fig.8(d), then each type of pesticide can be used one more time compared with  
 346 when  $m = 3$ . These results confirm that the dynamic complexity of the pest population  
 347 can result in more complex pesticide switching strategies if the EIL guided method is  
 348 employed.

## 349 6 Discussion

350 Pest control is an important part of agricultural management, for which chemical control  
 351 by spraying pesticides is the main method. However, more and more pests have developed  
 352 resistance to pesticides with the frequent use of only one or two kinds of pesticides for  
 353 lengthy periods. This can lead to pest resurgence and serious losses for farmers so pest  
 354 resistance management is important.

355 Control in pulses such as pesticide sprays or natural enemy releases is a common method  
 356 for pest control in IPM and can be modelled with impulsive equations. For instance, recent  
 357 studies of impulsive equations have been applied in the analysis of pulsed pest control in  
 358 theory, such as the spraying of pesticides at critical times and killing pests instantly  
 359 [11, 12, 13, 14, 15, 29, 30] and for biological control by releasing natural enemies at critical  
 360 times [16, 17, 31, 32, 33, 34, 35, 36, 37]. The existence of high density pest populations with  
 361 overlapping generations was a common assumption in those studies, which mainly focused  
 362 on the effects of chemical control on the extinction or permanence of pest populations  
 363 and the effects of pesticide resistance were seldom considered. However, in this paper, we  
 364 developed a discrete pest population growth model which addressed pesticide resistance.  
 365 Furthermore, the effects of the spraying period and the number of pesticide applications  
 366 or the frequency of pesticide applications on the development of pest resistance, and  
 367 consequently on the success or failure of pest control, were investigated.

368 In order to fight pesticide resistance and avoid pest resurgence, many principles have  
369 been proposed. Switching pesticides between two or more types is a common and effective  
370 tactic to delay or reduce the evolution of pest resistance. For instance, for controlling the  
371 peach potato aphid *Myzus persicae*, farmers have had to switch successively since the late  
372 1940s from organophosphate pesticides to cyclodienes, to carbamates to pyrethroids and,  
373 finally, to neonicotinoids and now there is also resistance to the latter [38]. However, if the  
374 aim of pest control is to eradicate the pest population, what is the optimal justification  
375 for switching from one type of pesticide to another or others? How to determine the  
376 period or the frequency of pesticide application for pesticide switches? And if the aim  
377 of pest control is getting the density of the pest population below an EIL, what is the  
378 optimal time for switching pesticides? Although our results show that modelling can aid  
379 in answering such questions, it is also important for decision-makers to be aware of factors  
380 such as the biochemistry of resistance mechanisms, the extent of cross-resistance to more  
381 than one pesticide type and the likelihood of resistance to novel compounds developing,  
382 as discussed by Bass et al. [38] regarding the management of peach potato aphids. If such  
383 approaches had been used more carefully in the past, resistance by rats to anticoagulant  
384 rodenticides [39] and many other such examples of pests developing resistance to a variety  
385 of products might have been avoided or at least delayed.

386 To answer these questions, we provided two methods including strong and weak thresh-  
387 old conditions, respectively, for pest eradication to judge when we should switch pesticides  
388 if the aim is eradication of the pest population. For the former method, we provided a  
389 strong threshold condition for pest eradication, and the optimal period of pesticide appli-  
390 cation for one type of pesticide. Moreover, we investigated the optimal switching time or  
391 frequency of pesticide applications for pesticide switches. In order to maximise the utiliza-  
392 tion of a pesticide, we provided a weak threshold condition for pest eradication in a second  
393 method and we also investigated the optimal switching time and the frequency of pesticide  
394 applications between pesticide switches and discussed the advantages and disadvantages  
395 of both methods.

396 According to the definition of IPM, the EIL is an important threshold value for pest  
397 control. Therefore, we provided one switching method with the EIL as a switching guide  
398 and the optimal number of sprays for one type of pesticide was investigated. In order to  
399 show how the dynamic complexity of the pest population influences the pest control and  
400 pesticide switching strategies, we extended the model using the generalized Beverton-Holt  
401 function. The main results from this model indicated that the switching frequency can  
402 be significantly affected by the dynamical behaviour of the pest population, as shown in  
403 Figs.7 and Fig.8.

404 IPM is another tactic for fighting pest resistance, which usually controls pest popu-  
405 lations by combining chemical control and biological control. Our future research will  
406 address questions such as how best to design IPM control tactics if the generations of  
407 pest populations do not overlap i.e. how to introduce biological control in discrete pest  
408 population growth models in theory? And what is the balance between the evolution of  
409 pest resistance and the rate of natural enemy releases?

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## 511 Figure Legends

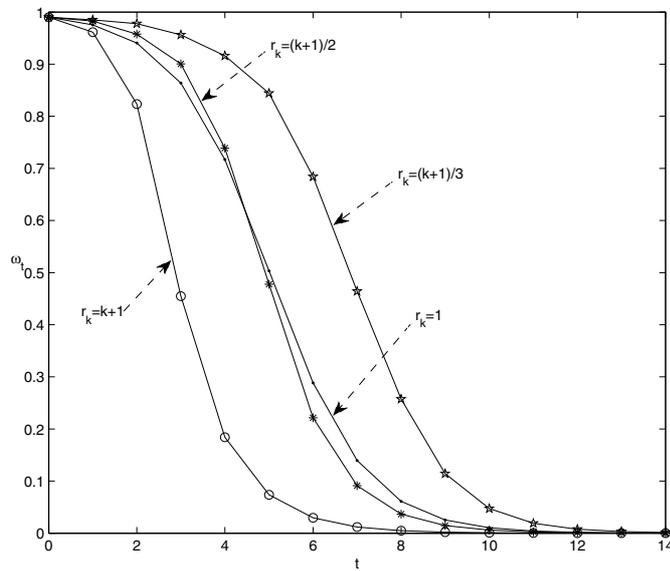


Figure 1: The effects of the frequency of pesticide applications on the evolution of  $\omega_t$  with  $d_1 = 0.6$ . Four curves for  $\omega_t$  are plotted with respect to  $r_k = k + 1, (k + 1)/2, (k + 1)/3$  and constant 1.

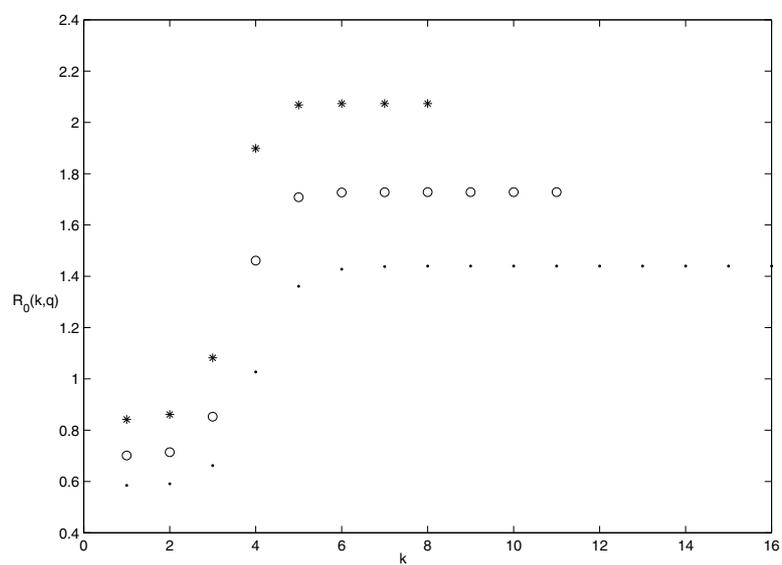


Figure 2: The effects of the period of pesticide applications on the threshold condition  $R_0(k, q)$  for  $q = 2(\bullet)$ ,  $q = 3(\circ)$ ,  $q = 4(*)$ , respectively.

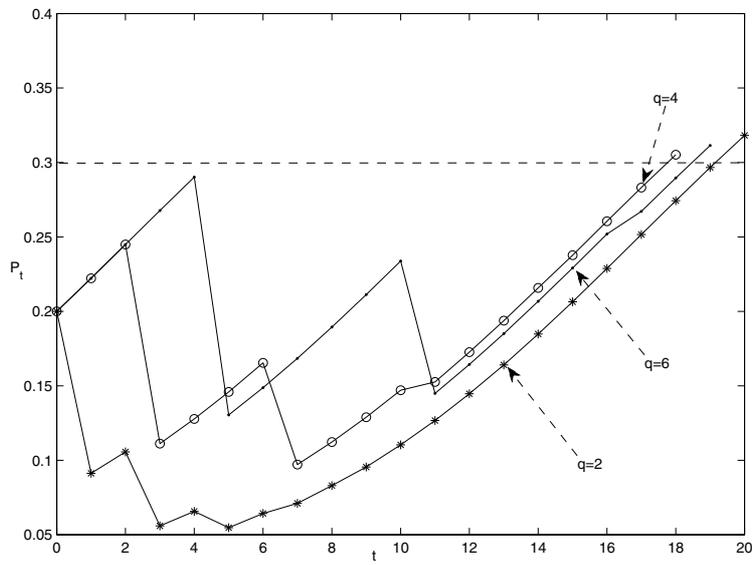


Figure 3: The effects of the period of pesticide applications on the density of the pest population predicted by model (10) for  $q = 2, q = 4, q = 6$ , respectively. The baseline parameter values were fixed as follows:  $d_1 = 0.6, a = 1.2, b = 0.4, \omega_0 = 0.99, EIL = 0.3$  and the initial value of  $P_0^+ = 0.2$ .

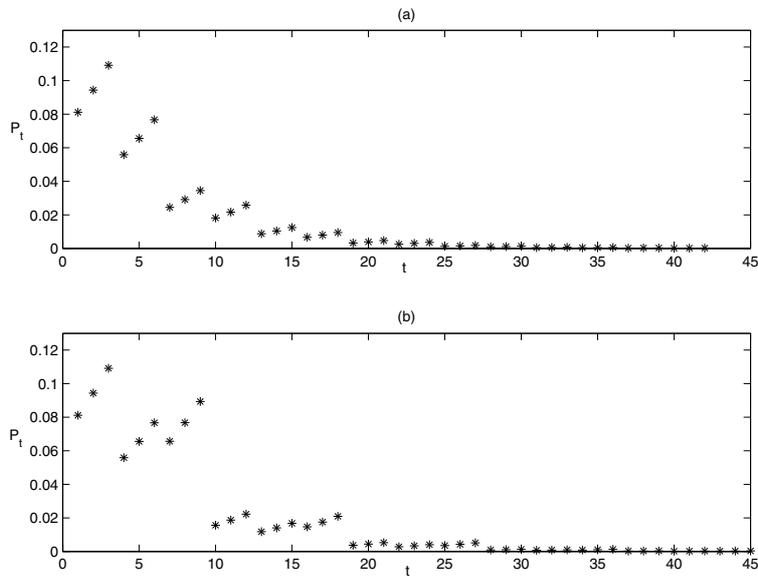


Figure 4: Illustrations of two different switching methods. The baseline parameter values are as follows:  $d_1 = 0.6, a = 1.2, b = 0.4, \omega_0 = 0.99, q = 3, P_0 = 0.2$ . (a) Numerical simulations of model (10) with several pesticide switches determined by the strong threshold condition; (b) Numerical simulations of model (10) with several pesticide switches determined by the weak threshold condition.

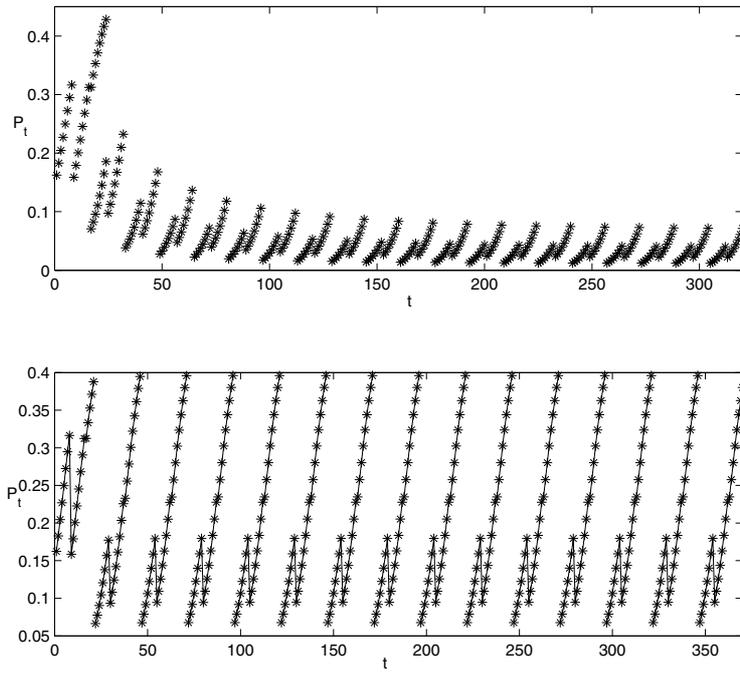


Figure 5: Illustrations of switching methods based on the weak threshold and on using the EIL-guided method. The baseline parameter values are as follows:  $d_1 = 0.6$ ,  $a = 1.2$ ,  $b = 0.4$ ,  $\omega_0 = 0.99$ ,  $q = 8$ ,  $P_0 = 0.2$  and  $EIL = 0.4$ . (a) Numerical simulations of model (10) with several pesticide switches determined by the weak threshold condition; (b) Numerical simulations of model (10) with several pesticide switches determined by the EIL guide.

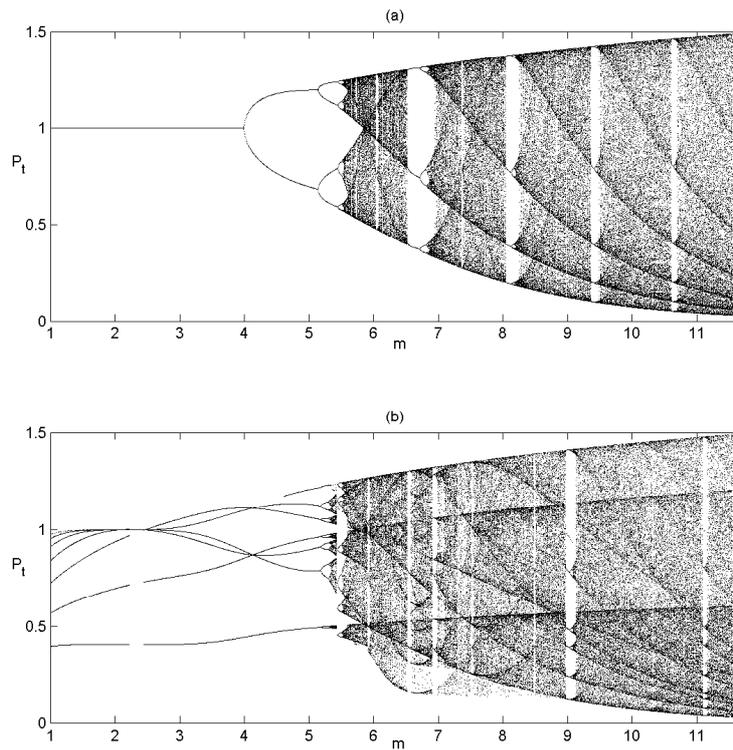


Figure 6: Bifurcation diagram for model (30) with bifurcation parameter  $m$ . The baseline parameter values are as follows:  $d_1 = 0.6, a = 2, b = 1, \omega_0 = 0.99, q = 3$ . (a) Pest control with no pesticide switching strategy; (b) Pest control with the switching strategy determined by the weak threshold condition.

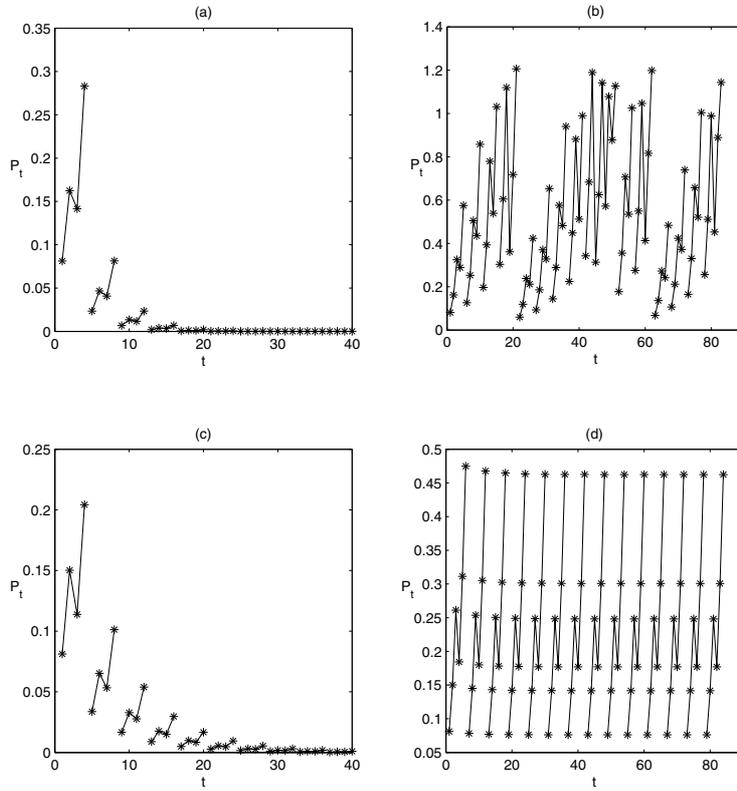


Figure 7: Illustrating the difference between model (30) and model (10) with switching strategies guided by the weak threshold condition. The baseline parameter values are as follows:  $d_1 = 0.6$ ,  $a = 2$ ,  $b = 1$ ,  $m = 5$ ,  $\omega_0 = 0.99$ ,  $P_0 = 0.2$ . (a) Numerical simulations of model (30) with several pesticide switches which are guided by the weak threshold condition and  $q = 2$ ; (b) Numerical simulations of model (30) with several pesticide switches which are guided by the weak threshold condition and  $q = 3$ ; (c) Numerical simulations of model (10) with several pesticide switches which are guided by the weak threshold condition and  $q = 2$ ; (d) Numerical simulations of model (10) with several pesticide switches which are guided by the weak threshold condition and  $q = 3$ .

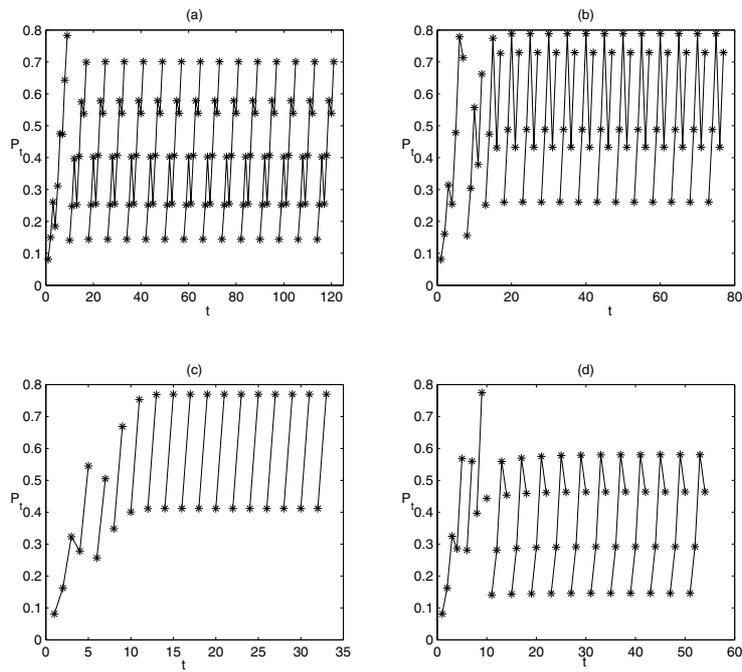


Figure 8: Illustrations of switching methods with the EIL-guided strategy for model (30) with different  $m$ . The baseline parameter values are as follows:  $d_1 = 0.6$ ,  $a = 2$ ,  $b = 1$ ,  $\omega_0 = 0.99$ ,  $q = 3$ ,  $P_0 = 0.2$  and  $EIL = 0.8$ . (a)  $m = 1$ ; (b)  $m = 2$ ; (c)  $m = 3$ ; (d)  $m = 4$ .