Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control[1]

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Economically important pests usually attack a crop or group of crops over a wide region in which there are geographic, local, and temporal variations in the environment. Effectiveness of any control program will therefore depend on the different responses of the crop, pest, and control organism to this pattern of environment. Usually the environmental heterogeneity is treated as an unavoidable complication in program evaluation, and attempts are made to work with "average" conditions.

The objectives of the control program do not depend only on the biology of the pest. We may want to achieve complete extirpation over part of the region, minimize average pest population over the whole region, hold total crop damage down to some acceptable level, or combine the costs of crop damage and control procedures to maximize some economic index. Therefore it is not possible to deduce an optimal strategy a priori. Rather, the purpose of this report is to show show that the pattern of environmental variation in space and time can be utilized in the control of pests and to indicate the information which is needed for the selection of the most promising predator.

MIGRATION AND EXTINCTION

Since the area over which control is sought is much greater than that of the local population, the control strategy must be defined for a population or populations in which local extinctions are balanced by remigration from other populations. This situation can be described as follows:

Let N be the number of local populations at a given time; let T be the total number of sites that can support local populations; M is the migration rate (the probability that migrants from any given population reach another site) and E is the extinction probability for a local population.

Then new populations are being established at a rate which depends on the migration rate times the probability that the site reached is vacant, or

$$m N \left(1 - \frac{N}{T} \right) \qquad \text{and}$$

populations are being eliminated at the rate EN. Thus the change of N with time is given by

$$\frac{dN}{dt} = mN(1 - N/T) - EN \qquad (1)$$

N will reach an equilibrium when the right side of the equation is 0. This gives the equilibrium level of

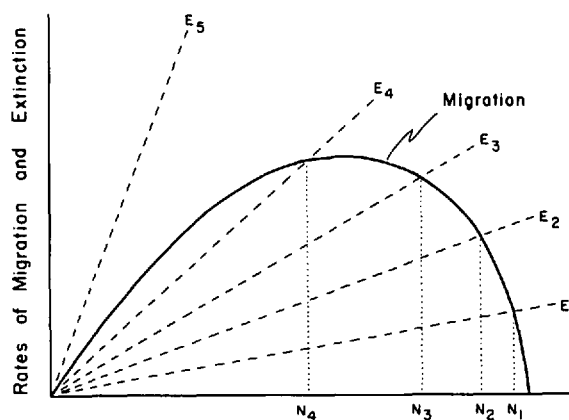$$\hat{N} = T \left(1 - \frac{E}{m} \right). \qquad (2)$$

Fig. 1. Equilibrium occurs at the N for which the migration and extinction rates are equal. When N is large, a given change in E (from E_1 to E_2) produces a small change in N. But near the flat part of the migration curve the same change form E_3 to E_4 has a greater effect. If the extinction rate exceeds migration as in E_5, the population disappears.

In Fig. 1 the process is shown graphically. We see that if E is small compared with m, N is near T, and changes in E have relatively little effect. But when E is large compared with m a small change in E is more important, and when E is greater then m the pest cannot persist.

The parameter E depends on uncontrollable environmental factors which vary in time and place, and also on control procedures. If E is varying in time then N does not reach an equilibrium level but fluctuates with some probability distribution. This probability density can be approximated by the method of diffusion equations (see Appendix 1) and to the extent that the assumptions are correct approaches a steady State distribution which is readily found. This distribution can be shown to have its peak value at

$$\hat{N} = T(m - \bar{E} - \sigma_E^2)/m. \qquad (3)$$

This reduces to (2) when E is constant. Since N is reduced by σ_E^2 best control is achieved for any given E when the extinction rate is most variable in time. If the factors which affect extinction are varying independently from place to place, local increases and decreases will cancel one another, and the overall variance from time to time will be small. Therefore it is to our advantage that control measures be applied simultaneously throughout the region. A parasitoid which can produce local extinction will be most effective if, for a given average effectiveness, it is least variable in space and most variable in time.

The migration parameter m is also subject to manipulation. It depends on the behavior of the insects, the average density of local populations, and the distance between sites. We do not know how m changes with distance, but for our purposes an exponential decay,

$$m = m_0 e^{-aD} \tag{4}$$

is sufficient to show the qualitative effects. Here D is the distance, a is a constant that depends on the scale of measure, and m_0 is the migration rate into an adjacent plot ($D = 0$). Suppose that a field adjacent to an infested field is reinvaded on the average in 2 days. The $m_0 = \frac{1}{2}$ Suppose further that a clear plot at a given distance D is reinvaded on the average in 10 days, so that m is 0.1.
Hence e^{-aD} is 0.2. Now let us double D. Then

$$m = m_0 e^{-2aD} \tag{5}$$
or
$$m = m_0 (e^{-aD})^2.$$

This would give
$$m = .5(.2)^2 = .02$$

and the waiting time to reinfestation is now 50 days. We can increase the distance between available sites in several ways. One would be elimination of alternate hosts for the pest. Or it is possible that the spatial variability of the environment is such that the same predator is unevenly effective in different sites. A predator which uniformly reduces all populations by half only halves m, but one which achieves nearly complete control in half the sites can reduce m severalfold. Finally, a given amount of insecticide in an integrated program might be most effectively distributed unevenly among sites to maximize D.

Note that the recommendations we would make to achieve control by reducing m are the opposite of those for control by increasing E. In the former case we want uneven effectiveness over space, in the latter we wanted uniform control in space and maximum variation in time. Therefore the formal analysis presented here does not lead to an unambiguous optimum strategy. Rather, we have shown that regional control may be attempted by acting on either local extinction or migration rates depending on the particular situation. For this approach to be relevant at all, we must first verify that in fact there is a distance-dependent migration rate, that after local extinction there is a waiting time of at least a week for reinvasion, that we are dealing with discrete populations.

LOCAL FLUCTUATION

Consider now a local population of size x which is growing at a rate
$$\frac{dx}{dt} = rx(1 - x/k) - px \tag{6}$$
where r is the environmentally determined intrinsic rate of increase, k is the carrying capacity of the environment, and p is the rate of predation by our control organism. Each of these parameters r, k, and p may be variables. Note that equation (6) is formally indentical with equation (1) although the terms have somewhat different meanings. Therefore if the only variable is p, x will have a probability distribution with a peak at
$$\hat{x} = k(r - \bar{p} - \sigma_p^2)/r \tag{7}$$
where p is the average predation rate and σ_p^2 its variance. For $r < \bar{p} + \sigma_p^2$ there is no peak and the population goes extinct.

We can also solve (6) directly as shown in appendix I. The solution is

$$x(t) = x_0 \Big/ \left\{ \exp\left(-\int_0^t r - p\,dt \right) \right.$$
$$\left. + x_0 \exp\left(-\int_0^t r - p\,dt \right) \int_0^t \exp\left(\int r - p\,dt \right) \frac{r}{k}\,ds \right\}. \tag{8}$$

If the average r is greater than the average p the population persists. The average x is reduced by all factors which increase the denominator of (8). However, only $p(\tau)$ is directly controlled by us through the choice of the control organism. (Integrated control programs could also modify r and k.) Clearly a large average p (high predation rate) reduces the average pest population. In addition a large variance in p reduces the average pest population and may even result in extinction if $\sigma_p^2 > \bar{r} - \bar{p}$. Therefore, it is not desirable to seek as our control organism one which does uniformly well in all the environments it is likely to encounter. Rather for a given average effectiveness we would choose that predator which is most variable in its predation, one which is specialized to a narrower range of environments provided this is compatible with its persistence. A further examination of equation (7) shows that a negative correlation between r(t) and p(t) is beneficial. The predator should not be chosen to do best when the prey is at its best but rather at its worst. Finally, a predator will be most effective if it is maximally adapted to the conditions at the beginning of the season. For this reason, the local population of predator most likely to be the best source for introduction need not be the one living in a similar climate as the region where it will be released. Rather we should look at climates that correspond to conditions at the start of the season in the area we are concerned with.

The treatment described here is too rough to be immediately applicable. For any real pattern of environment we could calculate the terms in equation (7) and evaluate potential control agents. However, at this point there is nothing to be gained by examining hypothetical cases to obtain numbers.

So far we have treated p as an environmental variable independent of x. But the rate of predation depends on the size of the predator population as well as the physical environment. Suppose the predator population expands with the prey, so that p(t) could be replaced by $p_0(t)x$. Then equation 6 becomes
$$\frac{dx}{dt} = rx(1 - x/k) - p_0 x^2. \tag{9}$$
Now the probability distribution of x has a peak roughly at $\dfrac{rk(1 - 2\sigma_p^2)}{r + \bar{p}k}$ when σ_p^2 is small. Thus in this situation too a variable p results in better control. However, the solution of equation (8) by the procedure in appendix I gives

$$x = x_0 \Big/ \left\{ \exp\left(-\int r(s)ds \right) + x_0 \exp\left(-\int r(s)ds \right) \right.$$
$$\left. \times \int \exp\left(\int r(s)ds \right) \left[\frac{r}{k} + p \right] dt \right\}. \tag{10}$$

Now this is minimized by p being concentrated in the period when the uncontrolled pest population would be greatest, usually late in the season. The source of the best control population would therefore be different from the previous case. The alternative models used here assume either that the predator abundance is independent of the prey or that it is proportional to the prey. The former case

corresponds to situations in which the predator has several hosts and is therefore not greatly changed by prey abundance, or to predators with much slower development or even fewer generations per year than the host so that it does not increase rapidly enough with prey density. The latter model makes the assumption that the predator is responding rapidly to its host population. But both models have the predation coefficient p depend only on physical environment. They ignore predator saturation, search difficulty, and other factors that would make p a function of x. The manner in which the model would have to be modified for particular cases will be dictated by the cases.

The treatment described considered population growth as a continuous process with overlapping generations. In many cases the pest has only one ot two discrete generations per year. Then a more exact method would be a discrete model in which population size in generation two is computed from pest and predator populations in generation one. When we deal with specific cases such a representation is likely to be preferable, but at the present stage of investigation the qualitative relations are brought out by the models used.

SELECTION OF PREDATOR GENOTYPES

Once an analysis of the population dynamics and environment enables us to determine the optimum properties of the predator population, the next step is to produce such a population. We have just indicated that the optimum predator may be adapted either to the early or later parts of the season depending on the dynamics of predator-prey relations. Therefore, what is best for us is not necessarily what is best for the predator, and it would be naive to expect that the best predator is the one already found in a similar region. Nor can we throw a lot of populations together, release the mixture, and expect natural selection to mold it into an optimal control organism.

In fact, the response of the population to natural selection may be deleterious even to the predator itself. The reason for this is that when a population is being selected in a varying environment its current gene frequency depends on the previous environment, whereas its survival value depends on the present environment. Therefore fitness is increased only if there is a strong positive correlation between the environments of successive generations. And this is possible only if there are many generations per year. Where there are few generations the correlation will be negative. For example if there are two generations in the course of a summer which begins hot and dry and ends cool and wet, the first generation will be selected for survival in dry heat. Its offspring will be even better adapted to dry heat, but will have to face a wet cool environment. Its offspring, selected for the cool wet conditions, will face the dry heat of early summer. The final result is a loss of fitness if there is genetic variability for a survival in these environments. Natural populations therefore will not normally adapt to such environmental fluctuations by a genetic response to selection. Rather each population will fix those genes which are the best compromise between the conditions at different times and will develop physiological or behavioral adaptations that vitiate the need for genetic change. But the genes which are fixed will be different in different populations, so that a mixture of populations will create a gene pool subject to deleterious fluctuations.

Hence it is undesirable to release a population with too much genetic variance. Rather, we should mix lines for the purpose of selection in the laboratory and then release the selected population.

The deleterious effects of response to selection in a rapidly changing environment are a danger to the control organism but offer a means of reducing pest populations by increasing their genetic variance with respect to traits whose selective value fluctuates. This is the general principle behind Klassen's concept of conditional lethality as a control technique. I have given more quantitative treatment of this problem (Levins 1965).

CONCLUSIONS

The study of population processes in a heterogeneous environment demonstrates the fallacy of several common sense notions about pest control.

1. The best control organism is not necessarily one which is uniformly effective in all the spatial or temporal variants of the environment. On the contrary we have shown for several models that a relatively specialized predator may give the best long-term control.

2. The best predator is not necessarily adapted to the same range of environments as the pest it is to control. Depending on the particular situation we may want a predator adapted to the very early or to the late season's climate, and there may be an advantage to having its adaptive level negatively correlated with that of the pest.

3. The optimal predator is not necessarily one from the most similar climate.

4. We cannot expect natural selection in the field to produce an optimal predator provided we supply enough genetic variation. On the contrary, some kinds of genetic variance will be positively deleterious. Therefore a heterogeneous gene pool should be selected in the desired direction in the laboratory prior to introduction.

Anybody who has worked with any real insect will recognize numerous ways in which each of our model is unrealistic or inapplicable for his animal. We have chosen to use these simplified models to demonstrate the qualitative nature of the processes, indicate possibilities, show what isn't necessarily so, and suggest how the properties of environmental heterogeneity can be considered in deciding on a control strategy. The mathematical analysis itself does not prescribe that strategy. Theoretical investigation is no substitute for entomological knowledge but may be a valuable supplement.

Appendix I

Several mathematical methods may be used to study the processes defined by the equation

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{k}\right) - px \qquad (11)$$

where any of the parameters r, k, or p may vary. A direct solution proceeds by the substitution

$$y = \frac{1}{x} \qquad \frac{dy}{dt} = \frac{1}{x^2}\frac{dx}{dt}.$$

Dividing (1) by $-x^2$ we obtain

$$-\frac{dx}{dt}\frac{1}{x^2} = -(r - p)\frac{r}{x} + \frac{r}{k}. \qquad (12)$$

This becomes

$$\frac{dy}{dt} = -(r - p)y + r/k. \qquad (13)$$

Adding (r-p)y to both sides and multiplying by the integrating factor

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$$\exp\left(\int r - pdt\right)$$

We obtain

$$\exp\left(\int r - pdt\right)\left[\frac{dy}{dt} + (r - p)y\right]$$

$$= \exp\left(\int r - pdt\right)r/k. \quad (14)$$

But the left side is readily seen to be

$$\frac{d}{dt}\left\{\exp\left(\int r - pdt\right)y\right\}. \quad \text{Therefore}$$

we can integrate both sides and divide by $\exp\left(\int r - pdt\right)$

Then

$$y = y_0 \exp\left(-\int r - pdt\right) + \exp\left(-\int r - pdt\right)$$

$$\times \int \frac{r}{k}\exp\left(\int r - pds\right)dt. \quad (15)$$

Finally, replacing y by $\frac{1}{x}$ and y_0 by $\frac{1}{x_0}$ we have the solution

$$x = x_0 \Big/ \left\{\exp\left(-\int r - pdt\right) + x_0 \exp\left(-\int r - pdt\right)\right.$$

$$\left. \times \int \frac{r}{k}\exp\left(\int r - pds\right)dt\right\}. \quad (16)$$

In the alternative model,

$$\frac{dx}{dt} = rx(1 - x/k) - p_0 x^2 \quad (17)$$

The same substitution $y = \frac{1}{x}$ and division by x^2 gives

$$\frac{dy}{dt} = -ry + \frac{r}{k} + p_0. \quad (18)$$

Proceeding as before,

$$\frac{d}{dt}\left\{\exp\left(\int rdt\right)y\right\} = \exp\left(\int rdt\right)\left(\frac{r}{k} + p_0\right) \quad (19)$$

and

$$y = y_0 \exp\left(-\int rdt\right) + \left\{\exp\left(-\int rdt\right)\int\left[\left(\frac{r}{k} + p_0\right)\right.\right.$$

$$\left.\left. \times \exp\left(\int rds\right)\right]dt\right\} \quad (20)$$

so that

$$x = x_0 \Big/ \left\{\exp\left(-\int rdt\right) + x_0 \exp\left(-\int rdt\right)\right.$$

$$\left. \times \int\left(\frac{r}{k} + p_0\right)\exp\left(\int rds\right)dt\right\}. \quad (21)$$

This method gives an exact solution to the differential equation and is therefore as valid as the model. If the probability distributions of the variables r, k, and p are known we can calculate the probability distibutions of population size. But there is not always an available substitution such as we used. Kimura (1964) has introduced the method of diffusion processes to go directly to the probability density distribution of variables defined by differential equations. He defines M(x) as the mean change in x as a function of x, and V(x) as the variance of the change conditional on x. Then if the random component has not correlation between successive intervals he gives the formal solution for the probability density of x:

$$\phi(x) = \frac{c}{v(x)}\exp\left(2\int\frac{m(x)}{v(x)}\right)dx. \quad (22)$$

The peak of ϕ is shown to be the solution of

$$M(x) = \frac{1}{2}\frac{dv}{dx}. \quad (23)$$

This method gives the final steady state distribution after a long time and requires that the random variations are not time-dependent. It is therefore only a crude description of the results of the process but more readily shows the influence of the random variation of the outcome.

References Cited

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KANSAS ENTOMOLOGICAL SOCIETY
(Central States Entomological Society)

The 45th annual meeting of the Kansas Entomological Society was held on May 2-3, 1969, at the University of Nebraska Center for Continuing Education.

Eighty-four persons attended a banquet on Friday evening, May 2, at which Robert H. Nelson, retired *Executive Secretary* of the ESA, was the featured speaker. Mr. Nelson was presented with a certificate signed by the Nebraska governor stating that he had been commissioned an Admiral in the Nebraska Navy.

The meeting was presided over by *President* Earle Raun, University of Nebraska. Fourteen papers were presented in two sessions. The reports of the *Editor* Peter Ashlock and *Secretary-Treasurer* Robert B. Mills were approved. The President reported that Dr. R. E. Hill had assumed the position on the editorial board left vacant by the death of Dr. Reginald H. Painter.

A motion was presented and passed to raise regular page charges of the Journal to $8 per page and to increase dues of individuals (except students) by $1.00.

Officers for 1969-1970 were elected. They are:

President: H. D. Blocker Department of Entomology Kansas State University
President-elect: Floyd D. Miner, University of Arkansas.
Secretary-Treasurer: Gerald E. Wilde, Kansas State University.

The newly-elected *President*, H. D. Blocker, announced the 1970 annual meeting at Kansas State University, and invited all to attend. Further information about the Society and its publication and membership may be obtained by writing the *Secretary-Treasurer*, Gerald E. Wilde, Kansas State University, Manhattan, Kansas 66502.