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QUALITATIVE ANALYSIS OF INSECT OUTBREAK SYSTEMS: THE SPRUCE BUDWORM AND FOREST

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SUMMARY

(1) A procedure has been described for the qualitative analysis of insect outbreak systems using spruce budworm and balsam fir as an example. This consists of separating the state variables into fast and slow categories.

(2) The dynamics of the fast variables are analysed first, holding the slow variables fixed. Then the dynamics of the slow variables are analysed, with the fast variables held at corresponding equilibrium values. If there are several such equilibria, there are several possibilities for the slow dynamics.

(3) In the case of the budworm, this analysis exhibits the possibility of 'relaxation oscillations' which are familiar from theory of the Van der Pol oscillator. In more modern terminology, the jumps of the system are governed by a cusp catastrophe.

(4) Such an analysis can be made on the basis of qualitative information only, but additional insight emerges when parameter ranges are defined by the kind of information typically available from an experienced biologist.

(5) At the least this can be a guide to assess subsequent priorities for both research and policy.

INTRODUCTION

As in all sciences, ecology has its theoretical and its empirical school. Perhaps because of the complexity and variety of ecological systems, however, both schools seem, at times, to have taken particularly extreme positions. And so the empiricists have viewed the theoretical school as designing misleading constructs and generalities with no relation to reality. The theoreticians, in their turn, have viewed the empirical school as generating mindless or mind-numbing analysis of specifics and minutiae.

This paper aims to apply some of the tools of the theoretician—specifically the qualitative theory of differential equations—to one of the most detailed and exhaustive empirical studies of an ecological system that has ever been attempted—the spruce budworm/forest interaction in eastern North America.

It has two purposes; the first is to demonstrate how far these mathematical tools can be pushed to give insight when information is available for a specific system at three different levels. The first level is purely qualitative and non-numerical. The second includes rough estimates of parameter values that are typically known by the informed biologist if he is asked the appropriate question. The third includes highly detailed quantitative data that, while rarely available, are provided in the extensive monograph of spruce budworm dynamics prepared by Morris (1963).

The development of the analysis described here in fact followed precisely that sequence. The first version of the equations was prepared by one of us (Ludwig) after hearing a 1-h lecture that was totally non-numerical and qualitative. Thereafter he relied on a one-half page summary description of the system (in Holling 1973, p. 14). After an afternoon discussion some modest modifications were made (particularly Step 5, in what follows) to complete the qualitative analysis as far as it could go.

We then moved to the next level of very general and easily obtained quantitative information. Our rule was to confine ourselves to guesses of parameter values that an informed entomologist or forester might reasonably be expected to have prior to the establishment of Morris' spruce budworm project.

The final step was to use the data from that detailed study to see what additional insights were added.

The second purpose emerges from that last step. Morris' detailed study has independently provided the basis for the development and rigorous testing of a simulation model (Jones 1976). Hence, the final set of differential equations, their parameter estimates, and the topological analysis could be directly compared to the functional content and behaviour of the full simulation model. The key question was to determine if there was value in compressing the detailed explanation contained in a simulation model into an analytically tractable set of three differential equations.

The paper is organized into the three levels of information. Since the approach seems to have considerable generality, we have also identified the specific steps as a kind of 'how-to-do-it' sequence.

LEVEL 1: QUALITATIVE INFORMATION

Step 1: divide the state variables into fast and slow categories

Associated with each state variable is a characteristic time interval over which appreciable changes occur. The budworm can increase its density several hundred fold in a few years. Therefore, in a continuous representation of this process, a characteristic time interval for the budworm is of the order of months. Parasites of the budworm may be assigned a similar, or somewhat slower scale. Avian predators may alter their feeding behavior (but not their numbers) rather quickly and may be assigned a fast time scale similar to budworm. The trees cannot put forth foliage at a comparable rate, however: a characteristic time interval for trees to completely replace their foliage is on the order of 7–10 years. Moreover, the life span of the trees themselves is between 100 and 150 years, in the absence of budworm, so that their generation time is measured in decades. We first conclude, therefore, that the minimum number of variables will include budworm as a fast variable and foliage quantity (and perhaps quality) as a slow variable.

In the case of the budworm, the main limiting features are food supply, and the effects of parasites and predators. In order to describe the former, we choose a logistic form: if B represents the budworm density, then, in the absence of predation B satisfies

$$\frac{dB}{dt} = r_B B \left(1 - \frac{B}{K_B} \right). \quad (1)$$

The carrying capacity K_B is assumed to depend upon the amount of foliage available. The logistic equation is chosen here because it involves only two parameters. The later mathematical analysis is facilitated by this choice, but the results would be analogous if any other form of self-limited growth were assumed.

The effect of predation is included by subtracting a term $g(B)$ from the right-hand side of eqn (1). A feature of predators is that their effect saturates at high prey densities; i.e. there is an upper limit to the rate of budworm mortality due to predation. The consumption of prey by individual avian predators is limited by saturation, and the number of birds is limited by such factors as territorial behaviour. Similarly, parasites have a low searching capacity that prevents a rapid build-up of their numbers during an outbreak. Thus their impact does not appreciably increase with increasing budworm density.

We conclude that $g(B)$ should approach an upper limit β as $B \rightarrow \infty$. This limit β may depend upon the slow variables (i.e. the forest variables), but that possibility is deferred until Step 5, below. There is also a decrease in the effectiveness of predation at low budworm densities. This is a characteristic of a number of predators and arises in birds in part because of the effects of learning. Birds have a variety of alternative foods, and when one of them is scarce, that particular prey item is encountered only incidentally. As the item becomes more common, however, the birds begin to associate reward with that prey and they begin to search selectively for it. Thus we may assume that $g(B)$ vanishes quadratically as $B \rightarrow 0$. A convenient form for $g(B)$ which has the properties of saturation at a level β and which vanishes like B^2 is

$$g(B) = \beta \frac{B^2}{\alpha^2 + B^2}. \quad (2)$$

This represents a Type-III S-shaped functional response (Holling 1959). The parameter α in eqn (2) determines the scale of budworm densities at which saturation begins to take place. The addition of vertebrate predation to eqn (1) thus produces a total equation for the rate of change of B :

$$\frac{dB}{dt} = r_B B \left(1 - \frac{B}{K_B}\right) - \beta \frac{B^2}{\alpha^2 + B^2}. \quad (3)$$

We emphasize that this particular form was chosen to require as few parameters as possible; our final conclusions are not dependent upon the specific form of the equation, but only upon its qualitative properties.

Step 2: analyse the long-term behaviour of the fast variables when the slow variables are held fixed

In the present case, this analysis is relatively simple, since only one fast variable is considered explicitly. In more complicated situations, phase plane or other more elaborate methods might be required (Bazykin 1974). The first step in the analysis is to identify the equilibria (where $dB/dt = 0$) and determine their stability. Equilibrium values of B must satisfy

$$r_B B \left(1 - \frac{B}{K_B}\right) - \beta \frac{B^2}{\alpha^2 + B^2} = 0. \quad (4)$$

Clearly, $B = 0$ is one such value. If B is near zero, the first term (growth) dominates the second term (predation). The derivative dB/dt is positive for B slightly greater than zero, and therefore $B = 0$ is an unstable equilibrium. The remaining roots of eqn (4) satisfy

$$r_B \left(1 - \frac{B}{K_B}\right) - \beta \frac{B}{\alpha^2 + B^2} = 0. \quad (5)$$

The number of roots for eqn (5) depends upon the four parameters r_B , K_B , β , and α . The next step is to combine some of these parameters where possible by scaling.

Step 2(a): Scale the equations to reduce the number of parameters

We introduce the scaled budworm density $\mu = B/\alpha$. Equation (5) takes the form

$$r_B \left(1 - \frac{\alpha\mu}{K_B} \right) - \frac{\alpha\beta\mu}{\alpha^2(1+\mu^2)} = 0. \quad (6)$$

We multiply through by α/β and (6) becomes

$$\frac{\alpha r_B}{\beta} \left(1 - \frac{\alpha\mu}{K_B} \right) - \frac{\mu}{1+\mu^2} = 0. \quad (7)$$

Now eqn (7) involves just two combinations of the original four parameters. We set

$$R = \frac{\alpha r_B}{\beta}, \quad Q = \frac{K_B}{\alpha} \quad (8)$$

and rewrite eqn (7) as

$$R \left(1 - \frac{\mu}{Q} \right) = \frac{\mu}{1+\mu^2}. \quad (9)$$

The interpretation of eqn (9) is both simple and important. The left-hand side of eqn (9) is the *per capita* growth rate of the scaled variable μ (with respect to a scaled time $t' = \beta/\alpha t$). The right-hand side of eqn (9) is the *per capita* death rate due to predation, also in scaled variables. The points where these curves intersect are the non-zero equilibria for μ (and equivalently, B). The two sides of eqn (9) are plotted in Fig. 1. The left-hand side is a straight line, with intercepts R and Q . The right-hand side is a curve which passes through the origin and is asymptotic to the μ axis at high densities.

Step 2(b): Examine the equilibria of the fast variables as a function of the parameter values

The equilibria for the budworm variable are defined where the straight growth curve

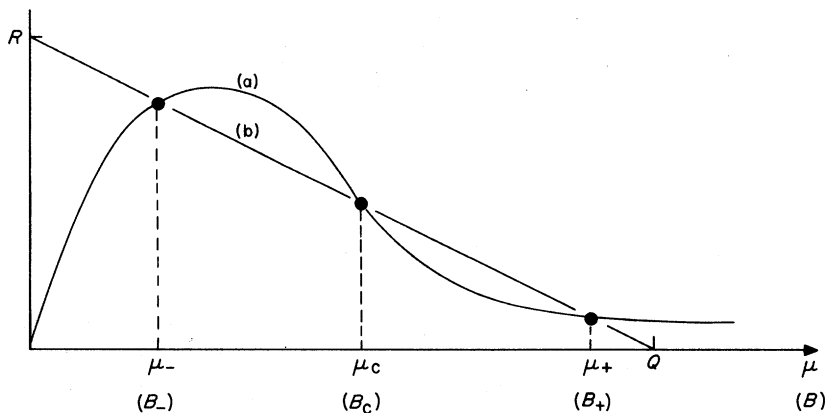


FIG. 1. The growth rate (a) $[R(1-\mu/Q)]$ and predation loss rate (b) $[\mu/(1+\mu^2)]$ of the scaled budworm density μ . Stable equilibria occur at μ_- and μ_+ ; an unstable equilibrium is at μ_c .

intersects the peaked predation curve (Fig. 1). The number and location of these intersections depends on the two parameters R and Q . In this section we examine the nature of this dependence.

Equation (9) provides a minimum of one and a maximum of three equilibria. A case of three is shown in Fig. 1 with the lower, middle, and upper values labelled as μ_- , μ_c , and μ_+ , respectively. Although eqn (9) and Fig. 1 are, strictly speaking, in terms of the scaled variable μ we shall henceforth substitute the original variable B , keeping in mind that they differ only by a constant factor, $1/\alpha$.

It should be clear from Fig. 1 that the locations of the intersections depend upon the relative positions of the growth and predation curves. In this particular choice of scaling, both of the system parameters, R and Q , appear in the straight (growth) function. This makes it easier to visualize how changes in R and Q will change the number and location of the equilibria.

Although we call R and Q parameters, we assume that they may turn out to be functions of the slow variables of forest development. The original purpose in separating slow from fast variables was to allow us temporarily to treat the slow ones as parameters. The definition of 'fast' is synonymous with the assumption that for any (R, Q) the value of B will converge rapidly to one of the stable equilibria, either B_- or B_+ .

The dynamics of the system can be visualized in Fig. 1 by imagining that initially $B = B_-$ and R is low. R is then slowly increased while keeping Q fixed. That is, the straight line is rotated clockwise about its right-hand intercept. The values of B_- and B_c will converge in an accelerating manner while B_+ increases only slightly. At the value of R where B_- and B_c coincide, the lower equilibrium is lost and the next increase in R sends the insect density to B_+ . If we now reverse the path of R , the level of B_+ will decrease very slowly, even beyond the time where B_- and B_c are recreated. It is only when R assumes even lower values that B_c and B_+ coincide and the upper equilibrium is lost. Very similar geometric arguments would illuminate the effects of changing Q .

It is clear that all the action occurs when the intermediate, unstable equilibrium, B_c , coalesces with either the upper or the lower equilibrium. When this happens the density may either jump from a low value to a high one or the reverse. This behaviour is similar

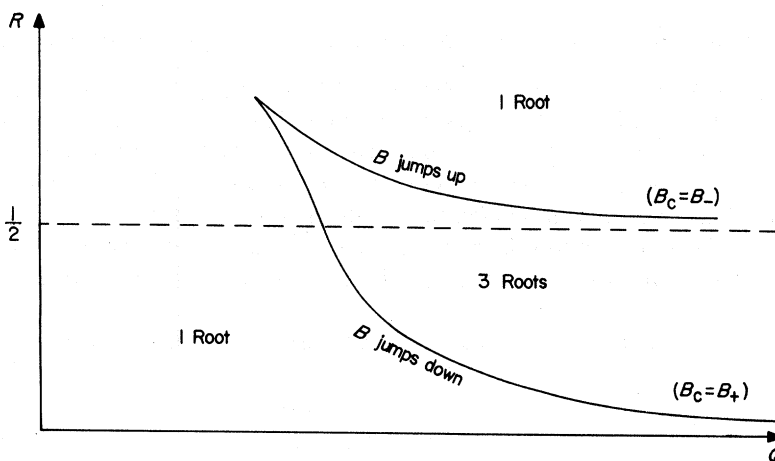


FIG. 2. The location of qualitative behaviour points in terms of the parameters R and Q . Regions with one root have one stable equilibrium. The region with three roots has two stable and one unstable equilibrium (as in Fig. 1). The critical curves separating these regions locate conditions where the budworm density changes radically.

to the sudden outbreaks and collapse that characterize the spruce budworm populations. The equilibria B_- and B_+ correspond to budworm limitation by predators and food, respectively. As forest conditions improve, budworm growth exceeds the control by predators and an outbreak occurs. On the other hand, if the forest is destroyed far enough, the predators can again regain control. Note that the conditions under which upward and downward jumps occur may be quite different since the critical combinations of R and Q may be widely separated.

The critical values of R and Q are where two roots of eqn (9) coalesce and disappear. This translates into the two critical curves of Fig. 2. (The details of the calculation are shown in the Appendix.) The upper curve is when B_c and B_- join and the lower equilibrium is lost, and the lower curve is for $B_c = B_+$, which eliminates the upper equilibrium.

The point where both critical curves meet is that unique combination of R and Q where $B_- = B_c = B_+$.

The two critical curves define a critical region, inside of which there are three equilibria—two stable separated by one unstable. Above this region there is one (high) equilibrium and below it there is one (low). The critical region can be thought of as two overlapping surfaces of stable equilibria. An R -value moving upward with $B = B_-$ must pass completely through the critical region before the upward jump occurs. It must then return completely through, past the lower curve, before B collapses.

The type of phenomena we have presented readily fits into the arena of Catastrophe Theory (Thom 1975). The application of this theory to dynamical systems can be found in Zeeman (1972, 1976) and Jones (1975). The particular case of two parameters and one fast variable has been given the name of a 'cusp catastrophe'. In fact a cusp appears in Fig. 2 where the two critical curves join. The important generality provided by that body of theory is that we may use all the lessons learned from other 'cusp catastrophes' in our current case. Thom's theory says that, at the appropriate qualitative level, all such systems are the same. The equivalence, seated in deep mathematical theorems, is in harmony with our opening assertion that the exact form of our equations was not important so long as they met certain biologically necessary, qualitative criteria regarding their shape.

Step 3: Decide upon the response of the slow variables when the fast variables are held fixed

In order to characterize the state of the balsam fir forest, one ought to keep track of the age or size distribution of the trees, their foliage quantity, and their physiological condition. However, periodic budworm outbreaks synchronize the development of the trees, and the age distribution may be replaced by a single variable S , which gives the average size of the trees. S will be identified with the total surface area of the branches in a stand. Similarly, the condition of the foliage and health of the trees will be summarized in a single variable E , which may be analogously identified with an 'energy reserve'.

Since the maximum value of surface area is bounded, we shall choose a logistic form for S ,

$$\frac{dS}{dt} = r_s S \left(1 - \frac{S}{K_s} \times \frac{K_E}{E} \right) \quad (10)$$

which allows S to approach its upper limit, K_s . The additional factor K_E/E is inserted into eqn (10) because S does not inevitably increase under conditions of stress; surface area may decline through the death of branches or even whole trees. However, during endemic

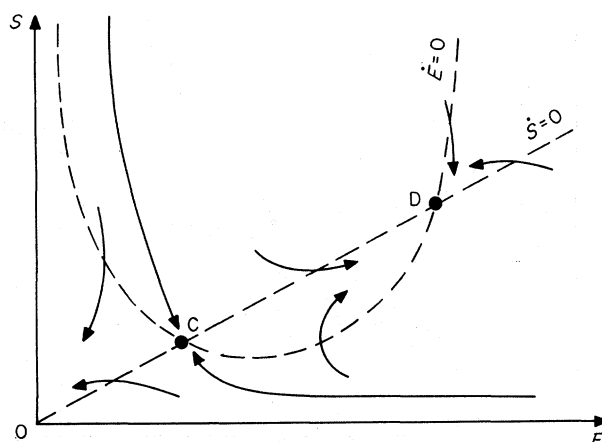


FIG. 3. The plane of the forest variables S and E . When there are few budworm the isoclines for no change in S and E intersect at the two points C and D .

times E will be close to its maximum value K_E and S will grow to its maximum, K_S .

We assume the energy reserve E also satisfies an equation of the logistic type:

$$\frac{dE}{dt} = r_E E \left(1 - \frac{E}{K_E} \right) - P \frac{B}{S} \tag{11}$$

If B is small, then E will approach its maximum K_E . The second term on the right-hand side of eqn (11) describes the stress exerted on the trees by the budworm's consumption of foliage. This stress is proportional to B/S . Since B has units of number per acre and S has units of branch surface area per acre, B/S is the number of budworms per branch. This is the natural density measure for the feeding process. The factor P may be regarded as constant for our present purposes.

Step 4: Analyse the long-term behaviour of the slow variables, with the fast variables held at their corresponding equilibria

The isoclines for the systems (10), (11), are obtained by setting their left-hand sides equal to zero. Thus $dS/dt = 0$ if

$$S = \frac{K_S}{K_E} E, \text{ or if } S = 0 \tag{12a}$$

and $dE/dt = 0$ if

$$S = \frac{PB}{r_E E \left(1 - \frac{E}{K_E} \right)} = \frac{PBK_E}{r_E} \times \frac{1}{E(K_E - E)} \tag{12b}$$

These curves are sketched in Fig. 3, for the case when B , and therefore PBK_E/r_E , is small and there are two equilibria for S and E at C and D . The point C is a saddle point, and hence unstable. There is a single pair of trajectories which reach C and which form a separatrix (heavy arrows). If E and S start out to the right of the separatrix, then (E, S) will approach D as $t \rightarrow \infty$. If E and S start out to the left of the separatrix, they move off into the direction of $E = -\infty$. While this is not realistic, it is a consequence of the form

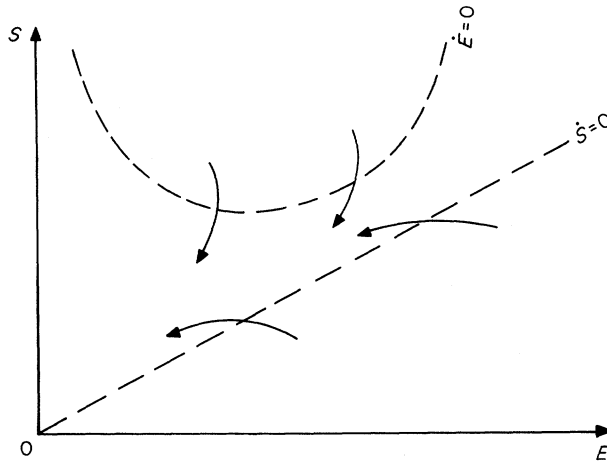


FIG. 4. The plane of the forest variables S and E . When there are many budworm the isoclines for no change in S and E separate and all trajectories head toward low E values.

of eqns (10) and (11). In full completeness we expect E to be limited by $E = 0$ and the origin of Fig. 3 would be a stable equilibrium. In a later section we shall patch up eqns (10) and (11) for low values of E and S . For the time being it is enough to know whether the point heads towards point D or toward the left. In the latter case we argue on logical grounds that it will eventually reach the origin. Even then we could conceptualize a source term that would regenerate a new forest after the old had collapsed. This circumstance is beyond the time frame of our present model.

Now if B increases, then the U-shaped isocline will move up, and the points C and D will approach each other, and the region to the left of the separatrix will take up more and more of the (E, S) plane. Finally, the U-shaped curve can move entirely above the straight S isocline, as shown in Fig. 4.

Now every trajectory converges to the left, presumably to the origin.

Step 5: Combine the preceding results to describe the behaviour of the complete system and identify the needs for additional coupling of the equations

Figures 2 and 3 imply the possibility of periods during which budworm populations are low and stable (at B_-). This condition holds if such populations start at low values and the system resides below the upper critical curve of Fig. 2. S and E will increase to the equilibrium condition at point D , noted in Fig. 3. The budworm will be limited primarily by predation.

However, if the upper branch of the critical curve of Fig. 2 is crossed, budworm populations will begin to increase on a fast time scale towards B_+ . If this happens, Fig. 3 must give way to Fig. 4. Given a complete separation of the two isoclines as shown in Fig. 4, both E and S will decrease. If, as a consequence, the lower critical curve (Fig. 2) is crossed, there will be a rapid decline of budworm density. The particular pattern described above represents one complete outbreak/decline cycle of the budworm/balsam interaction.

A number of other possibilities also exist, however. For example, if budworm populations are partially controlled, the two isoclines of Fig. 3 might never separate to the extent shown in Fig. 4. In such a case, the complete system would reach an equilibrium,

with B , S , and E all at relatively high values. This corresponds to the phenomenon of 'perpetual outbreak' that has been observed in New Brunswick as a consequence of insecticide spraying. Conditions under which this may occur will be given below.

Moreover, the above patterns are only generated if the critical curves are crossed in a particular direction. That depends on the movement across the (R, Q) plane of Fig. 2. In the present form R and Q seem to be constants. As a first departure we expect that Q would increase as the forest grew. Movement in the R direction would seem to be possible if an external driving variable changed one of its component parameters. For example, weather might increase r_B , the instantaneous rate of increase of budworm, enough to carry R across the upper curve in Fig. 2.

However, for sake of clarity, and our step-by-step format, we have left the issue of careful coupling of these equations to this point.

Let us first determine whether the budworm eqn (3) has any terms that should be expressed as functions of the slow variables. In order to do this, we refine our interpretation of B and S to represent quantities per acre of forest. Since the amount of foliage available per acre is roughly proportional to S , K_B should be proportional to S :

$$K_B = K' S. \quad (13)$$

Thus K_B measures carrying capacity in larvae per acre, while K' measures carrying capacity in larvae per unit of branch area.

Similarly, terms in the predation rate (eqn 2) are also dependent upon the branch surface area. Predators, such as birds, search units of foliage, not acres of forest, so that the relevant density is larvae per unit of surface area. Thus the half-saturation density for B is also proportional to S :

$$\alpha = \alpha' S. \quad (14)$$

The new parameter α' is measured in larvae per unit of branch area.

If eqns (13) and (14) are substituted into eqn (8), the result is

$$R = \frac{\alpha' r_B}{\beta} S, \quad Q = \frac{K'}{\alpha'}. \quad (15)$$

Note that Q is independent of S , while R is proportional to S . When the forest is young, R will be small, but Q may be quite large. Thus R and Q will be below the critical region in Fig. 2. Budworm densities will be low, not only in larvae per acre, but in larvae per branch. The densities per branch will be low because the predators will find it easy to search the small number of branches per acre. As the forest grows, control by predators becomes more uncertain, because of satiation of their appetites. Finally, the upper critical curve in Fig. 2 will be crossed and control by predators becomes ineffective as B rapidly increases to a high level (B_+) being limited now by food.

The effect of a rapid increase in B may be to change the dynamics of the slow variables from that depicted in Fig. 3 to that in Fig. 4. If this happens, the budworm outbreak will lead to a collapse of the forest. From eqns (3) and (13), we see that B/S is close to K' ($B \simeq K_B$) during a budworm outbreak. Can the forest reach an equilibrium in that case? Equation (12b) may be rewritten as

$$\frac{E}{K_E} \left(1 - \frac{E}{K_E} \right) = \frac{P}{r_E K_E} \frac{B}{S} \sim \frac{PK'}{r_E K_E}. \quad (16)$$

Since the left-hand side of eqn (16) is dimensionless, we denote the right-hand side as a dimensionless parameter M :

$$M = \frac{PK'}{r_E K_E}. \quad (17)$$

M is easily interpreted as the ratio of a rate of energy consumption by budworm (by eating foliage) to the rate of energy production by the trees. The maximum possible value of the left-hand side of eqn (16) is $1/4$. We conclude that no equilibrium is possible if $M > 1/4$. The preceding analysis indicates that an equilibrium is likely if $M < 1/4$.

Now, assuming that $M > 1/4$, a budworm outbreak must lead to a decline of the forest. Since R depends upon S , eventually the lower branch of the critical curve in Fig. 2 will be crossed, and the budworm population must collapse. However, it is not clear whether the budworm collapse will occur in time to save the forest from complete destruction. On the other hand, if the budworm density begins collapsing too soon, the effect on the forest may be reduced enough to establish a stable equilibrium for all three variables. In fact, the numerical values of the parameters in our equations will determine which of these behaviours will occur.

When realistic parameter values are substituted into our eqns (3), (10) and (11), budworm outbreaks lead to collapse of the forest. That is, E and S decline sharply during a budworm outbreak, and eventually E becomes negative. Negative values of E are unrealistic, and our model is not valid when extensive tree deaths occur. This situation can be remedied in two ways. The first (simplest) way is to recognize that the system eqns (3), (10) and (11) represents a cohort of trees and its resident budworm population. This cohort is only capable of going through one severe decline. If this were to happen, then the model must be started again with a small value of S and with E near K_E in order to generate the next outbreak. Regeneration from one cohort of trees to the next is a discontinuous process, and one might as well represent this fact explicitly in the model.

On the other hand, for mathematical convenience, it might be desirable to devise a system of differential equations which adjusts the behaviour of E and S for small values in order to simulate the growth of a new cohort. We have no need for such an adjustment in the present investigation, but we shall indicate how it might be carried out.

According to eqn (13), the carrying capacity for the budworm is independent of E , i.e. the trees put forth the same amount of foliage, regardless of their physiological condition. It would seem more reasonable that K' should depend upon E , and that K' should decline rather sharply if E falls below a certain threshold T_E . Therefore, we may replace eqn (13) by

$$K_B = K'S \frac{E^2}{T_E^2 + E^2}. \quad (18)$$

If T_E is small compared with K_E , then K_B will show a sharp decline near $E = T_E$. A corresponding change should also be made in eqn (11). We may set

$$P = P' \frac{E^2}{T_E^2 + E^2} \quad (19)$$

because the stress on the trees is related to the amount of foliage consumed.

The resulting equations are as follows:

$$\frac{dB}{dt} = r_B B \left(1 - \frac{B}{K'S} \cdot \frac{T_E^2 + E^2}{E^2} \right) - \beta \frac{B^2}{(\alpha'S)^2 + B^2} \quad (20)$$

$$\frac{dS}{dt} = r_S S \left(1 - \frac{S K_E}{E K_S} \right) \quad (21)$$

$$\frac{dE}{dt} = r_E E \left(1 - \frac{E}{K_E} \right) - P' \frac{B}{S} \frac{E^2}{T_E^2 + E^2}. \quad (22)$$

This system appears to be much more complicated than eqns (3), (10) and (11), but its qualitative behaviour will be exactly the same, except for small values of E . If the parameter T_E is chosen properly, the system eqns (20)–(22) will exhibit a regeneration similar to that obtained by re-starting eqns (3), (10) and (11). However, we shall use eqns (3), (10) and (11) in the sequel.

This is as far as we can go if we restrict ourselves exclusively to qualitative information. Some effort is now needed to quantify parameters in order to define, more precisely, the behaviour of the system. Since we are interested in determining how far one can predict with different levels of information, it is useful to identify two levels of quantitative information to add to the first qualitative level—one very general and based on estimates by experienced field naturalists and one more detailed and specific.

LEVEL II—GENERAL QUANTITATIVE INFORMATION

In order to complete our model, we must estimate its parameters. Especially important are the combinations of parameters which form Q , R and M , eqns (15) and (17). These will determine the qualitative behaviour of the system. Most of the other parameters are rate constants which determine the speed with which certain processes occur, but do not alter the basic qualitative picture.

The parameter K' in eqn (13) measures the carrying capacity of the forest in larvae per branch. An entomologist with cursory knowledge of budworm can confidently state that from 100 to 300 larvae can be supported by an average branch of balsam foliage in good condition. The parameter α' is likely to be low. Knowing, roughly, the speed of movement and distance of perception of birds for insect prey, α' can be estimated as one to two larvae per branch. [This particular analysis has been expanded by Holling, Jones & Clark (in preparation).] These ranges then permit a calculation of the likely range for Q from eqn (15). The results range from $Q = 50$ to 300, and strongly suggest that the system resides in or below the critical region (Fig. 2) during the endemic phase.

But still, outbreaks will only occur if R increases above $1/2$, and crosses the upper critical curve. Again, rough estimates of the elements determining the value of R (eqn (15)) can be obtained as follows:

- r_B The budworm is capable of a five-fold increase in density per year. Since we are using a continuous time model, we set $e^{r_B} = 5$, and conclude that $r_B = 1.6/\text{year}$.
- β The value of β has been estimated in the literature using the most general information on size of birds, their maximum daily consumption, the proportion of budworm in their diet, and their ranges of densities (Kendeigh 1947; George & Mitchell 1948; Mitchell 1952; Dowden, Jaynes & Carolin 1953; Morris *et al.* 1958). These estimates of the maximum consumption range from 20 000 to 36 000 larvae per acre per year.

S A maximum value for S is K_S .

K_S A fully recovered forest contains about 24 000 average branches per acre.*

If the preceding estimates are combined (eqn (15)), we find that R , for a mature forest, lies between 1.1 and 3.8. Because R need only be 0.5 we have considerable leeway in the value of S below K_S that will initiate an outbreak. A forest is fully mature at age 80, while outbreaks have a period of about 40 years. Actually, numerical results show that an outbreak is not immediate when the upper branch of the cusped curve is crossed. It requires a number of years for the budworm to show an appreciable rise in density. Although predation cannot control the budworm when $R > 0.5$, the predation does appreciably slow the rate of growth. Hence, a value of 1.1 for R at $S = K_S$ is not unreasonable.

Now we turn to the estimation of M . As mentioned above, M is a ratio of energy consumed by budworm to energy produced by trees. The critical value for M is 0.25 as trees collapse if $M > 0.25$. The time required for such a collapse will depend upon M . A forest can withstand defoliation for approximately 4 years, which implies that Mr_E must be approximately 0.3, since B does not in fact reach the value $K'S$ as assumed in the derivation of M (eqn (17)).

Some rates which should be estimated are r_S and r_E . The time of regeneration of the forest after an outbreak depends on r_S . It can be adjusted to make the period between outbreaks approximately 40 years. A value of $r_S = 0.15/\text{year}$ gives satisfactory results. Likewise, r_E sets the rate at which trees recover from the stress of defoliation. Since this recovery is fairly rapid, a value of 1/year is assumed for r_E . Since E is a synthetic variable we can set its maximum value as $K_E = 1$.

The only remaining parameter is P , the rate of energy consumption by budworm. From eqn (17)

$$P = \frac{Mr_E K_E}{K'} \simeq 1.5 \times 10^{-3}.$$

As an independent measure, it is known that 150 to 200 larvae per branch can consume approximately 25% of the foliage. Therefore

$$P = \frac{0.25}{150} = 1.7 \times 10^{-3}.$$

All the parameters for eqn (20) through eqn (22) are summarized in Table 1.

LEVEL III—EMPIRICAL QUANTITATIVE INFORMATION

Level I, the development of the model, utilized only qualitative information about the system's behaviour. In Level II we made a first attempt at estimating parameter values, but restricted ourselves to general quantitative information. This is the type of information that an experienced biologist might provide without specifically examining the New Brunswick budworm.

In Level III we examine the field data that have been collected over many decades and determine the best values for the parameters as we have defined them. This step is made easier in this particular instance because much of the work has already been done in

* The standard field measure for an 'average branch' is one that can be circumscribed by a polygon of 10 ft² area.

TABLE 1. Parameter values for Level II and Level III information

Symbol	Description	Units	Level II	Level III
r_B	intrinsic budworm growth rate	/year	1.6	1.52
K'	maximum budworm density	larvae/branch	100–300	355
β	maximum budworm predated	larvae/acre/year	20 000–36 000	43 200
α'	$\frac{1}{2}$ maximum density for predation	larvae/branch	1–2	1.11
r_S	intrinsic branch growth rate	/year	0.15	0.095
K_S	maximum branch density	branches/acre	24 000	25 440
K_E	maximum E level	–	1.0	1.0
r_E	intrinsic E growth rate	/year	1.0	0.92
P'	consumption rate of E	/larvae	0.0015	0.00195
R	$\alpha' r_B S / \beta$	–	1.07–3.84	0.994 (S/K_S)
Q	K' / α'	–	50–300	302
M	$PK' / r_E K_E$	–	0.15–0.45	0.71

connection with the construction of a detailed simulation model of this system. That simulator is a central element in a program of ecological policy design—a program to synthesize the methodologies and concepts of systems ecology and modelling, optimization, and decision theory in a case study framework. A review of that project and some of the lessons learned can be found in Holling *et al.* (1976).

The primary source of data for the simulator was Morris (1963), with considerable additional expert opinion from the personnel and files of Environment Canada's Maritimes Forest Research Centre. The simulator mimics the univoltine character of the insect as a difference model with yearly time steps. As a result, its parameters are not all appropriate for a continuous model formulation without some adjustments. These adjustments could be made in the original data, but for convenience we choose to let the simulation serve as a surrogate for the real world, and we consult it for measures that are analogous to the parameters needed for our model—eqns (3), (10) and (11). The errors and discrepancies generated by going through this 'middle-man' are on the same order as those when we assume the simple continuous form that we have.

Specific details about the budworm simulation model can be found in Jones (1976). We now briefly check off the parameter values suggested by that reference and indicate the discrepancies with Level II values. First, consider the intrinsic role of growth, r_B . We find in the simulation that the maximum growth rate between generations in a mature forest with low budworm densities is 4.56. Thus, $r_B = \ln(4.56) = 1.52/\text{year}$, in close agreement with that found above.

The hypothetical carrying capacity per branch K' is the most difficult to interpret. The simulation has a comparable equilibrium at $K' = 355$ larvae/branch. However, numerical experience shows that there can be a transient overshoot to values of 600 or more. This wide range is a consequence of the discrete nature of the insect population. We adopt K' as 355 because of the conceptual parallel of that value, but note that the continuous model will not overshoot to the high values seen in the simulation and in nature.

The parameters of bird predation are taken from the data summarized in Holling, Jones & Clark (in preparation). That paper specifically identifies three groups of insectivorous birds that represent three distinct size classes and, to some degree, three different modes of search. This more detailed, but still qualitative, analysis of field data identifies an expected value for β of 43 200 larvae/acre/year. This maximum consumption level is significantly higher than that found in the literature and reported in Level II. That literature only considered one class of birds—the arboreal feeders (e.g. warblers). Two other classes of birds were not previously recognized as important because they are

normally ground nesters (e.g. juncos and grosbeaks) and because their numbers do not increase during an outbreak. However, their large size and appetite make them at least equally as important as the smaller species and β is increased accordingly. Because the density of budworm which produces half-saturation of predation is different for each bird class we take an average for each, weighted by their contribution to the total predation. Thus, $\alpha' = 1.11$ larvae/branch.

The parameters for tree growth are taken by fitting eqn (10) (with $E = K_E$) to a typical history of branch surface area following the collapse of an outbreak. This gives a growth rate of $r_S = 0.095$ /year and an asymptotic level of $K_S = 25.4 \times 10^3$ branches/acre.

It was recognized early in the simulation development that something analogous to an 'energy reserve' was affecting the response dynamics of trees. However, there were insufficient data to incorporate this process adequately. The solution taken was to deputize foliage for this function, and we continue that here. As E is an intensive factor we lose no generality by defining $K_E = 1$. The value of r_E is evaluated from the rate of increase in foliage. The maximum that foliage can increase in the simulation is 1.26-fold per iteration. Thus $\exp r_E = 1.26$ gives $r_E = 0.23 \text{ yr}^{-1}$. This maximum occurs when foliage is about half its maximum; and so, as a consequence of the logistic form, $r_E = 4 \times 0.23 = 0.92$ /year.

P is the maximum rate that an individual feeds on 'E', which is $P = 1.95 \times 10^{-3}$ /larvae.

Using the above values, the three aggregate parameters R , Q and M assume the following values. First

$$R = 1.72(S/K_S)$$

$$Q = 302$$

(or $Q = 540$ if $K' = 600$).

Finally,

$$M = \frac{PK'}{r_E K_E} = 0.71$$

(or $M = 1.27$, if $K' = 600$).

The parameter values for Level III are also summarized in Table 1. There is remarkable agreement between the values found from extensive and intensive collection and analysis of field data and those estimated from a first field estimation.

One can go a lot further than traditionally assumed with informed, but qualitative, insight into ecological process. Extensive data collection efforts need not always be carried out and completed before the system is abstracted into an analysable model.

We have been emphasizing that the central and important aspect of this analysis is a process and not a product. The actual numerical integration of our model using the estimated parameters is a final, though anticlimactic, step to be performed for completeness. Because the parameter values from Level II and Level III information are so similar we adopt only Level III and use these values in our model (eqns (3), (10) and (11)). The integrated time course is shown in Fig. 5 through one outbreak cycle (ending in year 43). Fig. 6 shows a typical outbreak cycle exhibited by the simulation model.

The qualitative behaviour is similar, as this analysis predicted. The major difference in the appearance is between the graphs of surface area S . This is an expected discrepancy resulting from our attempt to mimic a 75 age class model of tree population with a single

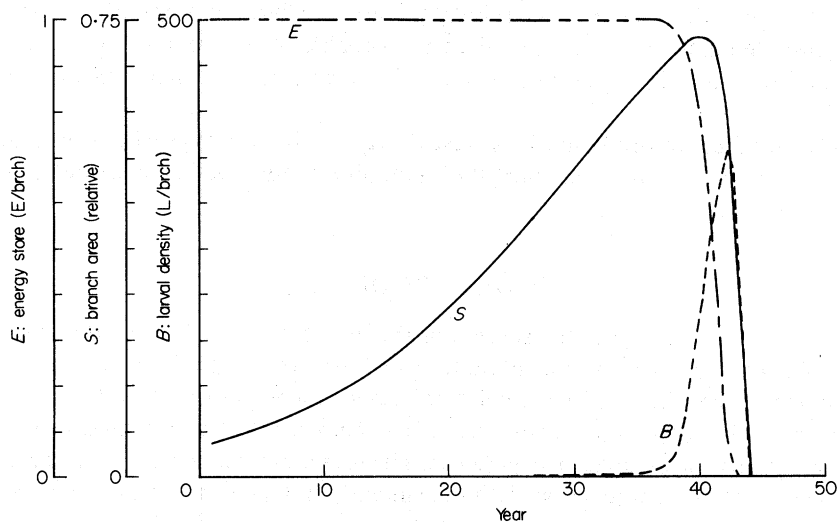


FIG. 5. A numerical solution of the differential equations using the parameter values of Level III information.

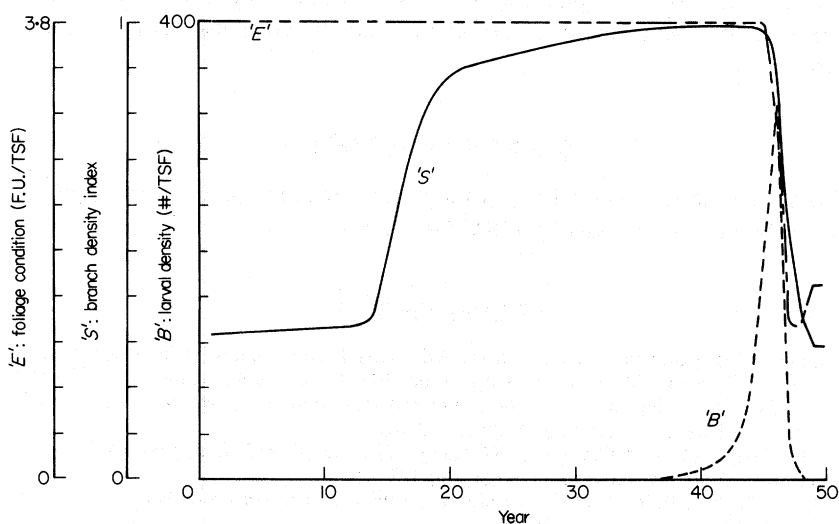


FIG. 6. A typical outbreak cycle from the detailed simulation model. The variables plotted are the ones most analogous to the differential equation model: 'E' is the total foliage available per unit of branch surface area in arbitrary 'foliage units'/10 ft² (F.U./TSF); 'S' is the density of surface area in TSF/acre scaled such that 'S' = 1 is equivalent to $S = 0.94$ in Fig. 5; 'B' is the density of third instar larvae in number 1 TSF

state variable. Other discrepancies between Figs 5 and 6 were also anticipated as they result from fundamental differences between discrete and continuous models. First, the maximum level of S is lower in Fig. 5 than in 6. Equivalently, the outbreak is triggered at a lower 'threshold' of S in Fig. 5. In the simulation model the process of competition between birds (not included in our differential equations) enhances their effectiveness in young forests (low S). Thus S must reach a higher value in the simulation model before

the control by predators is overcome (Holling, Jones & Clark, in preparation). Secondly, the differential equations as conceptualized are capable of only one outbreak while the simulation model output is periodic because the regeneration of new trees is explicitly modelled.

The differential equations could be adjusted, expanded, and otherwise 'tuned' so that their time traces more closely matched the simulation model, but we elect not to follow that procedure.

DISCUSSION

An obvious requirement for the success of this procedure is a good understanding of the basic phenomena, to know which are the most important variables, and to know the main features of their interactions. Such knowledge is never completely available at the beginning of an investigation. In the case of the budworm we had behind us extensive field investigations and simulation experience. The present methods have been exceedingly useful when applied in conjunction with the simulation. One can narrow the reasonable parameter ranges using these procedures. Perhaps most important, the analytic model is likely to extend our understanding of the phenomena, since the full armory of mathematical techniques is available (Ludwig, Weinberger & Aronson, in preparation). This raises a final question about the level of mathematical training or ability required to carry out such a program. In principle, the methods which were applied to the budworm do not go beyond first year calculus; however, their effective use requires considerable mathematical confidence.

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Documents and Publications
International Institute for Applied Systems Analysis
Schloss Laxenburg
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Austria

Publications (att'n: Ralf Yorque)
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APPENDIX

The double roots of equation (9)

Equation (9) has a double root if the straight line given by the left-hand side of eqn (9) is tangent to the predation term of the right side. We adopt the following expressions for the two sides of eqn (9):

$$f(\mu) = R \left(1 - \frac{\mu}{Q} \right) \quad (\text{A1})$$

$$g(u) = \frac{\mu}{1 + \mu^2}.$$

A double root occurs if

$$f(\mu) = g(\mu)$$

and

$$\frac{df}{d\mu} = \frac{dg}{d\mu}. \quad (\text{A2})$$

We treat eqn (A2) as a pair of simultaneous equations and solve for R and Q parametrically with respect to μ . These relationships can be written as

$$\frac{R}{Q}(Q - \mu) = \frac{\mu}{1 + \mu^2}$$

and

$$\frac{R}{Q} = \frac{\mu^2 - 1}{(1 + \mu^2)^2}.$$

It follows after some algebra that

$$R = \frac{2\mu^3}{(1+\mu^2)^2} \quad (\text{A3})$$

and

$$Q = \frac{2\mu^3}{(\mu^2-1)} \quad (\text{A4})$$

The cusp point of Fig. 2 where both critical curves meet (or begin) is the point where the derivatives of R and Q with respect to μ both vanish. This corresponds to the inflection point of $g(\mu)$, which occurs at $\mu = \sqrt{3} = 1.73$. This value in eqn (A3) and (A4) gives the cusp point for (R, Q) as

$$R_c = \frac{3^{3/2}}{8} = 0.650 \quad (\text{A5})$$

$$Q_c = 3^{3/2} = 5.196.$$

Further, the axis of the cusp is oriented as

$$\frac{dR}{dQ} = -1/16$$

Equations (A3) and (A4) also generate two limiting conditions. When $\mu \rightarrow \infty$, $Q \rightarrow \infty$ and $R \rightarrow 0$. As $\mu \rightarrow 1$, $Q \rightarrow \infty$, but $R \rightarrow 1/2$. Figure 2 is based upon this information.