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Dynamic Modelling of Pest Control Using a Pesticide

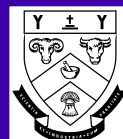
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Dynamic Modelling of Pest Control Using a Pesticide

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Abstract:

A general differential equation model of the temporal evolution of a pest population density when subjected to control measures using a pesticide, is investigated. The model is based on logistic growth combined with population dispersal described by diffusion, and pesticide action is characterised by its LD90 toxicity measure and a consumption limited by a saturation pesticide density. Solutions are found for a number of assumed scenarios concerning the initial pest distribution and pesticide application strategy. Criteria are established for pesticide toxicity and application density to ensure eradication, and the efficiency of the strategies investigated are compared with regard to total pesticide consumption. It is shown that rather general conclusions can be reached, such as that it is inevitable that a pesticide residue is left after full eradication has been accomplished.

1. INTRODUCTION

The use of pesticides in agriculture and industry has long been common practice, and they are also used by environmental control agencies against intruder species. However, as environmental awareness increases, their use is becoming increasingly controversial. It is an obvious paradox to control species that damage the environment with a toxin that itself contaminates natural resources and may be detrimental to the species that are being protected. Nevertheless, in many instances pesticides are the only effective way to achieve the desired goal.

To alleviate this dilemma, it is important to obtain as much understanding as possible of the interaction between the poison and both target and non-target species. To this end many studies have been done to study the action of a particular pesticide on a specific species, including empirical studies and statistical analysis of the observations. An example is a series of studies on possum extermination by 1080 poison by Ross, Hickling et al [1-7].

This article attempts to complement such studies by investigating a mathematical model that represents the dynamics of the interaction between the pest species and the pesticide that is applied. The model is formulated in general terms to make it applicable to any pesticide and pest species to which the model assumptions apply. The purpose of the study is to explore the kind of information that can be extracted from such a model, and its use in optimising the strategy that is used to apply the pesticide. Once more, there are many studies in the literature using ideas and techniques from population dynamics for detailed modelling of specific phenomena such as insecticide resistance; for example, see the work by Peck [8] for further references. It is not the intention of this article to focus on a single pest or pesticide or to make accurate quantitative predictions, but rather to

present a relatively simple model for understanding the mechanisms and identifying the variables that determine the outcome of chosen pesticide application strategies.

The criteria for deciding what is an optimal strategy may vary widely according to the circumstances. Some examples may serve to illustrate the issues that are involved.

Eradication. In this case we consider a population that is already established, and is stable and homogeneously distributed over the region under consideration. The purpose of control may be to eliminate the population completely, or to reduce and keep pest numbers low enough to make their impact on the environment negligible. A common strategy in this case is to apply pesticide homogeneously e.g. by aerial spraying or dropping. Another is to place bait, in which case accessibility may be an issue, and may make it necessary to place bait only on the periphery of e.g. a mountain forest. In either case one may either apply a large amount of toxin at once, or apply small amounts regularly to replenish it as it is consumed. One plausible optimisation goal may be to minimize cost by minimizing the total amount of pesticide used; or the cost of applying it, which may favour a single large application rather than repeated application of small amounts; yet another might be to minimize the toxin residue after eradication is completed.

Biosecurity. Here, a typical situation would be a population that starts strongly localised but is spreading with time. The first goal would be containment, and subsequent eradication. Again, there would be choices between pesticide application on the periphery or homogeneously, and instantaneous or continuous application, and the strategy which would be most effective might be different from the eradication scenario.

Toxicity. The use of a pesticide that is highly toxic but short-lived, might favour a different combination of strategies from a low-level but persistent toxin. In addition to the factors mentioned above, this would involve a comparison between the rate at which the population grows naturally, the rate at which the toxin reduces the population, and the rate at which the toxin decays.

Pest behaviour. The rate at which the target species (and perhaps non-target species) consume the poison is obviously important, and may even change over time e.g. as survivors become bait-shy.

These examples are not exhaustive, but illustrate that there are a wide variety of issues that can be addressed by suitable modelling.

Global modelling of the entire population as done here can be expected to be most successful when there are a large number of individuals involved. In the case of a colony of bacteria to which an antibiotic is applied, for example, the predictions should be very realistic, while in the case of only a few predators roaming over a large forest only a prediction of average trends can be expected.

Nevertheless, even in the case of small numbers, a dynamic model of the kind described here can be used as the basis of a risk analysis approach, e.g. using Monte Carlo simulation techniques, to incorporate statistical fluctuations away from the average.

The same applies to the incorporation of uncertainties in the parameters that are needed to specify the characteristics of the population, behaviour patterns of individuals, toxin properties, and any other parameters which may be hard to measure in practice.

2. MODEL FORMULATION

The quantity of primary interest is the pest density, i.e. the total number n of individuals in the pest population per unit area. For simplicity we work in SI units, e.g. n is expressed as a number per square meter (m^{-2}). In the case of bacteria in a liquid, we may instead define n as the number per unit volume.

The pest density is assumed to vary with time, as a result of the balance between the natural population growth and the number eliminated by the pesticide.

In many realistic problems the pest density will also vary with position. For this study, we assume that it only varies along the single direction labelled as the X-axis. This simplifies the mathematics, and is adequate to illustrate some of the phenomena that occur and how they are characterised in terms of pest and poison properties. Detailed application of the ideas developed here to particular cases will generally require more elaborate models to be developed.

For the growth we assume a logistic model with an initial pest density n_0 , a growth rate r per second and a saturation value k . In addition, we assume that as the population grows, it will tend to spread spatially according to a diffusion model, i.e. proportional to the local concentration gradient with a rate determined by a diffusion coefficient D (m^2s^{-1}). So in the absence of the pesticide the population growth rate is given by

$$\frac{\partial n}{\partial t} = r n \left(1 - \frac{n}{k}\right) + D \frac{\partial^2 n}{\partial x^2} \quad (2.1)$$

Population models of this type had been introduced in the ecological context by Skellam [9] and used by many other authors since; see Okubo [10] for a review.

We represent the pesticide density as p (Kg/m^2). Define c (Kg/s) as the poison consumption rate, i.e. the pesticide mass that one individual of the pest species consumes per second given unlimited access, e.g. in a laboratory experiment. In a typical application, pesticide might not be applied at a density that will give such unlimited access. But in principle if one should slowly increase the pesticide density, it is reasonable to expect that eventually a saturation density ρ will be reached where a pest individual will consume the pesticide at the rate c . Beyond ρ further increase will not cause the individual to consume any more poison.

At the other extreme, when p is small, it is plausible that the consumption rate will be reduced to (cp/ρ) . In the case of a homogeneously distributed pesticide application, that would happen because the area that the individual needs to cover in order to collect the same amount of pesticide as for a density ρ , would increase by a factor (ρ/p) . Alternatively, for application in the form of localised bait stations, the probability of encountering bait would be reduced by a factor (p/ρ) .

The behaviour described is expressed by introducing a sloped step function σ defined by

$$\sigma(x) = \begin{cases} 0 & \text{for } x < 0 \\ x & 0 \leq x \leq 1 \\ 1 & x > 1 \end{cases} \quad (2.2)$$

in terms of which the change in pesticide concentration due to consumption, is written by multiplying the individual consumption rate by the pest density, leading to

$$\frac{\partial p}{\partial t} = a - nc\sigma\left(\frac{p}{\rho}\right) \quad (2.3)$$

Here, a ($\text{Kg m}^{-2} \text{s}^{-1}$) represents the rate at which the pesticide density increases in the absence of any pests; this might include a positive contribution from the rate at which pesticide is being applied, as well as negative contributions from any applicable spoiling rate, consumption by non-target species, etc.

The rate at which pests are killed will depend on the toxicity of the poison and the rate at which it is consumed. A common measure of toxicity is the LD90 value, i.e. the poison mass per unit body weight, that will kill 90% of the population. Let us call this value L and the average body mass of the pests under consideration, m kg. Then the dose that will kill an individual with a probability of 0.9, is (mL) . So, as according to the second term in equation (2.3) the pesticide mass per unit area that is consumed in a time Δt is $(nc\sigma\Delta t)$, it follows that the number of pests that are killed per unit area in that time is $0.9\frac{nc\sigma\Delta t}{mL}$. Hence we can extend equation (2.1) to the case where pesticide is present,

as

$$\frac{\partial n}{\partial t} = rn\left(1 - \frac{n}{k}\right) + D\frac{\partial^2 n}{\partial x^2} - 0.9\frac{nc\sigma}{mL} \quad (2.4)$$

The model as described contains a rather large number of unknown constants, each measured in appropriate physical units. Considerable insight can be gained even before attempting a solution, if we allow the differential equations to dictate appropriate combinations of the constants. The form of the equations suggests transforming to scaled, dimensionless variables defined as follows:

$$N = \frac{n}{k}; \quad P = \frac{p}{\rho}; \quad T = rt; \quad X = x\sqrt{\frac{r}{D}} \quad (2.5)$$

Essentially this means that the pest and poison densities are expressed as fractions of their respective saturation values, time is measured in terms of how fast the population grows and distance in terms of the rate at which diffusion takes place. Substituting equations (2.5) into (2.3) and (2.4) leads to

$$\frac{\partial N}{\partial T} = N(1-N) + \frac{\partial^2 N}{\partial X^2} - \alpha N \sigma(P) \quad (2.6)$$

$$\frac{\partial P}{\partial T} = \gamma - \beta N \sigma(P) \quad (2.7)$$

where the 7 original parameters have been replaced by only the 3 dimensionless combinations defined as

$$\alpha = \frac{0.9c}{mLr}; \quad \beta = \frac{kc}{\rho r}; \quad \gamma = \frac{a}{\rho r} \quad (2.8)$$

Not only is this a major reduction in degrees of freedom, but even if we need to resort to numerical solution of the model equations (2.6) and (2.7) it will be possible to recover some of the analytical dependence through equations (2.8). Expressed in a different way, the model equations yield universal solutions in which all quantities are of order unity, and the physical solution for any concrete physical situations is obtained by merely transforming back to the original variables by substituting equations (2.5) and (2.8) into it and in the process the applicable units of measurement are automatically restored.

Solutions to the model equations depend on the parameters $\alpha, \beta,$ and γ , as well as the initial (scaled) pest population N_0 and pesticide density P_0 . The former set of parameters are determined by the properties of the pest population, the pesticide and their interaction, and so generally assume fixed values for a situation where one is confronted with a particular pest species and have selected a particular pesticide. Similarly N_0 would be given in such a situation, and the only control parameter that can be freely chosen is P_0 . In our analysis below we therefore concentrate on how P_0 can be chosen to achieve the desired effect, assumed to be the extermination of the pest population.

In the next section we construct solutions for some special cases, chosen both to represent some of the strategies mentioned in the introduction and as a progression from simple to more complex solutions.

3. SOLUTIONS FOR SPECIAL CASES

The introduction of a saturation pesticide density ρ is useful to formulate a consistent model that is guaranteed not to produce an unrealistic consumption rate. But it is

plausible to expect that the actual application of pesticide will always be kept well below this rate – at least, that would be a reasonable goal, unless for example the model predicts that extermination cannot be achieved in any other way. That point will be addressed later. For now we assume that at all times $p \ll \rho$, i.e. $P \ll I$. In that case it is sufficient to simplify equation (2.2) to $\sigma(P) = P$ and substitute this into equations (2.6) and (2.7).

3.1 Pest population initially localised, sustained pesticide level.

This example might apply to a biosecurity situation. The basic assumptions are

- There is a localised initial pest density which can be described by a normal (i.e. Gaussian) distribution; the centre of the Gaussian is chosen as the origin of the spatial axis. This is represented for illustrative purposes by

$$N(x,0) = e^{-\frac{x^2}{2}} \quad (3.1)$$

With this choice the initial peak density at $x = 0$ is equal to the saturation value k (in the absence of pesticide) and falls off over a length scale of the same order as that determined by diffusion.

- The pesticide is applied homogeneously over the range accessible to the pests, and this is continuously augmented as pesticide is consumed or spoiled to maintain a constant value of $P = P_0$.

The effect of the second assumption is that the second of the pair of model equations is trivially satisfied and we are only left with the single equation

$$\frac{\partial N}{\partial T} = N(A - N) + \frac{\partial^2 N}{\partial X^2} \quad (3.2)$$

where we have introduced a new dimensionless constant A defined as

$$A = 1 - \alpha P_0 \quad (3.3)$$

The form of equation (3.2) looks similar to the well known Fisher population growth model [Hastings (1997)], but contains a variable value A instead of the fixed Fisher model saturation value of 1. The equation can be solved numerically for any given A value, and shows the behaviour demonstrated by figure 1:

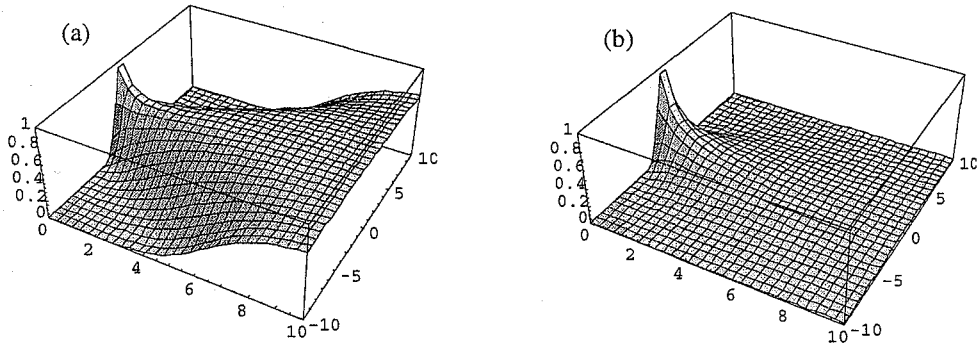


Figure 1. Pest population growth when the pesticide density is kept constant, for (a) $A = 0.75$ and (b) $A = 0$

If either the pesticide density is zero ($P_0 = 0$) or it is not toxic ($\alpha = 0$) we regain the case of population growth without limitation by the pesticide and this is the maximal A value $A = 1$.

Figure 1(a) shows a typical behaviour for a low pesticide density that gives an A value between one and zero. The initial population peak at first decreases as the population diffuses away from the starting point, then starts growing but eventually saturates at the value A . In other words, as long as $A > 0$ the pest population is controlled rather than exterminated.

To achieve extermination, we need $A = 0$, i.e. $\alpha P_0 = 1$. Figure 1(b) illustrates how the population changes in this case. Substituting in the definitions of α and P_0 , the minimum pesticide concentration that will achieve extermination is given by:

$$p_e = \frac{mLr}{0.9c} \rho \quad (3.4)$$

For any pesticide concentration p lower than p_e , the pest population will stabilise at the value

$$n_s = k \left(1 - \frac{0.9cp}{mLr\rho} \right) \quad (3.5)$$

The fact that extermination requires a minimum poison concentration and that below this it merely suppresses the saturation pest concentration, may come as no surprise, but in addition to that we have quantified these phenomena in terms of measurable parameters. Conversely, it may well be easier to measure p_e and n_s directly and use that to determine less accessible parameters such as k , r and ρ .

A striking feature of the result is that p_e and n_s are independent of the initial distribution of the pests – something that may well be unknown in a practical situation.

If the pesticide density is increased beyond the value p_e , A becomes negative and cannot be interpreted as a saturation density any more. In this range its effect is to determine the time scale over which the pest population is exterminated. That is illustrated by figure 2,

which shows the total pest population calculated by integrating the density over X , as a function of scaled time T , for some negative A values.

It is seen from figure 2 that the extermination poison density p_e is the borderline value for which extermination is only just achieved, but only over a very long time. For practical purposes somewhat higher values will be needed and the effect can be judged by calculating the value of A that applies to the particular pest species, pesticide, etc of interest. The figure also shows that the curves tend to converge as A decreases, suggesting that there is a law of diminishing returns in increasing the pesticide density beyond p_e .

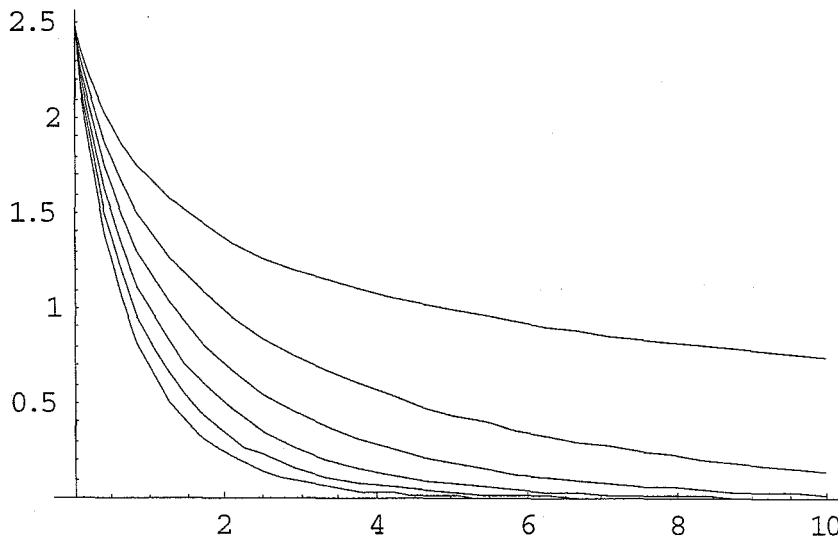


Figure 2. Total localised pest population as function of scaled time T , for $A = 0, -0.2, -0.4, -0.6, -0.8, -1$, curves taken from top to bottom in the plot.

Figure 1 illustrates that p_e is also a crucial density value from another perspective, as it is the minimal value that will allow *containment* of the originally localised pest population. Any lower value allows the population density to stabilise to a finite value, and so if the X -interval shown in the figure represents the area over which the pesticide is applied, it follows that the population eventually reaches the edges of the area and can escape beyond it.

The analysis above applies to a pesticide density less than the limiting value ρ , beyond which, according to equations (2.2) and (2.3), the factor P_0 in the definition of A is simply replaced by 1. In that case the condition to obtain extermination becomes $\alpha \geq 1$, i.e.

$$\frac{0.9c}{mLr} \geq 1 \quad (3.6)$$

This can be interpreted as a limitation on c and/or L . In other words, given the population growth rate r of a certain species, no matter how much pesticide is applied, extermination can only be achieved if the pesticide is toxic enough (L small enough) and consumed at a

sufficient rate (c large enough) that equation (3.6) is satisfied. This conclusion is once more qualitatively plausible, but equation (3.6) gives a quantitative test to evaluate the suitability of a particular pesticide.

To summarise, extermination is only possible if $\alpha \geq 1$, i.e. equation (3.6) is satisfied; and when this does hold, the minimal pesticide density that will give extermination is $P_0 = 1/\alpha$, i.e. the p_e value in equation (3.4).

Finally we consider the pesticide application rate that is required to ensure that the pesticide concentration stays constant at the level represented by P_0 . From equation (2.7) the condition that P does not change is given by

$$\gamma = \beta N P_0 \quad (3.7)$$

Substituting back the dimensionless parameters and bearing in mind that N depends on x and t , we have

$$a(x,t) = k c P_0 N(x,t) \quad (3.8)$$

This shows that more pesticide needs to be applied where the pest density is greatest, and the amount changes with time and position. That may seem an impractical goal as the pest density would not normally be known in such detail, but in the case of bait stations it can be achieved approximately by merely monitoring and replenishing the bait regularly.

Equation (3.8) may also be used to find the total amount of pesticide used, by integrating $a(x,t)$ over both x and t . This will clearly only be a finite number if $A \leq 0$, since otherwise the stabilised pest population will continue to consume pesticide indefinitely. Taking $A \leq 0$, the total amount of poison C consumed by the pests is obtained as

$$C(A) = \frac{k c p \sqrt{D}}{\rho r^{3/2}} I(A) \quad \text{where} \quad I(A) = \int N(X,T,A) dXdT \quad (3.9)$$

Here $I(A)$ is an integral that can be evaluated once and for all for any given A value, and for the assumed gaussian initial pest distribution we obtain the values shown in figure 3.

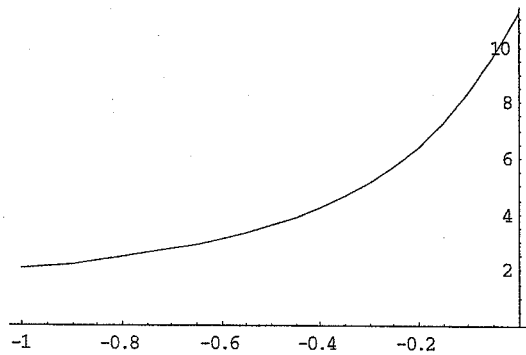


Figure 3. Integral I(A) for calculating total pesticide consumption by localised pest distribution.

Figure 3 shows that the total amount of pesticide consumed can be reduced by a factor of 5 or more by increasing the pesticide density beyond the minimal value corresponding to $A = 0$, but once more there is a diminishing return once A values around $A = -1$ have been reached. It should be borne in mind that to get the total amount of pesticide needed, we need to add to C the amount used to establish the initial concentration value p over the area of application; depending on how this amount compares with C it may or may not be worthwhile to increase p in order to reduce the value of C . No general conclusions can be drawn without detailed evaluation of a particular case.

3.2 Uniform initial pest distribution, sustained pesticide level

A practical example of this case would be an established pest population being eradicated from an isolated area by applying pesticide uniformly at the start and then continuously topping it up to maintain a constant pesticide density p . It is also of interest because it amounts to repeating the analysis of the previous section that was based on an assumed initial pest distribution, for a different initial distribution. Comparing the two cases gives an indication of which results depend on the initial values and how sensitive they are.

If the initial pest distribution is uniform, and pesticide is applied uniformly, the population has to evolve identically at every point and so the pest distribution must also stay independent of the position variable x at later times. That simplifies the mathematics greatly because the second derivative term in equation (3.2) that represents diffusion, falls away and we are left with a variation on the well-known logistic population growth equation [Hastings (1997)]. This equation can be solved analytically and the result is

$$N(T) = \frac{A N_0 e^{AT}}{A - N_0 + N_0 e^{AT}} \quad (3.10)$$

where N_0 is the initial uniform scaled pest density. To make a quantitative comparison with the previous results we arbitrarily take $N_0 = 0.5$ and adjust the size of the X-region in which the pest population occurs to such a value that the total number of pest individuals is the same as that represented by the localised distribution (3.1). Then equation (3.10)

gives the population evolution shown in figure 4, as compared to figure 2 obtained previously for the localised gaussian distribution.

The population trend is qualitatively similar in both cases, but for the same value of A the decrease is faster in the case of the uniform pest distribution. Curves for positive A values can be calculated similarly and it is easy to see directly from the form of equation (3.10) that these will all saturate to the value $N = A$ as T becomes very large, just as happened for the localised population.

All the results pertaining to the limits on pesticide concentration, toxicity and consumption in order to obtain extermination, discussed in the previous section, apply without change here as they were based on the form of equation (2.7) and hence (3.3) which apply equally well here.

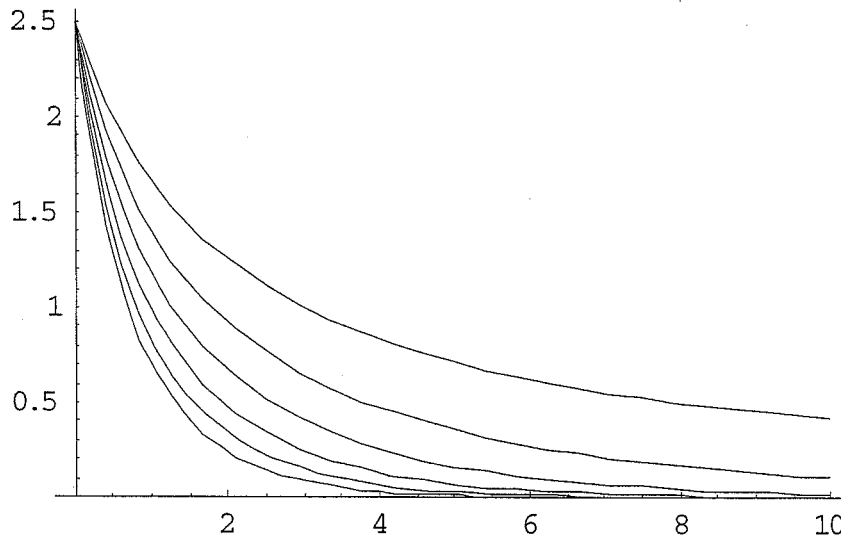


Figure 4. Evolution of uniform pest population for $A = 0, -0.2, -0.4, -0.6, -0.8, -1$, curves taken from top to bottom in the plot.

To obtain the total amount of pesticide consumed in a scaled time T , equation (3.9) is applied again but this time an analytical formula is obtained for $I(A)$:

$$I(A) = \Delta X \log \left(\frac{A - N_0 + N_0 e^{AT}}{A} \right) \quad (3.11)$$

Here ΔX is the size of the X-region and taking as before the values $N_0 = 0.5$, $\Delta X = 2\sqrt{2\pi}$ and $T = 10$ to compare with the localised distribution calculation, we obtain the trend shown in figure 5. Again the result is very similar to figure 3, but showing a slightly smaller pesticide consumption especially where the pesticide density is low enough that the marginal value $A = 0$ is approached.

To summarise the comparison, while the time development of the pest population depends to some extent on the initial distribution, the final population value attained for

an insufficient pesticide density is given by equation (3.5) and the criteria for extermination by equations (3.4) and (3.6) independently of the initial distribution.

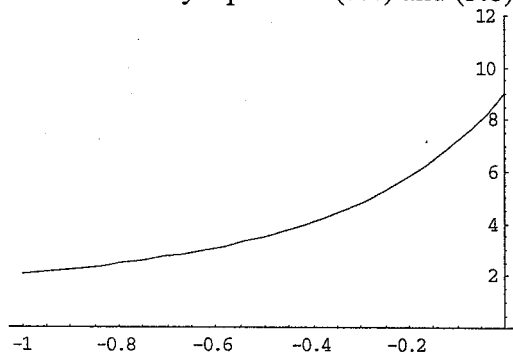


Figure 5 Integral I(A) for calculating total pesticide consumption by uniform pest distribution.

3.3 Uniform pest population, single initial pesticide application

In a practical situation the easiest way is to apply pesticide only once, at the beginning of an eradication operation, but this is harder to model mathematically because then P changes with time and the two differential equations (2.6) and (2.7) remain coupled. We first consider the case that we may neglect the diffusion term in (2.6) because the initial pest distribution is uniform.

As no pesticide is applied after the single application at time $T = 0$, $\gamma = 0$ and equation (2.7) is formally solved for $P < 1$ by the expression

$$P(T) = P_0 \exp[-\beta \int_0^T N(\theta) d\theta] \quad (3.12)$$

As $N(T)$ is still unknown, this solution is not immediately usable. In principle it could be used to eliminate P from equation (2.6), but the resulting equation and alternative forms of it obtained by various variable substitutions are too complicated to solve analytically. In addition, as will be shown below, for the single application case it does make sense to allow values of $P > 1$ and then the full function $\sigma(P)$ has to be retained in both equations further complicating their solution.

We therefore return to the original pair of 1st order differential equations and solve them numerically. Some examples of the calculated evolution of the pest density and pesticide density with time are shown in figure 6.

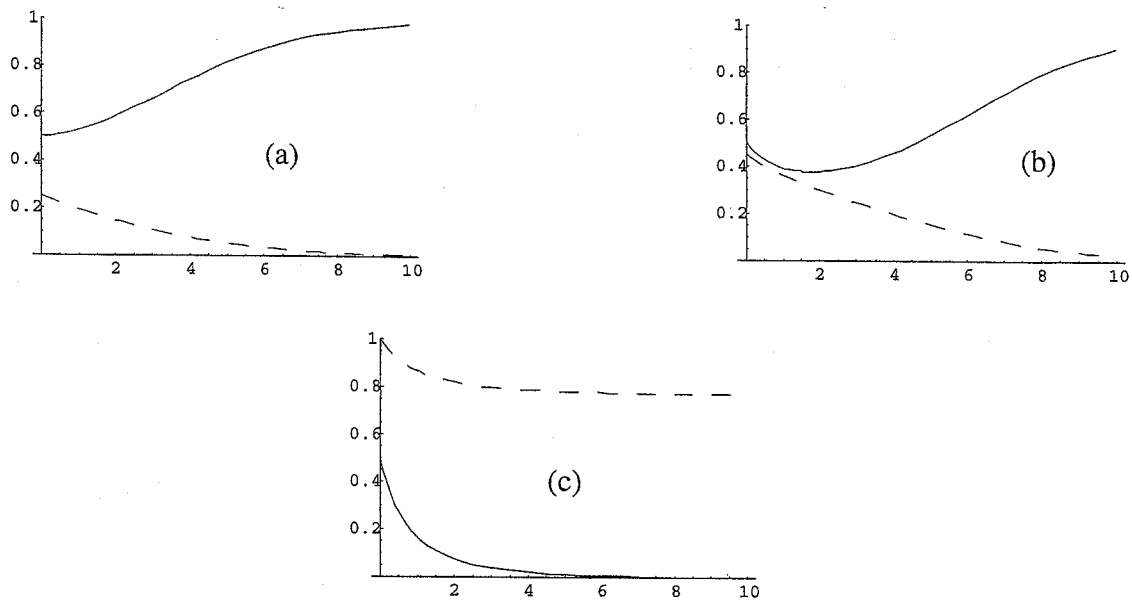


Figure 6. Pest population density $N(T)$ (solid line) and pesticide density $P(T)$ (dashed line) as function of time, for $\alpha = 2$, $\beta = 0.5$ and $N_0 = 0.5$, and three different P_0 values.

The figure shows three distinct behaviours depending on the initial pesticide density P_0 . At low values the pest density N may either still increase or initially decrease but reach a minimum, and then rises to its full saturation value while the pesticide density is depleted. For a high P_0 value on the other hand the pest density is reduced to zero and the pesticide density reaches a constant non-zero value.

The following argumentation shows that these three alternatives are in fact the only possible combinations that can occur. We first notice that $P(T)$ is a monotonically decreasing function, since for $\gamma = 0$ the derivative of P can never be positive according to equation (2.7). The derivative can become zero, but only if P becomes zero (i.e., $P = 0$ is approached asymptotically), or for non-zero P if N becomes zero as in fig 6c. For large times, a constant P value, either positive or zero, are the only two possibilities consistent with a monotonic decrease from an initial positive value, since negative P values are incompatible with its physical interpretation. If P approaches zero at large times, its contribution in equation (2.6) falls away and the equation reduces to a simple logistic growth law that saturates at $N = 1$. So there are only two possibilities at large time values: either $(P = P_\infty, N = 0)$ where $P_\infty > 0$ is the value to which the pesticide density stabilises at infinite times, or $(P = 0, N = 1)$. This means that i) it is not possible to suppress the pest population to a low density by a single pesticide application, as was the case for continuous application, and ii) it is also not possible - even theoretically - to choose the initial pesticide density such that both the pest density and the pesticide density will reduce to zero in the end, as might have seemed to be a desirable outcome.

Next, we consider the initial behaviour of N . Suppose that we start from a value $0 < N_0 < 1$. We have seen that it must eventually reach either 0 or 1. But can it reach a maximum or minimum in the meantime? To investigate that, we differentiate equation (2.6), set

$dN/dT = 0$ in the result as must be true at an extremum of N , and eliminate dP/dT by using (2.7). The result is that

$$\frac{d^2N}{dT^2} = \alpha \beta N^2 \sigma(P) \quad \text{for } 0 < P < 1, \quad 0 \text{ otherwise} \quad (3.13)$$

The right hand side of equation (3.13) cannot be negative, showing that N cannot have a maximum, although it can have a minimum as illustrated in figure 6b. Consequently, if at $T = 0$, N is increasing, it will inevitably rise to 1 and so a necessary condition to achieve extermination of pests is that the derivative dN/dT at $T = 0$ should be negative, i.e.

$$\alpha \sigma(P_0) > 1 - N_0 \quad (3.14)$$

This condition ensures that the pest population initially decreases, but is not strict enough to guarantee that N will become zero because it might only reach a minimum and then increase again as in figure 6b. To obtain a sufficient condition, we need to have $dN/dT < 0$ as $T \rightarrow \infty$ and $N(T) \rightarrow 0$, and from equation (2.6) that means

$$\alpha \sigma(P_\infty) > 1 \quad (3.15)$$

Since the maximum value that $\sigma(P_\infty)$ can achieve is 1, we once more obtain the minimal condition that $\alpha > 1$ which reduces once more to equation (3.6). Given that the pesticide that is selected satisfies this criterion, it follows that the minimum value of P_∞ that will give extermination is

$$P_\infty = \frac{1}{\alpha} \quad (3.16)$$

This condition specifies the minimum pesticide residue that will be left after extermination, and it is interesting to note that it is exactly the same as the extermination density p_e given by equation (3.4) for the continuous application example. One might have thought that maintaining a constant pesticide density is wasteful and would leave a larger residue than allowing the pests to consume it gradually; but this result means that to the contrary, extermination with a single application can only be achieved if the initial pesticide density is larger and gradually reduces down to p_e .

For practical use, equation (3.16) needs to be formulated in terms of P_0 rather than P_∞ . That requires solving the differential equations for $P(T)$, finding the limit of the solution as $T \rightarrow \infty$, putting that equal to $1/\alpha$ and solving for P_0 as a function of α, β and N_0 . As analytical solution of the differential equations is not possible, all these steps have to be done numerically and the result is illustrated in figure 7.

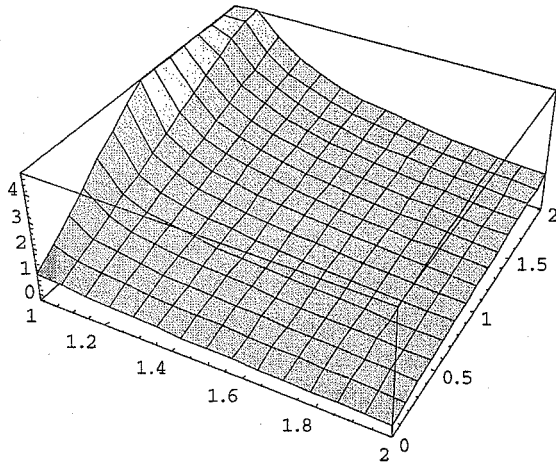


Figure 7. Minimal P_0 value required for extermination for $1 < \alpha < 2$ and $0 < \beta < 2$, at the uniform initial population density $N_0 = 0.5$.

The figure shows a smooth variation of P_0 , rising sharply when β becomes large and α is near 1, the minimal limit for which extermination is at all possible. It is only shown for $N_0 = 0.5$, but the behaviour is similar for other values.

It was remarked above that there is no point in having $P_\infty > 1$, as any density excess above 1 will by equation (2.2) have no effect on the pest population. In the sustained application example this carries through to pesticide densities at earlier times because a constant density is maintained. However, figure 7 shows that the situation is different for the single application case – initial densities considerably larger than 1 are generally required, the excess serving as a reservoir that is consumed at a later time.

Numerical solution for P_0 is a very cumbersome procedure, and to alleviate this we suggest the following approximate formula:

$$P_0 \approx \frac{1}{\alpha} + \frac{2.25\beta\sqrt{N_0}}{\alpha^2} + 0.2\alpha N_0 \quad (3.17)$$

The first term in this equation is justified by the fact that if $\beta = 0$, the pesticide density is constant according to equation (2.7) and so the solution $P = P_0 = 1/\alpha$ of the previous section is recovered. The other terms are purely empirical and were found to represent the numerical calculation with an accuracy of the order of 10% for the range $1.2 < \alpha < 3$ and $0 < \beta < 5$.

A final comparison between the continuous and single pesticide application scenarios is the total amount of pesticide consumed. In the present case, the application rate is zero so the consumption is simply obtained by subtracting the final density from the initial value. To facilitate comparison we cast this in the same form as equation (3.9) by defining an equivalent $I(A)$ function as

$$I(A) = \Delta X \left[\frac{1}{\beta} \left(1 - \frac{P_\infty}{P_0} \right) \right] \quad (3.18)$$

where A is again defined by equation(3.3) and we take the case of a minimal residue, i.e. $P_\infty = 1/\alpha$.

Comparing the continuous application analogue (3.11) with equation (3.18) with, we note that the former becomes infinite when $A = 0$ (i.e., $\alpha P = 1$) whereas the latter stays finite. In other words, if we choose to apply pesticide at only the minimal concentration residue that is necessary for extermination, it is far more efficient to apply a sufficiently large amount at once in the beginning rather than the lower amount continuously.

However, this is not necessarily true if a larger final residue can be tolerated. For example, we concluded from figure 5 that $A = -1$, i.e. twice the minimal density, would give a total pesticide consumption approaching the lowest achievable. Assuming this same residue density for the single application scenario, we calculate from equation (3.18) the comparison as shown in figure 8.

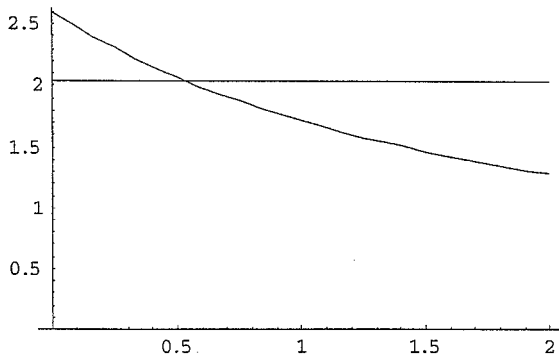


Figure 8. Total pesticide consumption function $I(A)$ for the single application model (descending curve) and the continuous application model (straight line) as function of β .

It is seen that for small values of β , continuous application requires less pesticide in total although the single application scenario is still better for large values of β . If the acceptable residue level is decreased, the straight line in figure 8 is shifted upwards (according to figure 5) and the β -value at which the single application model becomes favourable is reduced.

3.4 Localised pest population, single initial pesticide application

The final scenario we discuss is where a single homogenous pesticide density is applied initially to a localised pest population, modelled as before by the Gaussian density of equation (3.1). We now have to solve equations (2.6) and (2.7) fully, the only simplification being that $\gamma = 0$. As in the previous case the solution has to be done numerically for assumed values of all parameters and initial conditions. For illustrative purposes we take $\alpha = 2$ as this is well above the minimal value required, and $\beta = 0.5$.

Two trial values for P_0 present themselves. The value of $P_0 = 1/\alpha = 0.5$ that was found to be the minimum sustained pesticide density that gives extermination, is found to be inadequate for the single application case and allow the pest population to escape containment and grow to the full extent of normal logistic growth, i.e. $N = 1$.

At the other extreme, we might take the maximum of the localised initial population density (in this case the value $N = 1$ at $X = 0$) and apply the value calculated for P_0 in the previous section for a homogenous pest distribution, which is found to be nearly 1 in the present case (or a slightly higher value using the approximate formula (3.17)). This indeed produces extermination, but in fact overestimates the required value because the population peak is reduced not only by the action of the pesticide but also by the spreading of the peak as a result of diffusion of the population.

In fact the required value lies somewhat above the average of these two values. Figure 9 illustrates the calculated evolution of both the pest population and the pesticide density for a value $P_0 = 0.7$, just below the average of 0.75.

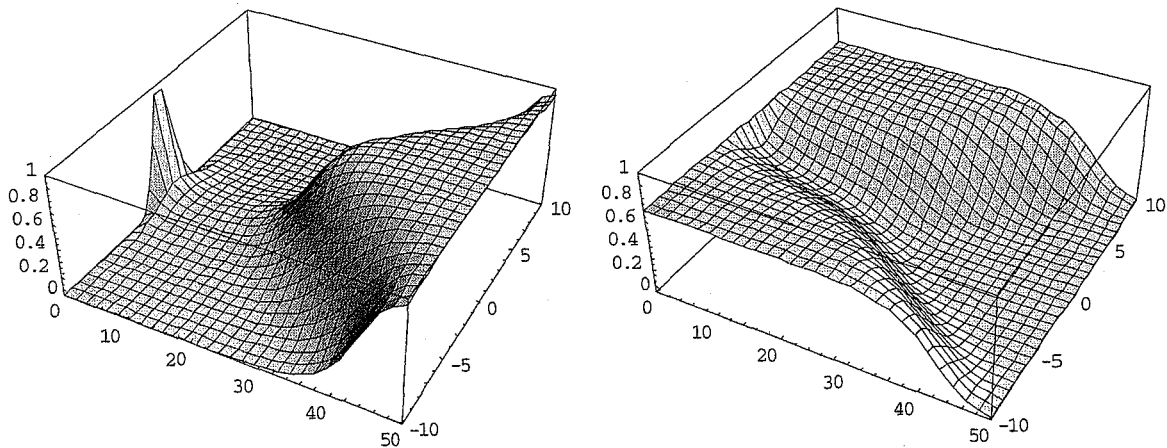


Figure 9 Scaled pest population density (a) and pesticide density (b) over the length interval $(-10,10)$ as a function of time $0 < T < 50$.

The figure illustrates that if the pesticide density is not quite high enough to exterminate the pests at the position of the original maximum (in this case, $X = 0$), once the pesticide has been consumed at this position the pest population starts growing again and serves as a source from which they diffuse outwards, eventually completely consuming the pesticide elsewhere and so allowing growth to $N = 1$ everywhere. This makes it clear that the extermination condition needs to be determined for the position of the initial population peak, i.e. the condition to be satisfied by $P(X, T)$ is that

$$P(0, \infty) = \frac{1}{\alpha} \quad (3.19)$$

As in the previous section, this may be reduced to a minimal value for P_0 that will produce extermination by numerically varying the numerical solution of the pair of differential equations as function of P_0 , until a value satisfying equation (3.19) is found. The result is shown in figure 10:

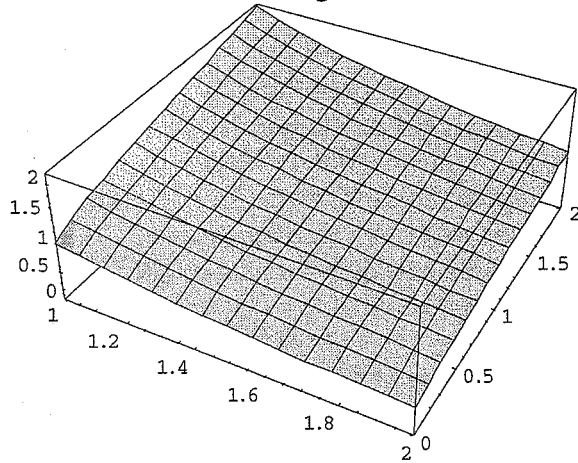


Figure 10. Minimal P_0 value required for extermination for $1 < \alpha < 2$ and $0 < \beta < 2$, for a localised initial population density with a peak value $N_0 = 0.5$.

To facilitate comparing this with figure 7, the assumed initial gaussian distribution of the pests was readjusted to have an initial peak value $N_0 = 0.5$ instead of unity as given by equation (3.1). The comparison shows that the required pesticide density is always lower for localised pests than for a uniform distribution. The underlying reason for this was already indicated above; in equation (2.6) the additional term that enters for a localised population is the second derivative d^2N/dX^2 term, and at a maximum of N this is negative, so that a smaller value of P_0 and hence of $P(X,T)$ in the last term of the equation is sufficient to ensure that N is eventually reduced to zero.

For a particular assumption of the pest distribution, such as the gaussian one we have used for illustration, it would be possible to make this argument more quantitative and estimate the reduction in P_0 obtained by estimating the 2nd derivative e.g. from the variance (i.e. spatial extension) of the gaussian. In this way an approximate formula for P_0 , similar to equation (3.17) might be found, but would have to depend on more parameters, such as the variance parameter of the gaussian. However, a different functional form would yield a different relation, possibly depending on even more parameters if a form that is more complicated than a gaussian is required.

We have therefore not pursued this line any further. However, it is still possible to give a general guideline for P_0 , namely that the value calculated for a uniform population at the same density as the peak, is an upper limit for that required to exterminate a localised pest population. So a value no larger than that of equation (3.17) is needed, and the latter value appears to be a good estimate for small ($\ll 1$) β values while for $\beta \approx 3$ the required value is in fact only of the order of half the upper limit.

3.5 Nonuniform pesticide application.

It appears from figures 1 and 10 that applying the pesticide uniformly over a large area within which a localised pest population is contained, is not very efficient since if the initial density is large enough to eradicate the population, it also prevents spreading and hence the pesticide outside the original population is not needed. This suggests that the pesticide application should be coordinated with the pest distribution, applying a higher density where the population is high. In principle it is no more difficult than it was in the previous section, to calculate the solutions of the differential equations if $P(X,0)$ is not a constant. However, inevitably this leads to a proliferation of the assumptions that need to be made and the associated list of parameters needed to specify initial distributions of both pests and pesticide. For this reason we have only performed very limited experiments in this regard, and considered the following two scenarios for $P(X,0)$:

- (a) $P(X,0)$ is a gaussian of the same shape as the initial pest density, i.e. simply a normalising constant multiplied by $N(X,0)$.
- (b) $P(X,0)$ consists of 3 discrete parts. One of these is a constant density in an interval centred at $X = 0$, and extending 3 standard deviations of the gaussian on either side (i.e., containing about 99% of the pest population). The other two are similar rectangular densities centred at 7.5 standard deviations on either side, i.e. forming an "outside" barrier to spread of the population.

In both cases the pesticide densities are kept constant with time, for comparison with the uniform density case in section 3.1 above. The normalising constants for both scenarios (a) and (b) are chosen in such a way that the total amount of pesticide used is also the same as for the uniform density case $P_0 = 1/\alpha$, i.e. the minimal extermination value.

In case (a) we find that while extermination is still achieved at the centre, some of the pest density escapes and hence grows to full saturation value outside of the gaussian pesticide density being maintained around the centre. Thus neither containment nor extermination is achieved in this case.

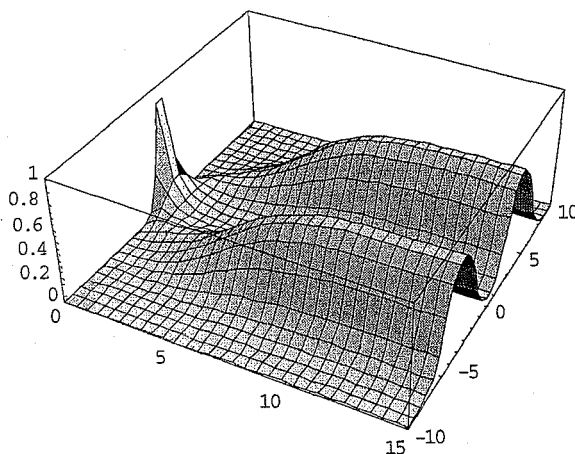


Figure 11. Evolution of pest density $N(X,T)$ for scenario (b), when a discrete central pesticide core in the interval $(-2,2)$ and outside pesticide barriers intervals $(-10,-6)$ and $(6,10)$ are maintained.

The result obtained for case (b) is illustrated in figure 11. The pests are again exterminated in the centre, and in addition the pest population stays contained within the outside barriers. Some pest population builds up and the region between the central and outside barriers, but the peak population density remains below saturation density.

These results are suggestive but far more work would be needed before general conclusions can be made. Provisionally it appears that a uniform spatial distribution of pesticide is more effective than a localised one even when the pest population is localised, because full extermination could be achieved with the same amount of pesticide only for the uniform distribution. It is also interesting to note that both containment and suppression of population density can be achieved by a pesticide barrier located outside of the localised population.

4. INTERPRETATION AND CONCLUSIONS

The model studied combines several established representations of population behaviour and response to toxins: a logistic natural population growth, its dispersion as a result of spatial mobility of individuals according to a density driven diffusion model, differentiated effects of the pesticide on individuals as characterised by a toxicity level such as LD90, and consumption proportional to availability but limited by a saturation pesticide density. Such a model could be elaborated to describe the behaviour of a specific pest, pesticide, environment, etc in more details, but our aim was to explore the insight that can be gained from universal features rather than specifics. In keeping with this only a 1-dimension model was studied, restricting the inclusion of geometrical detail to a minimum as well.

Even before application to specific situations, some conclusions could be drawn from the mathematical structure of the model about the appropriate variables and constants to use in describing a system of this nature. A natural time scale is defined by equation (2.5) in terms of the unconstrained population growth rate r ; essentially, this measures time in terms of how long it takes for a pest individual to reproduce itself, i.e. the time span of a generation, adjusted for the number of offspring. This leads to a natural scale for lengths, being in essence the distance by which a localised population spreads in one unit of the natural time scale. Using these natural scales, situations as different as microbes and mammals can be reduced to the same universal length and time variables X and T which are numbers independent of the units of measurement in the original system. Similarly the main independent variables of the model, the pest density and poison density, are reduced to universal variables N and P respectively by scaling them according to their respective saturation values. The behaviour of these universal scaled variables are in turn fully determined by only three combinations of the 7 system-dependent constants included in the model – the dimensionless constants α , β , and γ defined in equation (2.8).

Solutions of the model were obtained and studied in some detail for four specific situations: either a uniform or a localised initial pest population, and a uniform pesticide density being applied either continuously or only as a single initial application. Our

discussion focussed on the main parameter under control of the pest control officer; the pesticide density P_0 applied initially, and aimed to determine the minimum value that will guarantee pest extermination. The main conclusions reached are as follows:

1. For extermination to be possible at all, there is a minimum requirement that $\alpha > 1$. This requirement has a simple interpretation, as seen by the following argument. The average pesticide mass needed to kill one pest individual is $(mL/0.9)$. If the pesticide is being consumed at the maximal rate (nc) that holds at the saturation pesticide density, the total number of individuals killed per second is $nc/(mL/0.9)$. On the other hand, the maximal number of new individuals per second when population growth is not constrained by saturation or pesticide, is (nr) . So if we rewrite the definition of α in the form

$$\alpha = \frac{nc}{mL/0.9} \frac{1}{nr} \quad (3.20)$$

it is clear that $\alpha > 1$ just expresses the requirement that the maximal rate at which pests can be killed, should exceed the maximal rate at which new individuals can be added to the population.

2. Assuming that α is large enough, extermination requires that a residual pesticide density of at least $P = 1/\alpha$ remains after the pest population has been removed. It is not possible to exterminate all the pests and consume all the pesticide in the process.
3. With sustained application, it is enough to maintain the density value $1/\alpha$ throughout the process. However, with only an initial application, the initial density P_0 that is required may be considerable more than this, depending also on the initial pest population and the parameter β . An approximate formula for estimating P_0 is given in equation (3.17) but accurate determination may require full solution of the model equations.

A more physical interpretation of β to help understanding this requirement might be based on equation (2.7); the latter implies that β measures the maximal rate at which the pesticide density can be reduced by pest consumption, i.e. by a pest population at saturation density with maximal access to the pesticide.

In the real world pesticide is often applied in a number of discrete events, which is a scenario intermediate between the single application and continuous application cases. So the values mentioned above may serve as outside limits to give a guideline in such cases.

4. Sustained application is very inefficient in terms of the total amount of pesticide consumed (and hence the time taken) if the concentration is only maintained at the minimum level $1/\alpha$. Raising the level up to double this value produces substantial improvements in this regard.

5. The single application approach is generally faster and uses less pesticide in total when leaving the same final residue level as sustained application, but the reverse is true for small pesticide consumption rates.
6. With a localised population, a sustained, uniform pesticide application at a density below the extermination value will not prevent spreading of the population, but will suppress the population density (inside the application region) to a lower value than the saturation density, as given by equation (3.5).
7. On the other hand, with a single application, it is not possible to merely suppress population numbers. Unless the initial application density is high enough to eradicate the population completely, all the pesticide will be consumed eventually and allow uncontrolled spreading and population buildup. As shown in the example of figure 9, this may take a considerable time and in the initial stages, it may be hard to determine whether eradication will be achieved or not merely by observing the population.
8. Preliminary experiments with sustained but spatially non-uniform pesticide application, suggests that this is less efficient. However, it is also found that it is possible to both prevent escape and limit the final pest density by "ring fencing" an initially localised pest population with an external pesticide barrier.

The latter observation raises the question of how wide such a barrier needs to be and what pesticide density is required. It may well be that substantially less pesticide is needed for containment than for eradication, and for reasons of access or limiting the environmental impact this may be a preferable strategy in many practical situations. Full investigation of such matters is left for subsequent work.

As in any modelling situation, care should be taken in applying the conclusions reached above to situations not covered by the model assumptions or parameter ranges investigated.

As one example of such a model restriction, the logistic growth model is somewhat unrealistic in that it asserts that a population density, no matter how small, will always grow back to the saturation value. In the present context, that has the implication that if at any position X_0 the pesticide runs out before the pest density N has been reduced to zero, N will not only grow at X_0 but also diffuse from it to other X -values, creating a source of new pest population that especially in the case of the single application scenario can eventually destroy all control of the population. At the cost of introducing another free parameter, the model could relatively easily be extended to include a so-called Allee – effect into the logistic law that has the more plausible effect that the population dies out naturally if it falls below some small value.

The anticipated effect of such an elaboration would merely be to slightly lower the P_0 values required for extermination. Therefore we choose to keep the model simple, and consider the resulting slight overestimation of P_0 as a desirable error margin allowed in the result.

Another example of an effect that may be important in some contexts, is the build-up of resistance to the pesticide by the pest species; that might be incorporated by allowing L to be time dependent. Or pest individuals may become bait-shy, i.e. c might be time dependent. Incorporating such effects requires detailed knowledge of the relevant time dependency either explicitly or as additional differential equations to be included. Either of these effects will cause an increase of the pesticide density that is required. On the other hand, the P_0 value calculated here or a suitable increased value may be sufficient to ensure that eradication is achieved over a time scale that is short enough that L and/or c does not change significantly. In that case explicit inclusion of resistance or bait-shyness may be circumvented if only a rough estimate of the time scale over which those phenomena occur is known. Similar considerations hold when pesticide toxicity deteriorates, or there is consumption by non-target species. In all of these cases the present model may be used as a baseline model against which the need for further refinements are evaluated.

Our overall conclusion is that while results calculated from a general model such as this should not be taken to be definitive to the last decimal, it does allow some very pertinent general insight into pest control issues. It can be used as a guideline in the absence of more detailed knowledge or in order to build more detailed models of particular situations encountered in practice.

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