DYNAMICS OF THE SPRUCE BUDWORM POPULATION UNDER THE ACTION OF PREDATION AND INSECTICIDES

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Dynamics of the Spruce Budworm Population Under the Action of Predation and Insecticides

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Abstract

In this paper we study the dynamics of the spruce budworm system under either bird predation pressure, insecticide budworm disease mortality, or both assuming that the biomass remains constant. A model with two equations describing the dynamics between birds and budworms is proposed. It is shown that under certain conditions this two dimensional system has limit cycles, that is, it predicts the existence of periodic budworm population outbreaks. Numerical simulations illustrate the action of insecticides on the budworm population size. The possibility of controlling the budworm population via insecticides is explored.

1 Introduction

The spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), is native to eastern Canada and does not occur elsewhere. There has been knowledge of its behavior since 1770.

We will first give the life cycle of a spruce budworm since we need to know at what stage(s) they will be affected by predators and/or insecticides. The spruce budworm may have either a one- year or two-year life cycle. This cycle is divided into three stages: six instars, pupae, and adults. Moths emerge from mid-July to early August. Females lay eggs over several days.The eggs hatch in approximately 10 days. Soon after hatching, the first instar larva disperse within tree or stand, or even beyond by wind. Surviving larva spin hibernacula within which molt to the second instar. Feeding occurs until next spring. Second-instar larva overwinter in hibernacula until early May. Soon after emergence, they disperse again and settle at feeding sites on host trees. During the third to sixth instars, from about early June to early July, larva feed on the current-year shoots and the sixth-instar larva typically webs two or more shoots together to form a feeding tunnel and feeds on the needles. Fifth-and sixth instar larva can complete their development on old foliage, but this causes a marked reduction in the size of the pupa and the fecundity of the adult. The pupal stage, which varies in length from 8 to 12 days, occurs about mid-July. Pupation may take place in the feeding site of the sixth-instar larva or the larva may move toward the centre of the branch to spin a pupation site. Adult longevity in cages is approximately two weeks and adults may be found in the field from mid-July to early August, depending on the development rate of the immature stages of the population.

The budworm population is affected by parasites, spiders, and bird predation, the last one being the most critical one. Bird predation is greater during the sixth instar larval and during the pupal stage. The spruce budworm generally remains at population densities so low that it could be called a rare species; but periodically, when forest conditions and weather are favorable, it is released from this low endemic level and erupts to cause severe defoliations and tree mortality over large areas. Periodic outbreaks of the spruce budworm appear to be part of the natural cycle of events associated with maturing of extensive areas of balsam fir and with climatic variation. The history of outbreaks in the Province of New Brunswick have been traced for the last two centuries, the average period between outbreaks being approximately 35 years.

Aerial insecticide spraying has been used to control budworm outbreaks since the fifties. Budworm outbreaks happens during the sixth instar larva, the insecticides are applied during this stage, which takes place during mid-July until early-August. These insecticides are applied using aircrafts, therefore this affects the way that the budworms get in contact with these insec-

ticides.

This paper aims to study the dynamics of the spruce budworm system under bird predation and under insecticide. Our paper has two purposes: the first is to demonstrate the existence of periodic budworm population outbreaks as a result of bird predation and the second is to predict the behavior of budworm functional response under the action of insecticide that causes increased budworm mortality.

2 Predator-Prey Model

2.1 The model

The dynamics of the budworm population without the action of predation will be described by the logistic equation

$$\frac{dw}{dt} = rw\left(1 - \frac{w}{K}\right) \tag{1}$$

where w represents the budworm density, r represents the maximum growth rate, and K represents the carrying capacity of the forest. We describe the effect of bird-predation by subtracting from the right-hand side of equation (1) the term

$$\alpha B\left(\frac{w^2}{A^2 + w^2}\right)$$

which represents a Type-III S-shaped functional response. Here the parameter α is the maximum predation rate of an individual bird (on average), B represents the bird density and A is the budworm population when the predation rate is at half of its maximum. Thus we have the following equation for the dynamic of the budworm density under bird-predation

$$\frac{dw}{dt} = rw\left(1 - \frac{w}{K}\right) - \alpha B\left(\frac{w^2}{A^2 + w^2}\right). \tag{2a}$$

Equation (2a) has been studied by Ludwig, Jones and Holling [5], under the assumption of a constant bird density B.

In this paper we assume that some birds may leave the system if the budworm population goes down. Let μ represent the rate at which birds

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leave the system either by migration or death and let c be the predation efficiency, that is the number of new birds for each budworm killed. Thus the equation for bird density is given by

$$\frac{dB}{dt} = -\mu B + c\alpha B\left(\frac{w^2}{A^2 + w^2}\right). \tag{2b}$$

Following [5] we rescale the variables involved. The substitutions $w = \bar{w}A$, $t = \frac{\tau}{c\alpha}$ and $B = cA\bar{B}$, lead to the rescaled system

$$\frac{d\bar{B}}{d\tau} = g(\bar{B}, \bar{w}) = -\bar{\mu}\bar{B} + \frac{\bar{B}\bar{w}^2}{1 + \bar{w}^2}, \tag{3a}$$

$$\frac{d\bar{w}}{d\tau} = f(\bar{B}, \bar{w}) = \bar{r}\bar{w}\left(1 - \frac{\bar{w}}{\bar{K}}\right) - \frac{\bar{B}\bar{w}^2}{1 + \bar{w}^2} \tag{3b}$$

where

$$\bar{r} = \frac{r}{c\alpha},$$

$$\bar{K} = \frac{K}{A},$$

$$\bar{\mu} = \frac{\mu}{c\alpha}.$$

Note that $\bar{w}$ is the proportion of budworms with respect to A, $\bar{B}$ is the ratio between bird density and the product of predation efficiency times A, and τ is the time rescaled by the time that birds take to eat budworms.

In the remainder of the paper we rename the variables $\bar{w}$, $\bar{B}$ and τ and the parameters $\bar{r}$, $\bar{K}$ and $\bar{\mu}$ as w, B, t, r, K and μ, respectively, to simplify the notation of our rescaled system.

2.2 Equilibrium points

System (3) has the following equilibria

$$E_1 = (0,0)$$

$$E_2 = (0,K)$$

$$E_3 = \left(\frac{r}{\sqrt{\mu - \mu^2}}\left(1 - \frac{\mu}{K(\sqrt{\mu - \mu^2})}\right), -\frac{\mu}{\sqrt{\mu - \mu^2}}\right)$$

$$E_4 = \left(\frac{r}{\sqrt{\mu - \mu^2}}\left(1 - \frac{\mu}{K(\sqrt{\mu - \mu^2})}\right), \frac{\mu}{\sqrt{\mu - \mu^2}}\right)$$

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We note that E_1 and E_2 always exist. Since E_3 has negative (or complex) coordinates, it does not have any biological significance, so it is not considered here. As for E_4, this point has biological significance only in the case where $\mu < \frac{K^2}{1+K^2}$, because in the contrary negative or non-real populations are managed. We denote the coordinates of E_4 as (B^*, w^*) where

$$B^* = \left(\frac{r}{\sqrt{\mu - \mu^2}} \left(1 - \frac{\mu}{K(\sqrt{\mu - \mu^2})} \right) \right)$$

and

$$w^* = \frac{\mu}{\sqrt{\mu - \mu^2}}.$$

2.3   Stability Analysis

To analyze the stability of each equilibrium point we linearize system (3) by calculating the Jacobian matrix

$$\begin{pmatrix} \frac{w^2}{1+w^2} - \mu & \frac{2Bw}{(1+w^2)^2} \\ -\frac{w^2}{1+w^2} & r\left(1 - \frac{2w}{K}\right) - \frac{2Bw}{(1+w^2)^2} \end{pmatrix}. \tag{4}$$

Since this is a two dimensional system its stability can be determined by looking at the trace T and determinant Δ of matrix (4) evaluated at each equilibrium point. Each point is stable provided that $\Delta > 0$ and $T < 0$.

2.3.1   Stability of the equilibrium point E_1

Evaluating the Jacobian matrix given in (4) at the equilibrium point $E_1 = (0,0)$ gives

$$\begin{pmatrix} -\mu & 0 \\ 0 & r \end{pmatrix}. \tag{5}$$

Since the determinant of (5) is negative, E_1 is a saddle point.

2.3.2 Stability of the equilibrium point E_2

Evaluating the Jacobian matrix given in (4) at the equilibrium point $E_2 = (0, K)$ gives

$$\begin{pmatrix} \frac{K^2}{1+K^2} - \mu & 0 \\ -\frac{K^2}{1+K^2} & -r \end{pmatrix}.$$

(6)

The matrix given in (6) has trace $T = \frac{K^2}{1+K^2} - \mu - r$ and determinant $\Delta = -\frac{K^2 r}{1+K^2} + r\mu$. Then the stability condition is $\mu > \frac{K^2}{1+K^2}$. Note that if E_2 is stable, then the equilibrium point E_4 does not exist.

2.3.3 Stability of the equilibrium point E_4

This stability is studied only when the conditions for the existence of E_4 hold. Substituting $E_4 = (B^*, w^*)$ in (4) we get

$$\begin{pmatrix} 0 & -\frac{2r(K(\mu-1)+\sqrt{\mu-\mu^2})}{K} \\ -\mu & r\left(2\mu - 1 - \frac{2\mu^2}{K\sqrt{\mu-\mu^2}}\right) \end{pmatrix}.$$

(7)

The matrix in (7) has trace $T = r\left(2\mu - 1 - \frac{2\mu^2}{K\sqrt{\mu-\mu^2}}\right)$ and determinant $\Delta = -\frac{2r\mu(K(\mu-1)+\sqrt{\mu-\mu^2})}{K}$. Since $\mu < \frac{K^2}{1+K^2}$ $\left(\text{i.e. } K > \frac{\mu}{\sqrt{\mu-\mu^2}}\right)$, we have $\Delta > 0$. Clearly $T < 0$ in the case $\mu < \frac{1}{2}$. Then E_4 is stable if

$$\mu < \frac{1}{2}.$$

Now, in the case $\mu > \frac{1}{2}$, we also need the condition

$$K < \frac{2\mu^2}{(2\mu - 1)\sqrt{\mu - \mu^2}}$$

for stability of E_4.

2.4 Periodicity of Solutions

Theorem 2.1. *Any solution to System (3) is bounded.*

Proof. This proof is done in several steps.

Step 1. The solution never leaves the first quadrant because $\frac{dB}{dt} = 0$ when $B \equiv 0$ and $\frac{dw}{dt} = 0$ when $w \equiv 0$. Thus the first quadrant is invariant under the flow.

Step 2. If $w \geq K$, then for every B

$$-\frac{Bw^2}{1+w^2} \leq 0,$$

and since $\frac{w}{K} \geq 1$,

$$rw\left(1 - \frac{w}{K}\right) \leq 0.$$

Therefore $w' = f(B, w) \leq 0$.

Step 3. If $w \leq w^*$, then $\mu \geq \frac{w^2}{1+w^2}$. Consequently

$$-\mu + \frac{w^2}{1+w^2} \leq 0.$$

Therefore $B' = g(B, w) = B(-\mu + \frac{w^2}{1+w^2}) \leq 0$.

Step 4. We write step 4 in the form of a lemma.

Lemma. *Suppose that $(B(t), w(t))$ is a solution of System (3). Further assume that for some t_0 and some $\epsilon > 0$ $B(t_0) = \bar{B}, w(t_0) = \bar{w}$ with $\bar{B} \geq \frac{rK}{4\mu} + \frac{\epsilon}{\mu}$ and $\bar{w} > w^*$. Then there exists $t^* > t_0$ such that $w(t^*) = w^*$.*

Proof of the Lemma. Since $B' = g(B, w^*) = 0$ and $h(w) = \frac{w^2}{1+w^2}$ is increasing, then for $\bar{w} > w^*$ we have that $B' > 0$. Thus we can see that

$$
\begin{aligned}
w' < w' + B' &= r\bar{w}(1 - \frac{\bar{w}}{K}) - \mu\bar{B} \\
&< \frac{rK}{4} - \mu\bar{B} \quad \text{(since max}\left\{r\bar{w}\left(1 - \frac{\bar{w}}{K}\right)\right\} = \frac{rK}{4}\text{)} \\
&< -\epsilon \quad \text{(as } \bar{B} \geq \frac{rK}{4\mu} + \frac{\epsilon}{\mu}\text{)}
\end{aligned}
$$

Then for our case $w'(t \geq t_0) < -\epsilon$ and the graph of $w(t)$ is always below the line
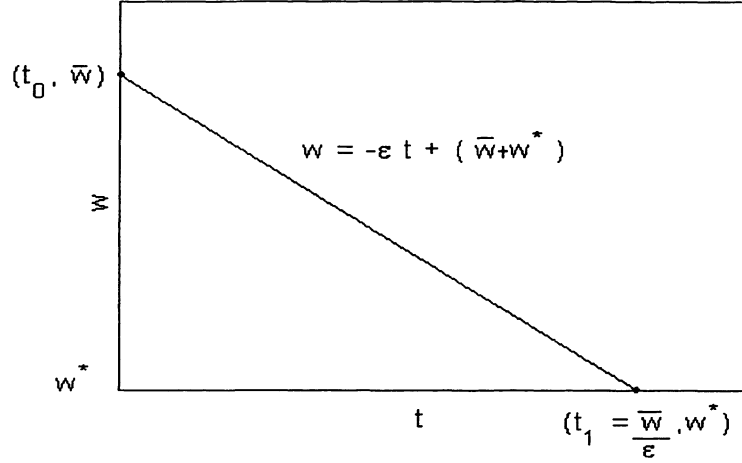
$$w = -\epsilon\, t + (\bar{w} + w^*) \tag{8}$$

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Figure 1: A trajectory that starts at point $\bar{w}$ will always be below the line
$w = -\epsilon\, t + (\bar{w} - w^*)$

which contains the points $(t_0, \bar{w})$, $(t_1 = \frac{\bar{w}}{\epsilon}, w^*)$ and has slope $-\epsilon$ (as shown in Figure 1). Then there exists $t^* < t_1$ such that $w(t^*) = w^*$. □

Step 5. For every solution such that $B(0) > \frac{rK}{4\mu}$ and $w(0) > w^*$, there exists some B_2 such that $B(t) \leq B_2$ for all $t \geq 0$. By the above lemma, there is some t^* such that $w(t^*) = w^*$. Let $B_1 = B(t^*)$. We can apply the lemma once more to conclude that there is an orbit $\Gamma(t)$ joining the point (B_1, K) and the line $w = w^*$, say in the point (B_2, w^*). Since for $w \leq w^*$ $B(t)$ is decreasing, and the orbit $(B(t), w(t))$ cannot cross the orbit $\Gamma(t)$, then $B(t) \leq B_2$ for all $t \geq 0$.

Step 6. The cases $B(0) < \frac{rK}{4\mu}$ or $w(0) < w^*$ lead to the previous cases. Therefore the theorem is proven. □

Corollary. *If $\mu > \frac{1}{2}$ and $K > \frac{2\mu^2}{(2\mu-1)\sqrt{\mu-\mu^2}}$, then System (3) has periodic solutions.*

Proof. Theorem (2.1) shows that all interior solutions are bounded. The analysis in (2.3.3) shows that under the hypotheses of the Corollary, E_4 is a source node. Then by the Poincaré- Bendixson Theorem (see for instance [8]) an interior solution is either a closed periodic orbit or approaches a closed periodic orbit as $t \to \infty$. □

3 Biological Considerations

In this section we study the biological interpretation of the previous results. To explain this, we use the notation of the original System (2). The trivial equilibrium point $(0,0)$ is unstable since without birds budworms present a logistic growth. In fact, $(0,0)$ is a saddle point since without budworms birds have an exponential decay (see Figure 2).
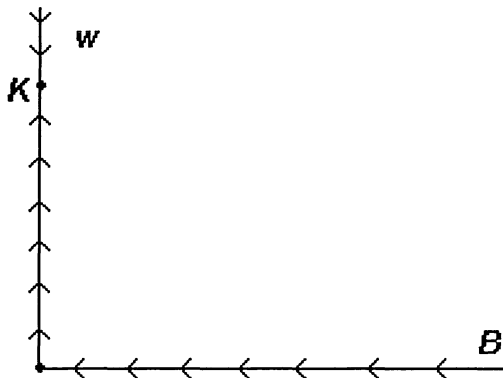

Figure 2: Field lines on the axes. Note that when $w = 0$, the bird population goes to zero, while if $B = 0$, then the budworm population goes to its carrying capacity K.

The equilibrium point $(0, K)$ is stable when $\mu > \frac{c\alpha K^2}{A^2 + K^2}$. This means that the birds are not sufficiently attracted by the budworms to stay, and so all birds leave and the budworm population establishes at its carrying capacity.

The interesting dynamics start when

$$\frac{c\alpha K^2}{A^2 + K^2} > \mu. \tag{9}$$

When (9) is satisfied budworms are attractive to the birds, that is, some birds will stay, hence there exists a nontrivial positive equilibrium (B^*, w^*). We have seen that this point is stable if

$$\frac{\mu}{c\alpha} < \frac{1}{2},$$

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i.e.

$$\mu < \frac{c\alpha}{2}.$$

This means that half the maximum density for predation is enough to attract and keep predators, and so birds stay. In this last case, we can show that $w^* < A$, so we conclude that a density of budworms equal to A is more than enough to sustain a stable number of birds.

In the case $\mu > \frac{c\alpha}{2}$, the following condition is required for the stability of (B^*, w^*):

$$\mu > \frac{c\alpha \left[\left(1 - \frac{c\alpha}{2\mu}\right) K \right]^2}{A^2 + \left[\left(1 - \frac{c\alpha}{2\mu}\right) K \right]^2}. \tag{10}$$

(Recall that we still need the condition $\mu < \frac{c\alpha K^2}{A^2 + K^2}$). That is, the mortality rate is larger than the predation efficacy rate when $w = \left(1 - \frac{c\alpha}{2\mu}\right) K$.

If condition (10) is not satisfied, then the point (B^*, w^*) is unstable, and as we have established in the previous section, the system has periodic solutions. Hence, our model predicts the existence of periodic outbreaks, as they have been observed in ecosystems in North America ([6]).

3.1   Quantitative Solutions

Now we discuss some numerical solutions to System(2). The parameters r, K and A are estimated as in [5]. According to the calculations in [5], $r \approx 1.52$, $K \approx 9,031,200$ and $A \approx 28,238$. Recall α is the maximum budworm predate. According to [4], a bird can eat 6 gr. of food per day. The weight of a budworm is about 0.08 gr., so that each bird eats approximately 75 budworms per day. Hence, a reasonable estimate for α is $\alpha \approx 75 \times 365 \approx 30000$.

Unfortunately, μ and c are unknown parameters. However, they can be chosen so that instability conditions of the point (B^*, w^*) are satisfied. Note that (B^*, w^*) exists and is unstable if

$$\frac{c\alpha}{2} < \mu < \frac{c\alpha \left[\left(1 - \frac{c\alpha}{2\mu}\right) K \right]^2}{A^2 + \left[\left(1 - \frac{c\alpha}{2\mu}\right) K \right]^2}.$$

The above values of r,K,A and α approximated above imply

$$15,047.2 < \frac{\mu}{c} < 29,998.8 \ .$$

Figures 3 and 4 were obtained for the cases $\mu = 0.4$ and $c = 0.00002$. Since μ is the difference between the birds' birth and death rates (as well as migration rates), $\mu = 0.4$ means the birds would decrease to 67% of the population within a year in the absence of budworms. Note that with these values, the budworm population has approximately three outbreaks within 100 years. This agrees well with existing data (see for instance, [6, 7]).
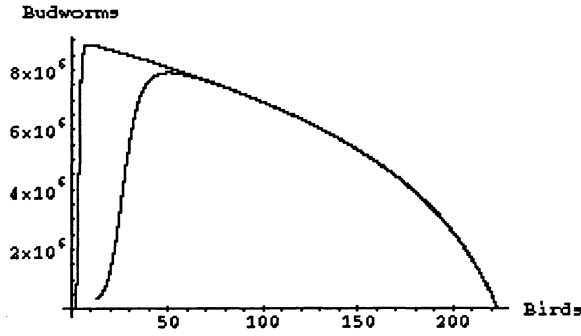
Figure 3: Bird-budworm densities phase-plane. Here, the initial conditions were Birds($t = 0$) = 13, Budworms($t = 0$) = 352,000. Note that the solution to the system stabilizes rapidly to the limit cycle.
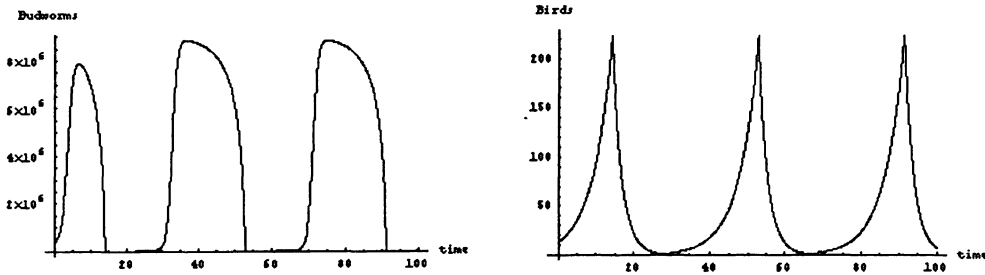

Figure 4: Outbreaks of budworm and bird population densities predicted by the model under study. Note that approximately three outbreaks appear every 100 years.

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4 Insecticide Response on Spruce Budworm Population Densities

4.1 Analysis

Now we introduce a functional response describing the action of insecticide. We propose the following response

$$\frac{\sigma\Omega\left(\frac{w}{\Omega}\right)^{n+1}}{1 + \left(\frac{w}{\Omega}\right)^{n}}$$

The parameter σ models the maximum budworm mortality rate due to the action of the insecticide. The highest mortality rate is only achieved for high values of w, since either insecticide is not sprayed in areas of small budworm density, or insecticide is not efficient when budworm density is smaller than some critical density, say Ω. Hence, budworm deaths due to insecticide are approximately σw, when $w > \Omega$, and proportional to $\left(\frac{w}{\Omega}\right)^{n+1}$ when $w < \Omega$. Thus our modified system of equations is:

$$\frac{dB}{dt} = -\mu B + c\alpha B\left(\frac{w^2}{A^2 + w^2}\right)$$

$$\frac{dw}{dt} = rw\left(1 - \frac{w}{K}\right) - \alpha B\left(\frac{w^2}{A^2 + w^2}\right) - \frac{\sigma\Omega\left(\frac{w}{\Omega}\right)^{n+1}}{1 + \left(\frac{w}{\Omega}\right)^{n}}$$

4.2 Determining the Parameters Values

By varying the parameters σ with respect to r and Ω we found the following three cases:

 CASE 1

Here we want to exterminate all the budworms as soon as they are born, thus we let $\sigma = 1.52$, and $\Omega = 1$. In this case we have that our functional term is linear and it goes to zero. Thus the periodic orbits are broken (See Figure 5).

 CASE 2

In this case we want to fumigate a small percentage of budworms $\approx 20\%$ whenever the maximum budworm growth population exceeds the control of the predators and the maximum scale of budworms density saturation level (which occurs when we let $\sigma = .03$, and $\Omega = 1,000,000$). In this case we are
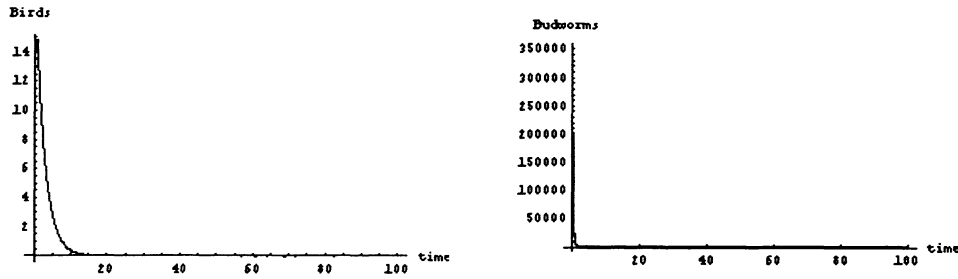
Figure 5: Linear response of budworm-bird population densities predicted by the model with insecticide.

going to have three full-periodic cycles in 100 years for both birds and worms (See Figure 6). Comparing this result with the model without insecticide we can see that the results on both cases are almost the same.
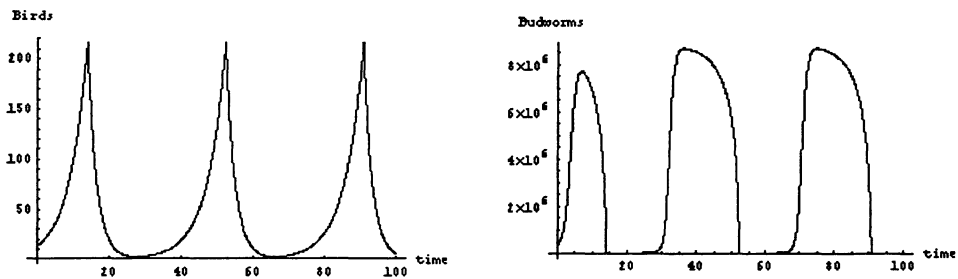

Figure 6: Outbreaks of large budworm-bird population densities predicted by the model with insecticide.

CASE 3

For the last case we want to kill a large percentage of budworms $\approx 90\%$ when the maximum budworm growth population exceeds the control of the predators and the maximum scale of budworms density saturation level (which occurs when we let $\sigma = 1.4$, and $\Omega = 1,000,000$). In this case we are going to have three and a half periodic cycles in 100 years for both birds and worms (See Figure 7).

The analysis shows that budworm survival is related to population density. In summary, we conclude that the use of insecticide has limited impact on the budworm population outbreaks. The use of insecticide does not break the periodic orbits; on the contrary, the generation survival is highest, thus
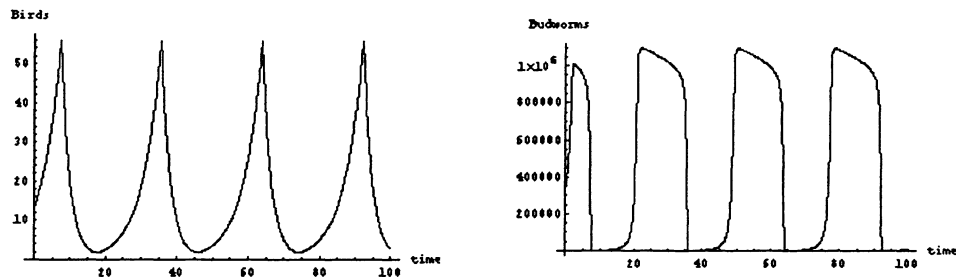
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Figure 7: Outbreaks of large budworm-bird population densities predicted by the model with insecticide.

having more outbreaks than before.

5   Conclusions and Future Work

Insecticide is currently applied only when we have a large budworm density. This could be an important factor for the insecticide's efficiency. One would have to analyze the result of applying insecticide before an outbreak occurs. In our simulations we notice that if we apply insecticide when we have a small budworm population our functional term is linear, thus the periodic orbits can be broken, although the ecological consequences could be disastrous[1]. As we have seen, periodic orbits which simulate the budworm outbreaks could not be easily broken by the use of insecticides. Insecticides are not necessarily an efficient method to control budworm outbreaks.

We obtained periodic solutions when studying the budworm-bird populations as a predator-prey model, and these periodic solutions corresponded to outbreaks. However, our model does not include possible changes in the biomass. We are not certain if the inclusion of the biomass dynamics support the existence of limit cycles (See Ludwig[2] et. al. in [5]).

Our model, while providing reasonable qualitative pictures, does not match the data. The amount of birds in our results is about 30 times the number given in the real data. These differences must be attributed to the absence of space considerations in our model. The results obtained in our

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[1] Recall that both species' equilibrium goes to zero when a linear insecticide response is considered.

[2] The system presented in the cited reference does not have periodic solutions.

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model are as expected. We assume that the bird population depends only on the budworm population and sufficiently large budworm densities lead to large bird densities. We also assume that birds leave the system in the case of null (or very small) budworm densities, which is not necessarily true since distinct bird species do not feed solely on budworms. Furthermore, it is known that migration, birth and mortality rates for birds depend on various factors, including climatological and seasonal characteristics of the environment.

We have not included the life instars of the budworms. Hence, we can not look at the impact of applying insecticides on different life stages of the budworms. However, it is known that existing insecticides do not affect the early life stages of the budworms (eggs or small larva). The lack of effectiveness of insecticides in the early stages of budworm development may be in fact critical for its dynamics and outbreaks. In future research, we would like to produce a model where distinct typical life instars are considered, in order to study the effects of insecticides in these stages, and consequently studying their impact on population outbreaks.

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