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Analytical methods for detecting pesticide switches with evolution of pesticide resistance

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ABSTRACT

After a pest develops resistance to a pesticide, switching between different unrelated pesticides is a common management option, but this raises the following questions: (1) What is the optimal frequency of pesticide use? (2) How do the frequencies of pesticide applications affect the evolution of pesticide resistance? (3) How can the time when the pest population reaches the economic injury level (EIL) be estimated and (4) how can the most efficient frequency of pesticide applications be determined? To address these questions, we have developed a novel pest population growth model incorporating the evolution of pesticide resistance and pulse spraying of pesticides. Moreover, three pesticide switching methods, threshold condition-guided, density-guided and EIL-guided, are modelled, to determine the best choice under different conditions with the overall aim of eradicating the pest or maintaining its population density below the EIL. Furthermore, the pest control outcomes based on those three pesticide switching methods are discussed. Our results suggest that either the density-guided or EIL-guided method is the optimal pesticide switching strategy, depending on the frequency (or period) of pesticide applications.

1. Introduction

Pesticide resistance is the adaptation of a pest population targeted by a pesticide, resulting in decreased susceptibility of the pest to the chemical. Pesticide resistance is increasing and farmers' and other pest managers' dependencies on chemical insecticides have led to a high frequency of insecticide resistance in some crop systems [1]. In the 1940s, farmers in the USA lost 7% of their crops to pests. Since the 1980s, the percentage lost has increased to 13%, even though more pesticides are being used, this is because more than 500 species of pests have developed resistance to pesticides since 1945 [2–4], and the situation is often caused by the same classes of pesticides being used repeatedly for a long time. Other problems ensue such as pest resurgence, acute and chronic health problems, environmental pollution and uneconomic crop production.

Therefore, knowledge of the mechanisms for the evolution of pesticide resistance is important for developing strategies to avoid the creation of resistance in pest populations, with the underlying principle being the preservation of susceptible genes in pest populations. Therefore, in order to fight pesticide resistance and based on a knowledge of the genetics of the development of pesticide resistance, a number of principles have been proposed aimed at delaying the emergence of resistance or avoiding it entirely. These principles include pesticide rotation or switching, avoiding unnecessary pesticide applications, using non-chemical control techniques [5], and leaving untreated refuges where susceptible pests can survive, within the concept of integrated pest management (IPM) [6–10].

When pesticides are the sole or predominant method of pest control, resistance is commonly managed through pesticide rotations or pesticide switches. This means after a pest species develops resistance to a particular pesticide, one method is to use a different pesticide, especially one in a different chemical class or family of pesticides that has a different mode of action against the pest. So far, switching among unrelated insecticides in response to detection of resistance has been the main method used. For instance, during the WHO Onchocerciasis Control Programme (OCP) in West Africa examples of different categories of pesticides were used in rotation after the blackfly vectors of Onchocerciasis developed resistance to the chemical of choice, the organophosphate temephos [11]. Similarly, in agriculture, insecticide rotation has been widely used to combat resistance in a major pest of brassica crops, the Diamondback Moth Plutella xylostella [12].

To achieve pest resistance management using pesticide switches or rotations, the key problems that we are facing are: What is the optimal frequency of pesticide use? How do the

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frequencies of pesticide applications affect the evolution of pesticide resistance and when does the pest population reach the critical threshold value?

In order to address those questions, mathematical models can be useful for determining the optimal frequency of pesticide applications, when is best to switch pesticides and for predicting how fast pesticide resistance develops. To do this, we have developed a novel pest population growth model concerning evolution of pest resistance and pulse spraying of pesticides. The model incorporates three different pesticide switching tactics for eradicating the pest or maintaining its population density below a given critical level.

The first justification for stopping the use of a given pesticide and switching a new type of pesticide (so called as pesticide switching method throughout this paper) is based on the threshold condition (the threshold condition-guided method) which ensures the extinction of the pest population, i.e. the pesticide is switched once the threshold value increases due to evolution of pesticide resistance and exceeds one, which determines the stability of pest eradication solutions.

The second pesticide switching method depends on the density of the pest population just before the pesticide is applied (the density-guided method). This switching action occurs when the efficacy of the pesticide begins to wear off, i.e. there is resurgence.

An important concept in IPM is that of the economic threshold (ET), which is usually defined as the number of pests in the field when control actions must be taken to prevent the economic injury level (EIL) from being reached and exceeded. The EIL is defined as the lowest pest population density that will cause economic damage [6,8–10]. For an IPM strategy, action must be taken once a critical density of pests is observed in the field so that the EIL is not exceeded. Thus, the third switching action is instigated when the pest population reaches the EIL (the EIL-guided method).

We provide analytical formulae for the optimal times to switch between different unrelated pesticides for all of the above three methods. Based on different situations, the optimal choices for each of these three methods, with the intention of eradicating the pests or maintaining their population density below a tolerable level, are discussed. Our results suggest that either the density-guided or the EIL-guided method is the optimal pesticide switching strategy, depending on the frequency (or period) of the pesticide applications.

2. Pest growth model with evolution of pesticide resistance

In this section, we will develop a simple pest population growth model concerning the evolution of pest resistance. In particular, the effects of the frequency of pesticide applications are modelled and investigated. One of our main purposes is to investigate how to implement a chemical control strategy and manage pest resistance such that the pest population dies out eventually or its density is maintained below the EIL. In order to address this topic, we focus on the threshold condition which guarantees the extinction of the pest population and discuss optimal strategies for pesticide switches.

2.1. Simple pest growth model with pesticide resistance

Throughout this study, the pest population is assumed to grow logistically with an intrinsic growth rate r and a carrying capacity parameter η. Then the pest population follows

$$\frac{dP}{dt} = rP(1-\eta P).$$

In the following, the total pest population is divided into two parts: susceptible pests (denoted by P_S) and resistant pests (denoted by P_R), and the proportion of susceptible pests in the population is denoted by a fraction ω, the remaining fraction $1-\omega$ is resistant, so we have $P_S = \omega P$ and $P_R = (1-\omega)P$. Susceptible pests are those that have not developed resistance to the pesticide. That is to say, ω may be thought of as the stock of effectiveness of the pesticide, and it is the proportion of the pest population to which the toxin is lethal. Naturally, the susceptible pests are assumed to die with a higher mortality rate, d_1, and the resistant pests are assumed to die with mortality rate, d_2, when chemical control is implemented. Then the growth of susceptible and resistant pests can be modelled as follows:

$$\begin{cases} \frac{dP_S}{dt} = \omega rP(1-\eta P) - d_1 P_S, \\ \frac{dP_R}{dt} = (1-\omega) rP(1-\eta P) - d_2 P_R. \end{cases} \tag{1}$$

However, for simplification we assume that the resistant pests display near-complete resistance to the pesticide, which means that $d_2 \approx 0$ [13]. Consequently, the evolution of the total pest population follows

$$\frac{dP}{dt} = \frac{dP_S}{dt} + \frac{dP_R}{dt} = rP(1-\eta P) - \omega d_1 P. \tag{2}$$

Since $\omega = P_S/P$, then the evolution of the fraction of the susceptible pests in the total pest population is

$$\frac{d\omega}{dt} = \frac{d}{dt}\left(\frac{P_S}{P}\right) = \left(\frac{dP_S}{dt}P - P_S\frac{dP}{dt}\right)/P^2 = d_1\omega(\omega-1). \tag{3}$$

Note that this resistance evolution equation has been widely used recently in different fields [13–17].

Therefore, the model (1) can be written as

$$\begin{cases} \frac{dP}{dt} = rP(1-\eta P) - \omega d_1 P, \\ \frac{d\omega}{dt} = d_1\omega(\omega-1). \end{cases} \tag{4}$$

In reality, the pesticides are applied instantaneously. Thus the model (4) can be developed by introducing an impulsive spraying of pesticide at a critical time and modelling the consequences of population densities changing very rapidly.

If the pesticides is applied at time point τ_{i-1} for $i \in \mathcal{N}$ with $\tau_0 = 0$, where $\mathcal{N} = \{1,2,3,\ldots\}$ and $0 = \tau_0 < \tau_1 < \tau_2 < \cdots$, then the number of pests killed at time τ_{i-1} is $d_1\omega(\tau_{i-1})P(\tau_{i-1})$. Therefore, we have the following impulsive differential equation

$$\begin{cases} \frac{dP(t)}{dt} = rP(t)(1-\eta P(t)), & t \neq \tau_i, \\ P(\tau_i^+) = (1-\omega(\tau_i)d_1)P(\tau_i), & t = \tau_i, \\ \frac{d\omega(t)}{dt} = d_1\omega(t)(\omega(t)-1), \end{cases} \tag{5}$$

where $P(\tau_0^+) = P_0$ and $\omega(\tau_0) = \omega_0$. This indicates that the initial condition of the pest population in model (5) is chosen as the population density after the first application of pesticide at time τ_0.

It is clear from model (5) that the efficacy of the pesticide on the target pest population depends on the evolution of pest resistance, as the killing efficacy will decrease as pest resistance develops. A detailed analysis of model (5) will be given in the coming sections.

2.2. The effects of frequency of pesticide applications on evolution of resistance

The formula (3) indicates how the pest resistance develops with respect to time. However, it does not involve the effects of the frequency of pesticide applications, the pesticide application period or the dosage of the applications on the evolution of resistance, and those factors do influence resistance patterns. Although it is difficult to involve these factors in the model (3), we note that the speed with which resistance develops depends on several factors including the rate, timing and number of applications made. Based on this fact, we assume that at each time point