

## PREDATOR–PREY MODEL WITH AGE STRUCTURE

J. PROMRAK<sup>1</sup>, G. C. WAKE<sup>2</sup> and C. RATTANAKUL<sup>✉3,4</sup>

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### Abstract

Mealybug is an important pest of cassava plant in Thailand and tropical countries, leading to severe damage of crop yield. One of the most successful controls of mealybug spread is using its natural enemies such as green lacewings, where the development of mathematical models forecasting mealybug population dynamics improves implementation of biological control. In this work, the Sharpe–Lotka–McKendrick equation is extended and combined with an integro-differential equation to study population dynamics of mealybugs (prey) and released green lacewings (predator). Here, an age-dependent formula is employed for mealybug population. The solutions and the stability of the system are considered. The steady age distributions and their bifurcation diagrams are presented. Finally, the threshold of the rate of released green lacewings for mealybug extermination is investigated.

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### 1. Introduction

Mealybug is a serious pest of food crops, fruit trees and many other cultivated plants such as cassava, cotton, mango, grape vine and orchid [9]. It is in the *Pseudococcidae* family. The commonly found species are *Phenacoccus manihoti*, *Ferrisiana virgata* (cockerell), *Phenacoccus madeirensis*, *Phenacoccus solenopsis* and *Phenacoccus jackbeardsleyi*. Mealybug at any stages can cause damage in plants.

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<sup>1</sup>Department of Mathematics, Faculty of Science, Mahidol University, Thailand;  
e-mail: [jpjairaj@gmail.com](mailto:jpjairaj@gmail.com).

<sup>2</sup>Institute of Natural and Mathematical Sciences, Massey University, Auckland, New Zealand;  
e-mail: [g.c.wake@massey.ac.nz](mailto:g.c.wake@massey.ac.nz).

<sup>3</sup>Department of Mathematics, Faculty of Science, Mahidol University, Thailand;

<sup>4</sup>Centre of Excellence in Mathematics, Commission on Higher Education, Thailand;  
e-mail: [chontita.rat@mahidol.ac.th](mailto:chontita.rat@mahidol.ac.th).

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It sucks sap from many parts of the plant, leading to reduction of photosynthesis, distortion of leaf and stem, and death [15]. In the absence of its natural enemies and other control management, this damage can reduce yields by more than 80% [9].

To control the spread of mealybugs, biological control by releasing their natural enemies has proved experimentally to be an effective method; one of the most powerful predators is green lacewing [11, 12]. There are many sources of guidelines to deal with the rate of releasing green lacewings to control the spread of mealybugs. In 1995, Papacek et al. [6] employed green lacewing (*Mallada signata* (Schneider)) to control aphid populations with release rates of 500–1000 lacewing larvae per hectare or 1–5 lacewing larvae per plant. Alternatively, pest management specialists in Australia suggested that a suitable release rate for biological control is about 2000–10 000 green lacewings per hectare [7]. In January 2010, the National Biological Control Research Center (NBCRC)-Central Regional Center suggested releasing 10 million green lacewing eggs to control the spread of mealybugs in the infested areas of Kanchanaburi and Suphanburi provinces in Thailand [32]. To verify the optimal rate of green lacewing release in farm work, an in-depth understanding of mealybug–green lacewing (predator–prey) interactions is necessary.

Traditionally, the population dynamics of two species have been described by Lotka and Volterra [25, 35] as follows:

$$\frac{dx}{dt} = cx - \alpha xy, \quad (1.1)$$

$$\frac{dy}{dt} = \gamma xy - dy, \quad (1.2)$$

where  $x(t)$  and  $y(t)$  denote the populations of the prey and predator species, respectively;  $c$  is the natural growth rate of prey,  $d$  is the natural death rate of predator,  $\alpha$  is the death rate per encounter of prey due to predation, and  $\gamma$  is the efficiency of conversion of eaten prey into predator. Over the past few decades, this model has been improved and applied by many researchers. Because of the difference of two behavioural time scales, Arditi and Ginzburg [4] suggested including a predator abundance term in the trophic function (the per capita rate of consumption), which led to ratio-dependent models. This new form of function is more appropriate for heterogeneous systems, and can solve the problems which may occur in the classical predator–prey model (1.1)–(1.2), including paradoxes of enrichment and biological control [3, 5]. Since the integer-order differential operator is local, the fractional-order differential operator is introduced to obtain non-local properties. The next state of the system is then dependent on the current state and all of the preceding states of the system [21].

A fractional Lotka–Volterra model was proposed by Das et al. [14]. Its solution was obtained through an analytical method called the homotopy perturbation method. The influence of the fractional order on both predator and prey populations was discussed [13]. On the other hand, approximate analytical solutions of the fractional Lotka–Volterra model were derived by using a hybrid approach which is the combination of

the homotopy analysis method, Laplace transforms and homotopy polynomials [21]. To handle spatial and individual behaviours of heterogeneity, Hugo et al. proposed a population-driven, individual-based model where the individual scale was used only for the predation process [33]. Their work demonstrated the link between individual and population scales. Recently, the Lotka–Volterra model with the state-dependent Riccati equation control technique was employed to study biological control of spider mite *Panonychus ulmi*. The results indicated that the approaches are efficient in stabilizing the system at the desired point, which can minimize economic damage [34].

Due to the widely recognized biological fact that age plays an important role in death and fecundity rates of a population, a partial differential equation in which time and age are independent was introduced. Let  $u(a, t)$  be the population density (or age distribution) of individuals of age  $a$  at time  $t$ ,  $a \geq 0, t \geq 0$ . A general age-structured model for the evolution process was proposed by Sharpe et al. [26]:

$$\frac{\partial u(a, t)}{\partial a} + \frac{\partial u(a, t)}{\partial t} = -\mu(a, t)u(a, t), \quad (1.3)$$

where  $\mu(a, t)$  is the mortality rates per capita. Equation (1.3) is also known as the Sharpe–Lotka–McKendrick equation used to describe the dynamics of population density of individuals.

The birth rate process is described by the renewal law

$$u(a, t) = \int_0^\infty \beta(a, t)u(a, t) da, \quad (1.4)$$

where  $\beta(a, t)$  is the renewal rate, and gives the proportion of newborn population at time  $t$  with parents of age  $a$ . The initial age distribution is given by

$$u(a, 0) = u_0(a). \quad (1.5)$$

The derivation and properties of this age-structure model are discussed (see, for example, [2, 16, 27]). Equations (1.3)–(1.5) have been developed in many directions, including partition into two subpopulations [18], spatial effect with diffusive process [8, 17, 22, 23], and age–sex-structured population [31]. Different numerical methods for age-structured population were reviewed and their numerical solutions were also presented [1, 24, 28, 36]. Solutions of common age-structured models (the Leslie matrix, the difference equation, the integral equation) were compared [20]. The approximation of equations (1.3)–(1.5) in various forms of mortality function was discussed [19]. Moreover, age-structured models have been tested with real data. Sharpe and Lotka derived the expression for fixed age distribution (independent of time), and applied this formula to calculate the population of England and Wales in 1871–1880. Their results indicated that the calculated values conform quite closely to the observed data [30]. Chiu [10] proposed some new algorithms for estimating parameter functions in the models by practical data. With these algorithms and a numerical method, the human population can be predicted.

Unlike the previous research which considers predator–prey interaction regardless of age or focuses on the age-structure model of a single population, in this work we study population dynamics of two species with age structure for prey by extending equation (1.3) and considering the equation for prey in the Lotka–Volterra model. We then also introduce a released-predator term in the system as a biological control. Therefore, this model will be useful in the field of pest management.

In Section 2 the predator–prey model with an age-dependent formula for prey is proposed. We initially derive the implicit solutions, one for predator and another for prey. To simplify the model, we analyse the steady age distributions in Section 3. Then the system can be solved explicitly. After the steady distributions are found, we investigate their stabilities and obtain the bifurcation diagrams presented in Section 4. In Section 5 we focus on numerical examples for the mealybug problem controlled by green lacewings. Finally, in Section 6, we summarize the discussion of the results and draw some conclusions.

## 2. The predator–prey model with age-dependent formula for the prey

Let  $P(a, t)$  be the population size density of prey over age  $a$  at time  $t$ , and  $M(t)$  be the predator population size at time  $t$  for  $a, t \geq 0$ . To investigate the population dynamics of prey, we extend the Sharpe–Lotka–McKendrick equation (1.3) by multiplying the mortality rate by the predator population size. Combining this equation with the integro-differential equation for the predator leads to a population model with age structure for prey as follows:

$$\frac{\partial P(a, t)}{\partial a} + \frac{\partial P(a, t)}{\partial t} = -\mu M(t)P(a, t), \tag{2.1}$$

$$\frac{dM(t)}{dt} = \mu \left( \int_0^\infty P(a, t) da \right) M(t) - \delta M(t) + g, \tag{2.2}$$

with initial and boundary conditions

$$P(0^+, t) = \lim_{a \rightarrow 0^+} P(a, t) = b \int_0^\infty P(a, t) da, \tag{2.3}$$

$$P(a, 0) = p_0(a), \tag{2.4}$$

$$M(0) = c, \quad c > 0. \tag{2.5}$$

We also define

$$K(t) = \int_0^\infty P(a, t) da.$$

Variables and their units are given in Table 1, where  $BM$  and  $T$  stand for biomass and time (usually in days), respectively. We have taken  $\beta$  in equation (1.4) as a constant and denoted it by  $b$  as shown in (2.3). Parameters  $\mu$ ,  $\delta$  and  $g$  are also constants for sampling where the rate of released predator  $g$  is used to control the growing population of prey (for more information see [29]).

TABLE 1. Details of variables and parameters used.

Variable	Symbol	Unit
Prey age population density	$P(a, t)$	$BM \cdot T^{-1}$
Predator population	$M(t)$	$BM$
Death rate of prey	$\mu$	$BM^{-1} \cdot T^{-1}$
Death rate of predator	$\delta$	$T^{-1}$
Introduced predator rate	$g$	$BM \cdot T^{-1}$
Total prey (all ages)	$K(t)$	$BM$
Renewal rate of prey	$b$	$T^{-1}$

**2.1. Implicit solution of prey** We solve equation (2.1) using the method of characteristics. Let  $s = t - a$  and  $\tau = t$ . Then equation (2.1) becomes the partial differential equation

$$\frac{\partial P(s, \tau)}{\partial \tau} = -\mu(\tau)P(s, \tau).$$

We solve this equation by integrating by parts and obtain

$$P(s, \tau) = F(s)e^{-\mu \int_0^\tau M(\tau') d\tau'},$$

where  $F$  is an arbitrary function to be found. The solution of the original equation is, therefore,

$$P(a, t) = F(t - a)e^{-\mu \int_0^t M(t') dt'}. \tag{2.6}$$

*Case I:  $t < a$ .* The initial condition at  $t = 0$  gives  $P(a, 0) = F(-a) = p_0(a)$ , so  $F(t - a) = p_0(a - t)$  and

$$P(a, t) = p_0(a - t)e^{-\mu \int_0^t M(t') dt'} \quad \text{for } t < a. \tag{2.7}$$

*Case II:  $t > a$ .* The renewal condition at  $a = 0$ : from equations (2.3) and (2.6),  $P(0, t) = F(t)e^{-\mu \int_0^t M(t') dt'} = b \int_0^\infty P(a, t) da$ . So

$$\begin{aligned} F(t) &= be^\mu \int_0^t M(t') dt' \left( \int_0^t P(a, t) da + \int_t^\infty P(a, t) da \right) \\ &= be^\mu \int_0^t M(t') dt' \left( \int_0^t F(t - a)e^{-\mu \int_0^t M(t') dt'} da + \int_t^\infty p_0(a - t)e^{-\mu \int_0^t M(t') dt'} da \right) \\ &= b \int_0^t F(t - a) da + b \int_t^\infty p_0(a - t) da. \end{aligned} \tag{2.8}$$

Let  $a'' = t - a$  and  $a' = a - t$ . Then equation (2.8) becomes

$$F(t) = b \int_0^t F(a'') da'' + b \int_0^\infty p_0(a') da',$$

which yields

$$F'(t) = bF(t)$$

and so

$$F(t) = Ce^{bt}. \tag{2.9}$$

From equation (2.8),

$$F(0) = C = b \int_0^\infty p_0(a) da.$$

Substituting for  $C$  into (2.9),

$$F(t) = be^{bt} \int_0^\infty p_0(a) da \equiv be^{bt} K_0,$$

where  $K_0 = \int_0^\infty P_0(a) da$ . Thus,

$$P(a, t) = be^{b(t-a)} K_0 e^{-\mu \int_0^t M(t') dt'} \quad \text{for } t > a. \tag{2.10}$$

**2.2. Implicit solution for the predator** Solving equation (2.2) by using the integrating factor  $e^{-\mu \int_0^t K(z) dz + \delta t}$  and the definition of  $K(t)$  in equation (2.3) yields

$$M(t) = g e^{\mu \int_0^t K(z) dz - \delta t} \int_0^t e^{-\mu \int_0^{t'} K(z) dz + \delta t'} dt'. \tag{2.11}$$

Later in Section 4, we find an equation for  $M(t)$ .

### 3. The steady age distribution of the system

Let  $P_s(a)$  and  $M_s$  be the equilibrium solutions of our age-structured population model (2.1)–(2.5) called the steady age distributions which are independent of time. We then obtain the corresponding system

$$\frac{dP_s}{da} = -\mu M_s P_s, \tag{3.1}$$

$$\frac{dM_s}{dt} = \mu K_s M_s - \delta M_s + g = 0, \tag{3.2}$$

with renewal condition

$$P_s(0) = b \int_0^\infty P_s(a) da \equiv bK_s. \tag{3.3}$$

Here we define  $K_s = \int_0^\infty P_s(a) da$ . So either there is no prey (the monoculture solution), or

$$P_s(a) = bK_s e^{-\mu a M_s}. \tag{3.4}$$

From equations (2.2) and (3.2)–(3.4), we obtain

$$M_s = \frac{b}{\mu}, \quad P_s(a) = \frac{b\delta - g\mu}{\mu} e^{-ab}, \quad \text{and} \quad K_s = \frac{b\delta - g\mu}{\mu b}.$$

Thus, the solutions of the system (3.1)–(3.3) are:

- (1)  $(P_s, M_s) = (0, g/\delta)$ ;
- (2)  $(P_s, M_s) = (e^{-ab}(b\delta - g\mu)/\mu, b/\mu)$  which is biologically feasible, provided that  $P_s(a) \geq 0$  if and only if  $g \leq b\delta/\mu \equiv \delta M_s$ .

#### 4. Stability

Recall from equation (2.2) that

$$\frac{dM(t)}{dt} = \mu \left( \int_0^\infty P(a, t) da \right) M(t) - \delta M(t) + g.$$

We substitute  $P(a, t)$  from (2.7) and (2.10) into the formula

$$\begin{aligned} \int_0^\infty P(a, t) da &= \int_0^t P(a, t) da + \int_t^\infty P(a, t) da \\ &= \left( \int_0^t b e^{b(t-a)} K_0 da + \int_t^\infty p_0(a-t) da \right) e^{-\mu \int_0^t M(r') dr'}. \end{aligned}$$

Let  $a' = a - t$ . Then

$$\begin{aligned} \int_0^\infty P(a, t) da &= \left( K_0 e^{bt} (1 - e^{-bt}) + \int_0^\infty p_0(a') da' \right) e^{-\mu \int_0^t M(r') dr'} \\ &= K_0 e^{bt-\mu \int_0^t M(r') dr'} \end{aligned}$$

leads to

$$\frac{dM(t)}{dt} = \mu K_0 e^{bt-\mu \int_0^t M(r') dr'} M(t) - \delta M(t) + g \quad (4.1)$$

with  $M(0) = c$ .

To obtain a local equation, we differentiate (4.1) with respect to  $t$ , which gives

$$\frac{d^2 M}{dt^2} = (\mu K_0 e^{bt-\mu \int_0^t M(r') dr'} - \delta) \frac{dM}{dt} + \mu K_0 M (b - \mu M) e^{bt-\mu \int_0^t M(r') dr'}. \quad (4.2)$$

From equation (4.1),

$$e^{bt-\mu \int_0^t M(r') dr'} = \frac{\delta}{\mu K_0} - \frac{g}{\mu K_0 M}.$$

Then equation (4.2) becomes

$$\frac{d^2 M}{dt^2} = -\frac{g}{M} \frac{dM}{dt} + (b - \mu M)(\delta M - g). \quad (4.3)$$

For stability of the steady age distribution, we let solutions of model (4.3) be

$$M(t) = M_s + m(t),$$

where  $|m(t)| \ll 1$ , that is,  $m(t)$  is a small disturbance from the fixed point. We get

$$\frac{d^2 m}{dt^2} = -\frac{g}{M_s} \frac{dm}{dt} + (b - \mu(M_s + m))(\delta(M_s + m) - g).$$

From the previous section, we have two steady-state age distributions, which are  $(P_s, M_s) = (0, g/\delta)$  and  $(P_s, M_s) = (e^{-ab}(b\delta - g\mu)/\mu, b/\mu)$ .

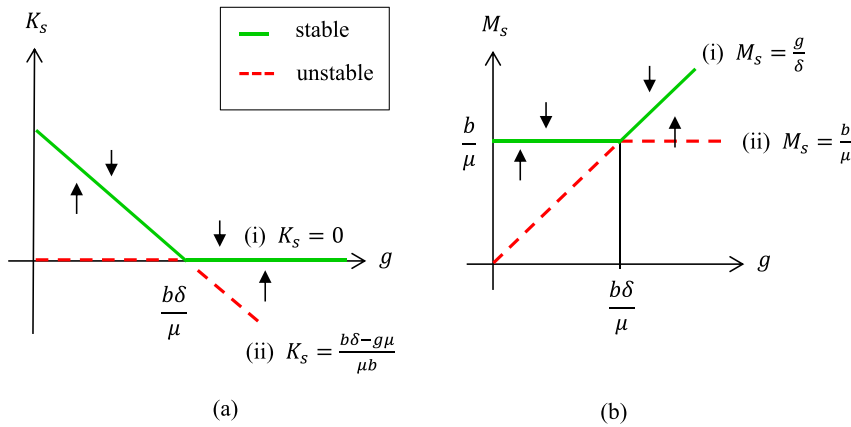


FIGURE 1. Bifurcation diagrams for (a) prey and (b) predator.

For  $M_s = g/\delta$ , we have

$$\frac{d^2m}{dt^2} + \delta \frac{dm}{dt} + (\mu g - \delta b)m + \underbrace{\delta \mu m^2}_{\text{higher-order term}} = 0.$$

We determine the stability of this system using the corresponding eigenvalues. We then obtain that  $(P_s, M_s) = (0, g/\delta)$  is stable when  $g > \delta b/\mu$ , and is unstable elsewhere.

For  $M_s = b/\mu$ ,

$$\frac{d^2m}{dt^2} + \frac{g\mu}{b} \frac{dm}{dt} + (\delta b - \mu g)m + \underbrace{\delta \mu m^2}_{\text{higher-order term}} = 0.$$

Again, the eigenvalue technique is employed, providing the stability condition for  $(P_s, M_s) = (e^{-ab}(b\delta - g\mu)/\mu, b/\mu)$  which is  $g < \delta b/\mu$ . Therefore, the stabilities of this system are found and shown on the bifurcation diagrams in Figure 1.

### 5. Numerical results: application to the control of mealybugs in crops

In this section, specific examples are presented to verify the theoretical results divided into two cases based on the steady state where the threshold is  $g = \delta b/\mu$ . Let  $b = 0.5, \mu = 1.6, \delta = 0.7, g = 1$  ( $g > \delta b/\mu$ ) for the first case, and  $b = 0.5, \mu = 0.2, \delta = 0.7, g = 0.3$  for the second. By breaking the second-order ODE (4.3) into two first-order ODEs, the predator population dynamics is carried out. Each of Figures 2 and 3 shows the behaviour dynamics of the system consisting of two first-order ODEs for a certain set of parameters. The long-term solutions for the first and second cases are  $M_{s1} = g/\delta = 1.429$  and  $M_s = b/\mu = 2.5$ , respectively. Observe that the behaviour of the predator population fluctuates considerably, and it takes more time to reach a stable period when  $g$  is smaller. In other words, the greater the number of predators added, the faster the control of mealybugs is achieved. Moreover, there is no overwhelming population of predators which may cause another problem.



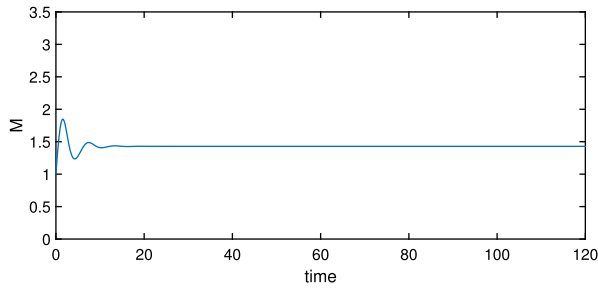


FIGURE 2. Population of predator for  $b = 0.5, \mu = 1.6, \delta = 0.7, g = 1$ .

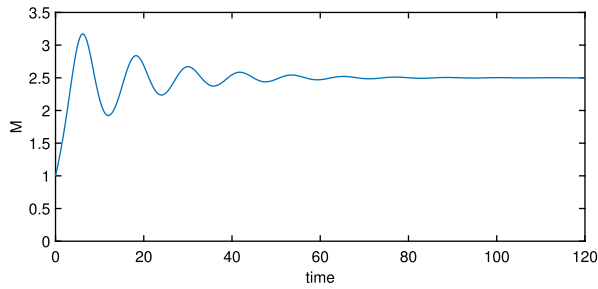


FIGURE 3. Population of predator for  $b = 0.5, \mu = 0.2, \delta = 0.7, g = 0.3$ .

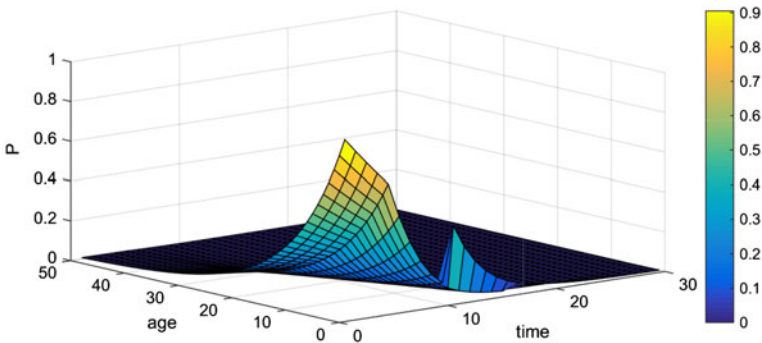


FIGURE 4. Population of prey for  $b = 0.5, \mu = 1.6, \delta = 0.7, g = 1$ .

After obtaining the numerical results for  $M$ , we can simulate the prey density using equations (2.7) and (2.10). Define the initial condition (2.4) as  $P(a, 0) = p_0(a) = Ce^{ka}$  for some positive constants  $C$  and  $k$ . This function represents the population of mealybugs over age  $a$  at the first observation time. We then evaluate the population density of prey for corresponding cases. The results are illustrated in Figures 4 and 5.

In the case where  $g > \delta b/\mu$ ,  $P(a, t)$  tends to zero for large  $t$ , that is, no mealybug survives. Otherwise,  $P(a, t)$  converges to  $e^{-ab}(b\delta - g\mu)/\mu = 1.45e^{-0.5a}$ .

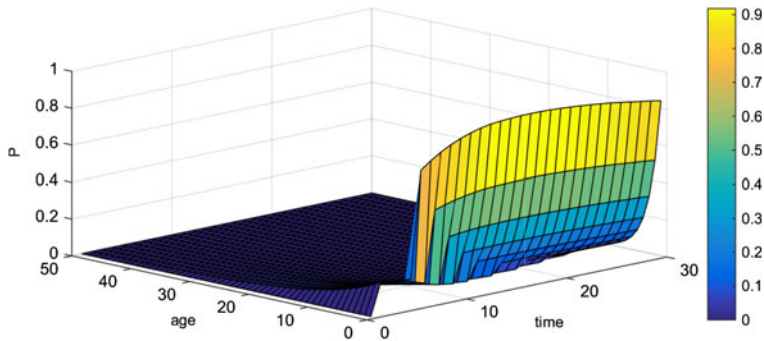


FIGURE 5. Population of prey for  $b = 0.5, \mu = 0.2, \delta = 0.7, g = 0.3$ .

## 6. Discussion and conclusion

We have analysed the predator–prey population model with age-dependent formula for the prey. The implicit solutions for both predator and prey are evaluated as equations (2.3), (2.10) and (2.11). By employing the steady age distribution, two steady states of the system are obtained: one is mono-species and the other is coexisting species. Then, local stability of both steady states is explained. Furthermore, we get the threshold of the introduced predator level leading to mealybug extinction. Numerical results with biological meaning are provided in Section 5, which is very useful for visualizing the mealybug control problem.

Here we have shown that this useful hybrid model, with one age-structured compartment coupled to an unstructured compartment, has exactly one asymptotically globally stable steady state. The solution of the transient model is obtained analytically, albeit implicitly, thus providing a check on computational solutions in more complex situations. This parallels the outcome in systems which are not age or spatially structured. The threshold for extermination of the mealybugs ( $g > \delta b/\mu$ ) will be useful for practical situations. Prevention of recurring outbreaks requires that this predator release rate should ideally be maintained. It is expected that a similar outcome will apply when the parameters are functions of time and/or age.

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