# 15
Man Versus Pests

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15.1 Introduction

Pest control constitutes an ancient war, waged by man for 4000 years or more against a great variety of small and remarkably persistent enemies. Surprisingly, although the war is old, its·dynamics seem poorly understood. Even the objectives, at least of man, are ill-defined. It is as though man, in the heat of the battle, has not had the time to analyse in any sophisticated fashion the conflict in which he finds himself. Battles have been won and lost but lessons have been learned slowly and painfully. It is only in recent years that people have begun to ask the fundamental questions of principle and to raise doubts about implicit beliefs and objectives.

The term pest connotes a value judgement. A pest is a living organism (insect, fungus, bacterium, weed, etc.), which causes damage or illness to man or his possessions or is otherwise, in some sense, 'not wanted'. Thus, at the outset, pest control is a problem for the social sciences and in particular for applied economics. Simply stated, the problem is to assess whether the damage or illness caused by a pest can be reduced in a manner which is profitable or satisfactory. Formal economic analysis requires that the damage or illness be quantified, usually in monetary terms, so that the potential benefits ensuing from control of the pest can be compared with the costs involved. Such costs may be economic, social or environmental.

The classical economist's tool for tackling this kind of problem is marginal analysis (Fig. 15.1). A control action is termed rational when its cost is less than or equal to the net increase in revenue it produces and is economically most efficient (i.e., most profitable) when the marginal cost of control equals the marginal revenue produced (Southwood and Norton, 1973). If we consider an agricultural crop, then the object of pest control is to maximize the quantity

$$Y[A(S)]\ P[A(S)] - C(S). \tag{15.1}$$
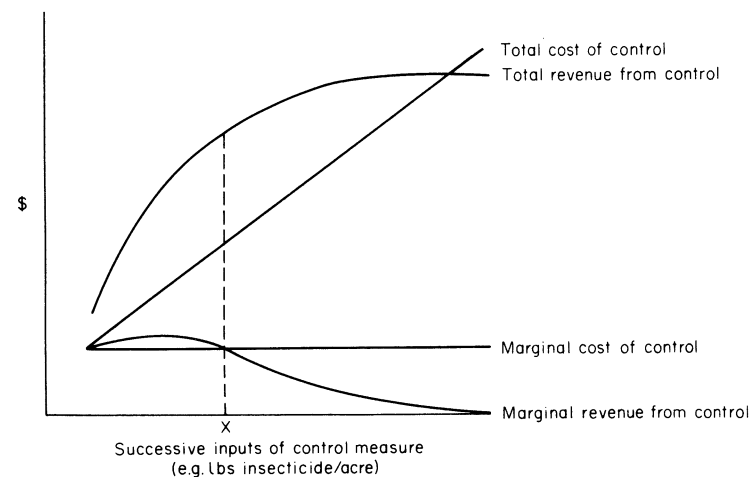
Fig. 15.1. Cost and revenue curves for pest control. The marginal curves give the increment in total cost or revenue for each successive input of control. Profit is greatest when marginal revenue equals marginal cost. (After Southwood and Norton, 1973.)

This expression, which subtracts the cost of control from the revenue, comprises four important functions.

(1) The quantity damage function $Y[A(S)]$, which relates yields to levels of attack $A(S)$.

(2) The quality damage function, $P[A(S)]$, which relates prices to levels of attack $A(S)$.

(3) The control function, $A(S)$, which relates levels of pest attack to the range of control strategies available S.

(4) The cost of control function, $C(S)$, which relates costs of control to the control strategies S.

Figure 15.2 illustrates how the functions are linked.

To this point analysis of the problem has been in purely economic terms. But, by definition, pests are also living organisms and as we dissect the constituent functions and investigate their properties biological, and in particular ecological, knowledge dominates the analysis. Populations of organisms—as the early chapters of this book make clear— respond, often in a complex and dynamic fashion, to outside interference. Only rarely will the level of pest attack be a simple function of control strategy. The kill produced by a pesticide may evoke a density dependent response, so that the pest population rebounds,
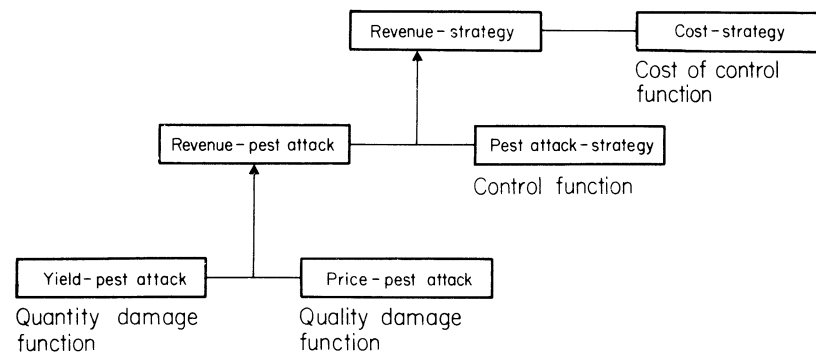
Fig. 15.2. Constituent functions of the relationship between revenue and cost of control.

sometimes to a new and higher level. Pesticides, for example, may kill off those predators and parasites which have an important function in regulating pest numbers. In the longer term there may be genetic responses. Pest populations may develop resistance to control, notably to chemical pesticides.

The damage function may also reflect complex ecological processes since the object of pest attack—usually a crop plant, domestic animal or man himself—is also a living organism. The outcome of attack is thus the product of the dynamic interaction of two or more populations. For example, the damage caused by a weed infestation is a function of competition between the weed and the crop population. Where crops are directly attacked by pests the outcome is complicated by the frequent ability of crops to compensate for low levels of attack. Similarly, where pests are vectors of disease, the ensuing incidence of illness in the animal or human population will depend on such features as the age structure and the level of immunity present.

In this chapter I shall discuss more fully how modern ecological and economic analysis illuminates the problem of pest control. I describe, in the next section, how the short and long term dynamics of pest populations determine the choice of appropriate strategies of control. I then show how knowledge of the damage function modifies this choice. Finally, I describe how optimal solutions to pest control problems can be theoretically attained and discuss the more difficult task of designing pest management systems which are resilient in both ecological and economic terms.

15.2 The control function

In traditional text books, pests are classified and dealt with in taxonomic order or according to the crop or other object of attack. A potentially more illuminating classification is according to the spectrum of ecological strategies which are described by Southwood in chapter 3. On this basis we can then speak of r-pests and K-pests with, in between, 'intermediate' pests.

15.2.1 r-pests

The word pest immediately conjures in the mind the image of a ravaging swarm devastating all before it and moving on; indeed the word derives from the Latin *pestis*, for plague. The classic pests which conform to this image, rats and locusts or the rusts of wheat for example, all show the typical r-strategy features of high potential rates of increase and strong dispersal and host finding ability.

An illuminating example of an r-pest is the plague caterpillar, *Tiracola plagiata*, of South East Asia. This belongs to the moth family Noctuidae which contains many other r-pests, including the armyworms, cutworms and bollworms. The adult moths are strong fliers and capable of laying batches of 1000 eggs or more. The life cycle from egg to adult takes only 30 to 40 days. Conway (1971a) describes an outbreak of this species in an area of cleared primary rainforest in Northern Borneo. A strip of forest about a quarter of a mile long had been cleared some five years earlier, but had been abandoned and was in the process of passing back through the long succession to primary forest. At the time of the outbreak the vegetation consisted of a variety of secondary forest trees standing six to fifteen feet high. When first seen the outbreak, a huge army of caterpillars comprising several million individuals, had progressed half way along the strip, removing the leaves from virtually every plant. Since the land was abandoned, with no value attached to the vegetation, the caterpillars were not pests. However, at the end of the strip was a young plantation of cocoa which had also been planted on cleared forest land. The population was not sprayed and two weeks later all the caterpillars pupated in the soil close to the cocoa plantation. Only a few adult moths emerged from the pupae, the majority dying from a viral or other infection, and the cocoa was spared. But in other countries in South East Asia the plague caterpillar has become a serious pest of cocoa.

The species is indigenous to the region, living within the boundaries of the primary rainforest, but adopting an r-strategy so as to exploit the scattered ephemeral clearings in the forest which, in the absence of man, are created by lightning strikes or by the overflowing of rivers. It is a species which is catholic in its food preferences, attacking many of the plants, themselves r-strategists, which characterize the early stages of secondary succession. This adaptation is clearly an excellent pre-adaptation to the role of agricultural pest. With the planting in the cleared forest of annual or perennial crops, species such as the plague caterpillar continue to pursue their life strategy but in a habitat that is no longer temporary.

This pattern of emergence of an r-pest, in this case from the tropical rain forest, has occurred many times in human history and in every part of the world, although in the industrialized, temperate regions the origins of the r-pests may be obscure. Agricultural and industrial development has greatly increased the availability of favourable habitats for r-strategists. For example, the natural habitat of the mosquito *Aedes aegypti,* which is a vector of yellow fever, is the primary forest where it breeds in the water contained in the forks and hollows of forest trees. Its invasion of urban areas and the accompanying spread of the disease it carries is a result of the numerous favourable sites provided by man, such as water containers, discarded tin cans, automobile tyres, etc., which furnish similar and often better breeding conditions than occur in nature. For this species there is evidence that there has been a shift from K- to r-strategy accompanying its move to the urban environment (Schlosser and Buffington, 1977). In comparable fashion mismanagement of the semi-arid regions of Africa and Asia, through over-grazing and repeated burning, has increased the availability of breeding sites for various locust species. The complicated and unique life cycle of the locust has evolved to exploit the ephemerally favourable habitats of semi-arid regions; human activity has both raised the probability of locust outbreaks occurring and extended their timespan.

In the temperate regions of the world perhaps the majority of pests are towards the r-end of the spectrum; they are species which have adopted this strategy in order to exploit the essentially short-lived plants which depend on each annual growing season. Often, as Southwood (1977b) points out, such r-pests spend part of the season at low population levels in one habitat, for example the sorghum midge on wild grasses, and then explode later onto the growing crops.

15.2.2   K-pests

K-pests, by contrast, have low rates of potential increase, greater competitive ability and more specialized food preferences.

A good example is another Southeast Asian pest, the bark borer, *Endoclita hosei,* which is a member of the Hepialidae, a family of large, slow flying moths with low fecundity and long life cycles. In nature the larvae bore in the trunk of a secondary forest tree, where they seem to cause little damage. But they also attack cocoa and there a single larva boring in a cocoa tree will cause its death. Thus even small populations can cause considerable damage.

Most organisms which show extreme K-strategies do not become pests; their specialized niche is not of interest to man. However, if man does expand the niche or provide a new niche of very similar composition then K-strategists can become important pests. On their natural primary hosts K-pests may cause little harm; the numbers are usually low and the damage is insufficient to cause the death of the host or seriously impair its reproductive capacity. K-pests thus act more in the manner of parasites than predators. Indeed many of the internal parasites of vertebrates such as the tapeworm or the schistosomes are characteristic K-pests.

Nevertheless even if the damage, at least in terms of biomass removed, is small it may be unacceptable to man when it affects him or his crops. Southwood (1977b) cites the example of the skylark which in eastern England often removes a small number of seedling sugar beet in the early summer. Until recently multigerm beet fruits were sown and the excess seedlings subsequently thinned by hoeing so that the skylark depradations were insignificant. Now fruit with a single seed is drilled to a stand and the skylark is a pest.

The codling moth provides another example of a pest towards the K-end of the spectrum. Its damage to fruits is biologically insignificant since few are attacked and normally they remain attractive to birds and mammals and the seeds are dispersed in the usual manner; but on cultivated fruit crops, such as apples, the damage becomes commercially important because of the high value we place on unblemished fruits.

The contrast between r- and K-pests is well illustrated by two important pests, the brown planthopper and the green leafhopper of rice in Japan (Table 15.1). For neither species are the indigenous parasites or predators (mostly spiders) significant in regulation. Each year the

Table 15.1. Comparison of two rice pests from Japan. (Data from Kuno and Hokyo, 1970.)

	Brown planthopper (*Nilaparvata lugens*) r-selected	Green leafhopper (*Nephotettix cincticeps*) K-selected
Population increase		
Generation time	similar	
Mean fecundity per female	429	47.6
Rate of growth in season	1855 ×	110 ×
Annual fluctuations		
Ratio highest to lowest numbers in peak generation	90.6	2.4
Regulation		
b-value (see Table 2.2,D)	$b \approx 0$	$b \approx 1$
Equilibrium density per hill	572	13.5
Spatial distribution	Patchy	Homogeneous
Mean crowding (Lloyd, 1967) (at density 20 per hill)	50	25
Vagility	Invasive, from China; density dependent migration	Local, within fields
Damage	Sapsucking causing loss of growth	Transmission of rice dwarf virus

brown planthopper invades from China and builds up rapidly in numbers, the eventual population size being primarily a function of climatic conditions. As the density increases the rice plants deteriorate and a growing proportion of the adults are of the large winged, migratory form. By contrast the green leafhopper persists throughout the year at a much lower, more stable level brought about by intraspecific competition. Both hoppers suck the sap of the rice plants, but the green leafhopper is never abundant enough to cause direct damage and is only a pest because it transmits a virus disease of rice.

15.2.3 *Intermediate pests*

Probably the great majority of pest species lie between these two extremes and can be classified as intermediate pests. As Southwood points out in chapter 3, there is a continuum, in nature, from r-strategist to K-strategist and a sharp demarcation between the categories is unrealistic. Intermediate pests may show any mixture of features, but probably their most important characteristic, from the viewpoint of

control, is the high degree to which they are normally regulated by natural enemies (see Fig. 3.6). Insects may be controlled by parasites or predators, including other insects, nematodes, birds and mammals, and by insect pathogens; weeds by herbivorous insects and plant pathogens; and plant and animal pathogens themselves by other pathogens.

Commonly this degree of natural regulation is sufficient to keep the damage caused to crops or livestock or man below a level at which artificial control is required. But the regulation may break down and the insect or weed or pathogen 'escape' to become a pest. This may be a seasonal phenomenon or may only occur every few years, but often it is a permanent or semi-permanent change resulting from human intervention.

Many temperate aphids, lying towards the extreme r-end of the intermediate spectrum, may annually escape following the disruption to natural enemy regulation caused by the winter. For example, the bean aphid which overwinters on the spindle tree may in some years outstrip the build-up of its enemies (general predators such as ladybird beetles, hoverflies and lacewing larvae), given a good starting population and favourable weather in the spring. Often the enemies will then only re-establish control when the aphid population has already crashed. In other years conditions may favour the enemies and the pests will be held below the release point.

The longer-cycle, periodic release from natural enemy regulation is typified by many forest pests such as the spruce budworm. The detailed analyses of the dynamics of this pest (Peterman et al., 1979) suggest that the epidemics have followed long endemic periods (approximately 40 years) in which the absence of severe budworm damage has resulted in a maturing of the forest and a change in the tree species composition. The resulting increase in foliage and branch density then permit an explosive increase in budworms sufficient to allow their escape from their predators (Fig. 15.3).

The best known intermediate pests are those which have been imported to new regions of the world, but in the process have left their natural regulating agents in the country of origin. The examples of classical biological control, where the regulation has been reimposed by the deliberate introduction of the original natural enemies, fall in this category. One of the earliest and most quoted instances is of the cottony cushion scale introduced into California, probably on wattle from Australia in the 1860's, and controlled with spectacular success by the sub-

sequent introduction of two of its natural enemies, the vedalia beetle and a parasitic wasp. Introduced pests, whether r or intermediate in strategy, are particularly important in North America. Over 60 per cent of the important insect pests of North America and of the weeds of Canada are introduced, mostly from Europe.
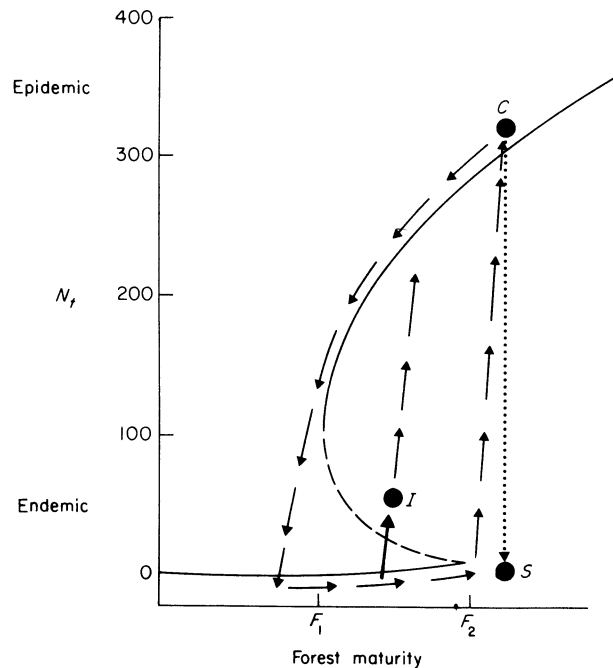
Fig. 15.3. Dynamics of spruce budworm as a function of forest maturity. Epidemics occur either because the forest matures beyond point F_2 or immigrants boost the population to point I. Spraying may only hold the population at an unstable point S. (After Peterman *et al.*, 1979.)

The final category of intermediate pests comprises all those pests which have become important because man-made changes have eliminated or reduced the efficiency of their natural enemies. Included are the 'secondary' or 'upset' pests which are the result of the inadvertent effect of pesticides on the natural enemies of hitherto insignificant pest species. Some of the earliest and now most serious upset pests are the spider mites, which attack various fruit trees. These mites first became important as a consequence of the application of tar oil winter washes to the trees. The tar oil destroyed the mosses and lichens which

gave protection to the hibernating predators (ladybird beetles and predacious mites) of the spider mites. Since the Second World War the problem has become worse because of the direct kills of the predators by modern insecticides.

15.2.4   *Strategies of control*

This conceptualization of pest strategies has important implications for control, since each different ecological strategy clearly invites an appropriate strategy of control. In practical terms a pest profile can be drawn up for the crop or host being attacked (Table 15.2) and used as a first step towards choosing a mix of control strategies.

Table 15.2. Crop pest profiles for cocoa in Northern Borneo and dessert apples in the U.K.

	Cocoa	Apples
r		
Intermediate	Bagworms	Red spider mite
	Nettle caterpillar	Winter moth Rosy apple aphid
	Cocoa looper	Apple grass aphid
	Branch borer	Codling moth Bullfinch
K	Bee bug Ring bark borer	Tortrix Apple sucker Apple blossom weevil

Five major techniques of pest control are currently practised.

(1) *Pesticide control:* the use of chemical compounds to kill pests directly.

(2) *Biological control:* the use of natural enemies, viruses, bacteria or fungi, either by augmenting those already present or by introducing species from other regions and countries.

(3) *Cultural control:* the use of agricultural or other practices to change the habitat of the pest.

(4) *Plant and animal resistance:* the breeding of animals and crop plant varieties resistent to pests.

(5) *Sterile mating control:* the sterilisation of pest populations by various techniques to reduce the rate of reproduction.

Unfortunately the history of pest control has been dominated by the search for panaceas. With the advent of organochlorine and organophosphorus insecticides at the end of the Second World War, it was believed that most pest problems would be quickly solved. But within 15 years the limitations of pesticides had become widely apparent. Control programmes failed or sometimes created worse problems than they solved because of the effects of pesticides on natural enemies, or the development of resistance. Moreover evidence grew that many pesticides pose serious hazards to wildlife and in some cases to man himself. Biological control became the new panacea. When it, too, was seen to be limited in scope, attention shifted to sterile mating techniques and most recently has focussed on the development of animal and crop resistance. An attempt at a more rational approach began with the concept of integrating biological and chemical control. Latterly the term integrated pest management has been used to denote the mix of all appropriate techniques in a given situation (Apple and Smith, 1976). However, as Way (1973) points out, it has been largely an empirical approach; successful integrated control programmes have depended on a combination of insight and trial and error. There has been little attempt, so

Table 15.3. Principal control techniques appropriate for different pest strategies.

	r-pests	Intermediate pests	K-pests
Pesticides	Early widescale applications based on forecasting	Selective pesticides	Precisely targeted applications based on monitoring
Biological control		Introduction or enhancement of natural enemies	
Cultural control	Timing, cultivation sanitation and rotation	→ ←	Changes in agronomic practice, destruction of alternative hosts
Resistance	General, polygenic resistance	→ ←	Specific, monogenic resistance
Genetic control			Sterile mating technique

far, to define a theoretical basis for choosing appropriate strategies. Recognition of the r–K categorization, I believe, provides a step in this direction (Table 15.3).

r-pests are the most difficult to control. Their frequent invasions and the massive damaging outbreaks they are capable of producing require a fast and flexible response. Natural enemies cannot provide efficient control and pesticides remain the most appropriate means of attack. But because r-pests are resilient to disturbance, rebounding after even very heavy mortalities, pesticides have to be used more or less continuously. Resistant varieties of crops and animals may provide some protection but if it is to persist resistance has to be of the general, polygenic type providing, through broad physiological mechanisms, an overall reduction in the rate of increase of the attacking pest or pathogen (Browning et al., 1977). Many r-pests, such as the cereal rusts, regularly produce new races which will overcome narrow based resistance. Cultural control may also be of help where it serves to reduce the likelihood and size of the pest invasion. Early or late planting, for example, may permit the crop to escape; rotation prevents the build up of pests such as nematodes, while against r-selected weeds the production of weed-free seed and mechanical cultivation are appropriate.

By contrast K-pests are theoretically more vulnerable. They may be forced to low population levels and, in some situations, eradicated; for this reason they are the most suitable targets for the sterile mating technique. Pesticides may also give efficient control where small populations cause high losses, for example when fruit is blemished, but they need to be carefully timed and precisely applied. In general, because K-pests are specialists occupying narrow niches in the man-made world, they are most vulnerable to strategies aimed directly at reducing or eliminating the effective pest niche. Resistant animal breeds or crop varieties are a powerful approach to K-pests since permanent success can often be attained with simple, monogenic resistance. Cultural control may also be very effective; small changes in agronomic practices such as planting density or pruning may render a crop unattractive, or the K-pest may be greatly reduced by eliminating its alternative wild host.

Biological control has its greatest pay-off against intermediate pests and this must be the preferred strategy in every case. If pesticides have to be used they should be selective either in their mode of action or in the way they are applied so that only the target pests are affected, and not their natural enemies and those of other pests. It also, of course,

follows that when r, K and intermediate pests coexist the pesticide applications against the r- or K-pests should not interfere with the biological control of the intermediate pests. Indeed the successful control of the intermediate pests on a crop or host should be seen as the initial taget, with which the strategies for control of the remaining r- and K-pests are then integrated.

15.2.5   *Pesticide resistance*

In much the same way that crops and animals can be artificially bred for resistance to pests, given sufficient time, pests can evolve resistance to virtually all of the control techniques devised by man (Corbett, 1978). The most serious contemporary problem, however, is the rapidly growing resistance of pests to pesticides. This is not a new phenomenon: in 1908 the San Jose scale was recorded as resistant to lime sulphur. But resistance has accelerated with the introduction of modern pesticides and more intensive use. Today there are 364 species of insect and mite resistant to one or more insecticides (Fig. 15.4) and resistance has occurred against every one of the insecticide groups, including the synthetic pyrethroids, juvenile hormone analogues and growth regulators,
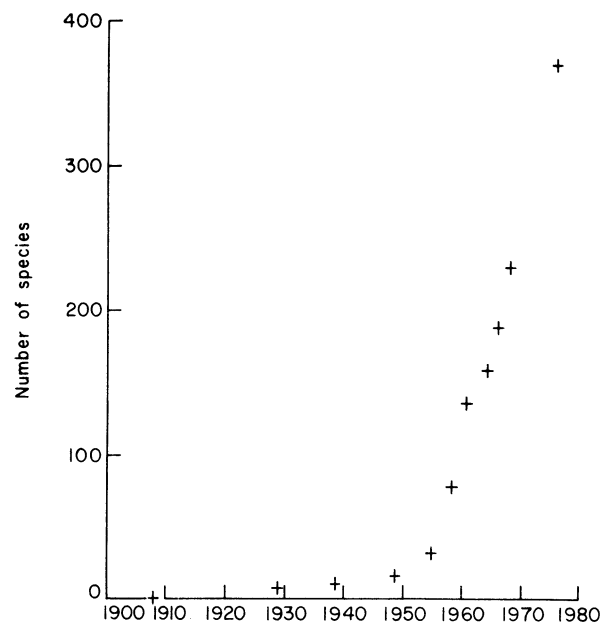

Fig. 15.4. Numbers of insect and acarine species resistant to one or more insecticides.

introduced in the last 5 years. There are fewer pathogens (67) and weed species (19) showing resistance, but certain fungicides and herbicides are very vulnerable.

Genes conferring resistance are often present in a pest population before the pesticide is applied and whether or not the population becomes resistant depends on the intensity of pesticide selection. In general, the more frequent the applications, the higher the kill produced and the more thorough the coverage of the population, then the more rapidly resistance develops. For these reasons resistance is more common among r-pests since their generally shorter generation times and high rates of population growth necessitate frequent pesticide treatment. Indeed the 23 insect and tick species which show resistance to all four of the major insecticide groups are all strongly r-selected. Resistance in mosquitoes has seriously hampered malaria control, while resistance in the cotton bollworm and tobacco budworm caused a near collapse of cotton production in the U.S.A. and great reductions in cotton acreage in Mexico.

It seems very unlikely that pesticides, and in particular insecticides, will be discovered against which pests cannot evolve resistance. The only practical way of minimizing the problem, and so extending the useful lifetime of existing or new pesticides, is to reduce the selection pressure. There is no shortage of tactical options for affecting the rate at which resistance develops. The dosage, distribution and timing of pesticide applications are important parameters, but unfortunately tactics for delaying resistance cannot be field-tested since resistance is essentially undetectable in its early stages. Moreover, resistance characteristically develops on a regional or even national scale, requiring a strategic rather than tactical response. These difficulties make the problem one which is particularly suited to mathematical modelling techniques.

Comins (1977a) has developed a model, based on a number of simplifying assumptions, which seems nevertheless sufficiently realistic as to provide guidelines that are generally applicable. The model assumes that the population is large and homogeneous with discrete generations. The resistance gene is also assumed to operate monofactorially and equally in both sexes. On these assumptions the typical pattern of development of the resistance gene occurs in three phases (Fig. 15.5). In the first phase, when the pesticide is not being applied, the resistance gene is likely to be a liability and hence will exist at a low equilibrium frequency determined by the opposing forces of mutation and adverse selection. In the second phase, once pesticide selection has commenced
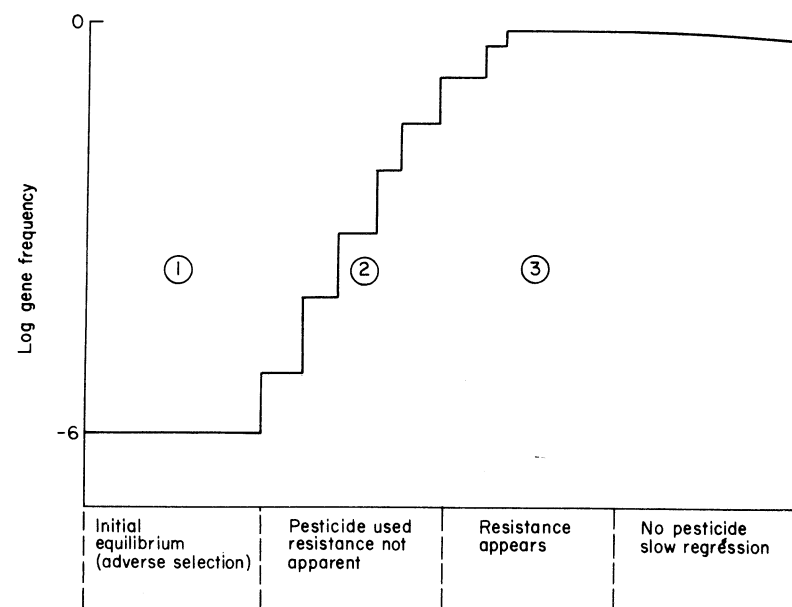
**Fig. 15.5.** The phases of development of pesticide resistance in a pest population. (After Comins, 1980.)

the resistance gene spreads rapidly through the population although still below the level at which control efficiency is noticeably reduced. Finally however, the crisis occurs; control measures fail, resistance is detected and after perhaps a period of increasing dosages, the pesticide is abandoned.

By concentrating on the second phase of resistance development it is possible to make a further important assumption, namely that the genes being selected exist at low frequencies. From this it follows that heterozygotes greatly outnumber homozygotes. Thus, in phase two, partially or fully dominant genes will be selected on the basis of the degree of resistance they confer in heterozygous individuals and this will be the most important factor determining the rate of development of resistance.

One of the most important questions that can be answered by this simple genetic model concerns the advisability of aiming for a high or low percentage mortality of the target pest population.

If we assume that 10 per cent of the target population escapes contact with the pesticide (there is some form of refuge due to incomplete pesticide coverage, for example) but otherwise every pest receives an

equal standard dose, then the selection factor for heterozygotes (ratio of heterozygote to susceptible survival) is as shown in Fig. 15.6. At low pesticide dosages it is high but at high dosages it declines. This implies
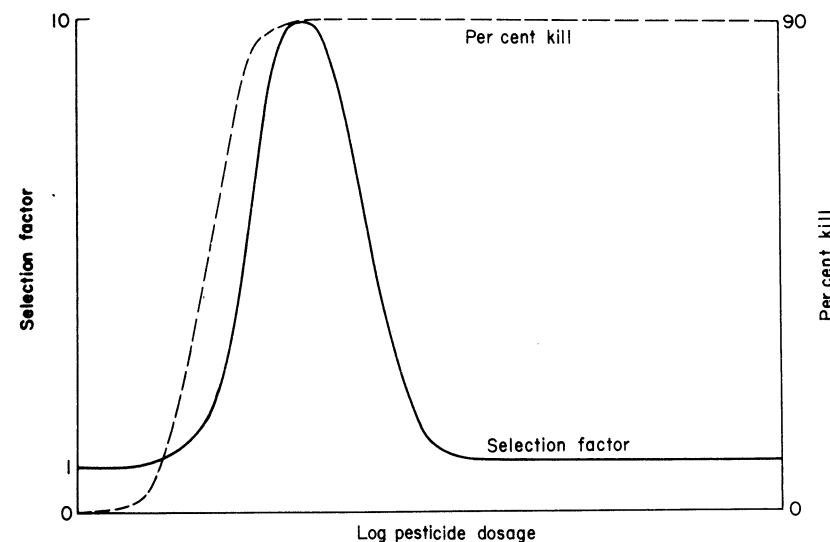

Fig. 15.6. Selection factor for heterozygotes (ratio of heterozygote to susceptible survival) as a function of pesticide dosage, where 90% of the pests receive the standard dosage. (After Comins, 1980).

that given a sufficiently high individual pesticide dose the resistant heterozygotes will be killed off, thereby permitting control of the pest population with negligible selection of the resistance gene.

This analysis suggests that, where individual dosage can be precisely controlled (for example when dipping cattle with non-residual acaricides against cattle ticks), resistance may be delayed by high kills.

In practice, however, the individual dose cannot be closely controlled under most field conditions. Applying more pesticide will simply tend to increase the proportion of the population subject to a low dose and this will simply accelerate the rate of selection. This situation can be conceptualized by a model which assumes that the pesticide, in effect, diffuses out from its point of application and individual pests or their descendants have a decreasing probability of entering the treated area (within a time that is short relative to the rate of resistance selection) the further they are from the centre. This model produces a graph of the form shown in Fig. 15.7 where the selection factor does not
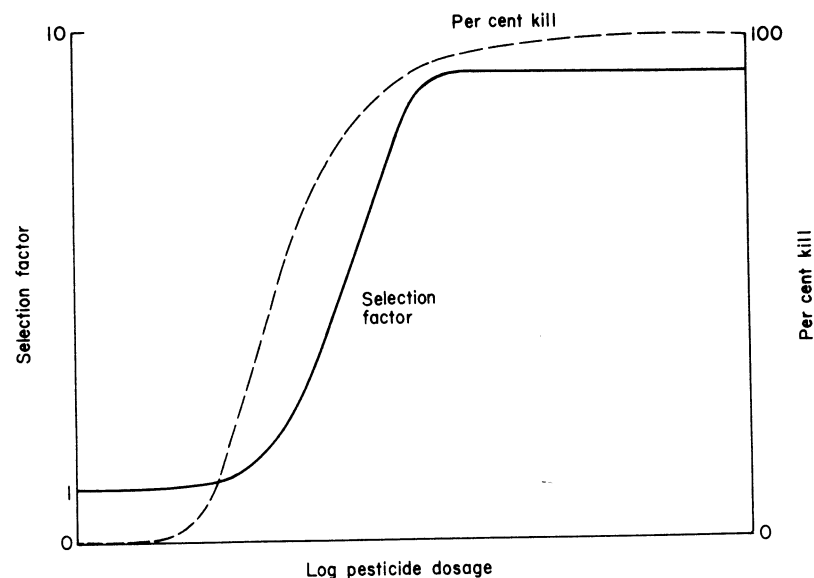
Fig. 15.7. Heterozygote selection where the dosage received is a function of the distance of the individual from the point of application. (After Comins, 1980.)

dip at high dosage. In this, which is probably the most common, field situation high kills will not delay resistance and indeed will markedly increase the selection rate for genes with high resistance factors.

The model also clearly demonstrates the importance of pest migration in delaying resistance. If the treated pest population in, say, a farmer's field is linked to a large untreated population in a wild habitat or in adjacent fields, then resistance in the treated population will develop much more quickly if the rate of migration from the untreated to the treated area falls below a certain critical threshold. Susceptible individuals migrating in provide 'susceptible' genes for the next generation and hence in effect 'dilute' the inheritance of resistance from the survivors in the treated area. Where the resistance gene is recessive the critical threshold is very sharply defined, the population suddenly jumping from a very low to a very high frequency of resistance (Fig. 15.8). However, even where the resistance genes are partially dominant the rate of development of resistance will accelerate as migration decreases.

In general any strategy which increases the effective migration rate or the effective relative size of the untreated population is to be recommended. Other considerations aside, it is good policy to leave untreated
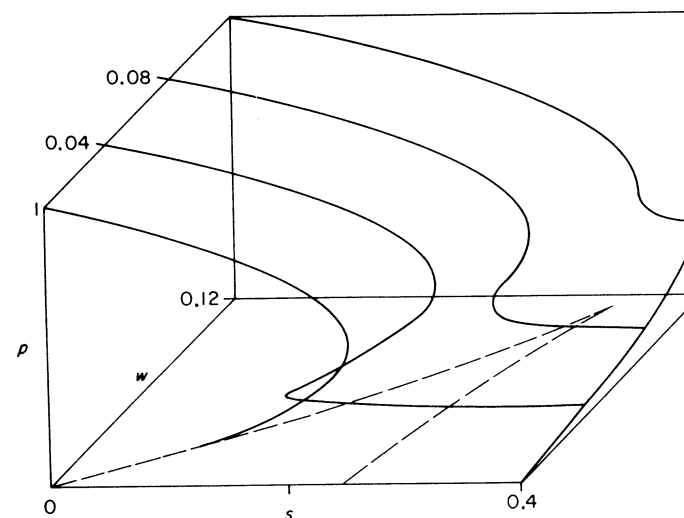
Fig. 15.8. Gene frequencies (p) for a recessive resistance gene in a pesticide-treated population; w is the initial gene frequency and $s = r/[(1 - r)(L - K)]$, where r is the migration rate and L, K are the survival rates of the resistant and susceptible homozygotes. (After Comins, 1977a.)

sub-populations of pests in neighbouring fields or on wild host plants. It also follows that for pests with discrete generations pesticides should be withheld in the period between immigration and reproduction, so producing the maximum degree of reproductive competition.

15.3   The damage function

It is common to find a linear relationship between the size of a pest population and the direct, immediate injury that it typically causes. For example, the leaf area of a crop consumed is roughly proportional to the number of pest individuals present in the crop, and the numbers of humans bitten by mosquitoes is proportional to the size of the man-biting mosquito population. The relationship becomes more complex, however, when we consider the yield of the crop or the ensuing incidence of illness.

15.3.1   *Crop compensation*

The basic form of the relationship between crop yield and pest population size is sigmoid (Fig. 15.9) but as Southwood and Norton (1973)
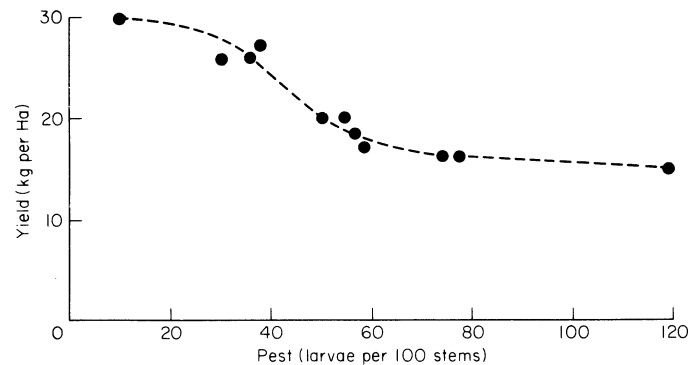
Fig. 15.9. The yield-pest relationship as shown by the African white rice borer, *Maliorpha separatella*, on rice. (After Brénière and Walker, 1970.)

point out, only a portion of this curve is usually exhibited. Where pests attack the foliage or roots and hence directly affect the growth of the plant, the plateau of high yields indicated by the left-hand portion of the curve is extended; severe losses are only caused by high populations. On the other hand, where pests attack the seeds or fruit, which are commonly the harvested product, there is a rapid decline in yields, as demonstrated in the right hand portion of the curve; losses can be severe from low populations. Most of the important pests of foliage and roots tend, therefore, to be *r*-strategists while many of the pests of fruit or seeds are *K*-strategists.

The plateau of high yields at low pest population densities, which is characteristic of foliage and root attacking pests, results from the ability of many crops to compensate for pest injury. Up to a certain level of attack a crop is able to replace the photosynthetic tissues removed by the pest population. The individual plant may respond by growing new leaves or shoots, or by extending the photosynthetic lives of existing leaves, or it may reallocate materials within the plant. Often when one plant is damaged, adjacent plants may produce extra growth to compensate. There are innumerable avenues for such compensation. In some cases it is so effective that pest injury early in the life of the crop actually produces higher yields than would have occurred in the absence of the pest.

It is thus important not to embark on control simply because of the presence in a crop of a population of pests known to cause injury. In order to make a rational decision both the density of the pest population and the current phenological condition of the crop have to be assessed

and an estimate made of the likely level of damage that will eventually arise, taking into account what is known of the crop's ability to compensate for injury. This is not easy and all too often control is attempted when it is not strictly necessary. Profitability is reduced and, if pesticides are used, there is an unwarranted risk of developing pesticide resistance or of contaminating the environment.

In an attempt to minimize insecticide application in a situation of this kind Wilson *et al.* (1972) built a computer model describing the effects of the bollworm *Heliothis* on cotton in Western Australia. Their model was based on three observations. First, there is a definite maximum crop of bolls that can ripen. Second, the bolls require a minimum number of day-degrees to mature and hence have to be protected for this period in order for the maximum crop to be obtained. Third, the day-degree requirement to set the full crop of bolls depends on the size of the plant. The bigger the plant the more quickly the crop is set. As the model clearly demonstrated (Fig. 15.10), if treatment is delayed then the period of protection can be shorter. Less insecticide is used and the control is cheaper and more efficient.

Unfortunately there is very little information on the pest–yield relationship, even for the most common pests, and only rarely is there a
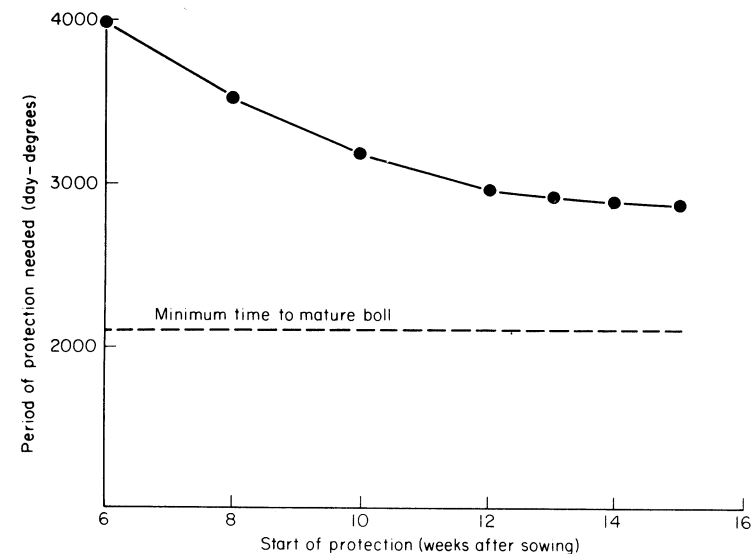

Fig. 15.10. Minimum period of time for which cotton in Western Australia needs to be protected from bollworm attack so as to ensure a maximum crop of bolls. (After Wilson *et al.*, 1972.)

good understanding of the compensatory mechanism, where present. If more were known, it would be possible not only to minimize wasteful control actions but also to enhance the degree of compensation which naturally occurs, using cultural techniques or plant breeding.

15.3.2   *Illness*

As discussed in chapter 14, where pests carry disease the relationship is a product of the dynamics of three populations: that of the pest or vector (e.g. a mosquito, *Anopheles* spp.); the host (e.g. man); and the disease organisms (e.g. the malaria parasite, *Plasmodium* spp.). Macdonald (1957) developed a simple and elegant mathematical model to describe this relationship for malaria. The basic model depends on six key parameters:

m = the density of anopheline mosquitoes in relation to man;

a = the average number of men bitten by one mosquito in one day;

b = the proportion of anophelines with sporozoites in their glands which are actually infective;

p = the probability of a mosquito surviving through one day;

n = the time taken for completion of the extrinsic cycle of the malaria parasite (neglected, for simplicity, in ch. 14); and,

r = the reciprocal of the period of infectivity in man.

When combined, these parameters give a measure of the rate of production of new infections arising from a single primary infection in a community. As explained more generally in chapter 14, this is called the basic reproductive rate of malaria and equals [see eq. (14.50)

$$\frac{m\,a^2 b\,p^n}{r\,\ln 1(/p)}. \qquad (15.2)$$

In contrast to crop damage the relationship between illness and pest density (m) is simple and linear. The critical population parameter is the survival probability (p) of the pest which is contained in eq. (15.2) both raised to a power and as a logarithm. In consequence small changes in survival probability produce large changes in the malaria reproductive rate. As Fig. 15.11 shows, a decrease in the mosquito's mean expectation of life from 20 days ($p \sim 0.95$) to under 3 days ($p \sim 0.7$) is sufficient to push the reproductive rate below unity, and hence to cause extinction of disease transmission. This explains why pesticides such as DDT, which reduce survival probability, have been so heavily relied upon in
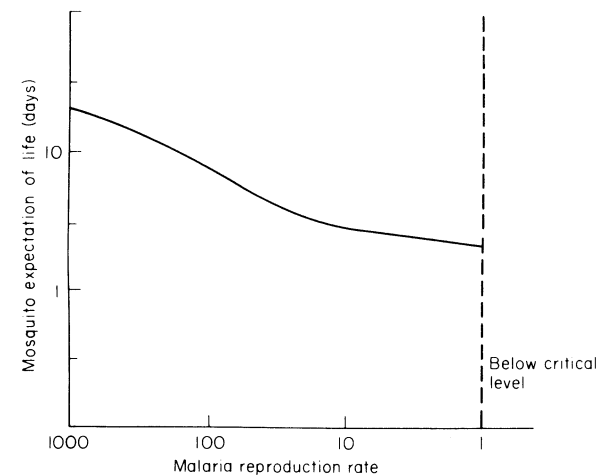
Fig. 15.11. Effect of change in the mosquito's expectation of life on the basic reproduction rate of malaria. (After Macdonald, 1961.)

malaria control campaigns. In practice, however, it has proved very difficult to achieve eradication (Harrison, 1978). The rapid rates of increase of mosquito populations, their powers of host finding, dispersal and adaptation to a wide variety of habitats, and their ability to evolve resistance, have limited the effective use of pesticides. Few nations have been able to provide the time, organization and funds which control of so powerful a pest requires.

Fortunately, the existence of three populations in the illness–pest relationship means that pest populations are no longer the sole target for control strategies. The disease pathogen populations can themselves be the subject of control, either through immunization or through chemotherapy. Macdonald *et al.* (1968) have suggested by means of a computer model how chemotherapy, based on drugs, and pesticides could be utilized in an integrated fashion for malaria control. The search is now on for a vaccine which will confer immunity against malaria. Other examples of the ecology of human diseases were discussed in chapter 14.

15.4   Ecology and economics

Knowledge of the dynamics of the pest and of the pest-damage relationship can provide a guide to those control strategies which, in ecological

terms, are most likely to succeed. But the final choice of strategy depends on the objectives of the decision-maker and on the context within which the decisions are made.

15.4.1   *Optimal control*

At the beginning of the chapter I assumed that the objective of pest control was profit maximization, i.e. the farmer or other decision-maker wished to maximize the difference between the revenue and the cost of control. This is an objective which is probably pursued by most large scale farming operations. A good example occurs on the West Indian island of Trinidad, where sugar-cane is grown over several thousand acres by a single company. The cane is attacked by a frog-hopper, *Aeneolamia varia saccharina*, the adult of which causes a loss in the quantity of cane produced (Conway *et al.*, 1975). Each brood or generation is readily described by a simple mathematical function which can be used to determine the effects of pesticide control. In this case there is little evidence of compensation and field experiments suggest that the loss of sugar-cane yield is a simple linear function of the number of adult days.

Two kinds of insecticide are available: (1) a cheaper non-residual compound which only acts on the day it is applied, and (2) a more expensive residual compound which persists for 5 days. These can be applied at any time and in any permutation. If a limit is set of three applications per brood, ten dominant strategies are possible (five further strategies exist but these eliminate fewer adult days than other permutations of the same combination of insecticides). Table 15.4 gives the optimal spraying times for these strategies.
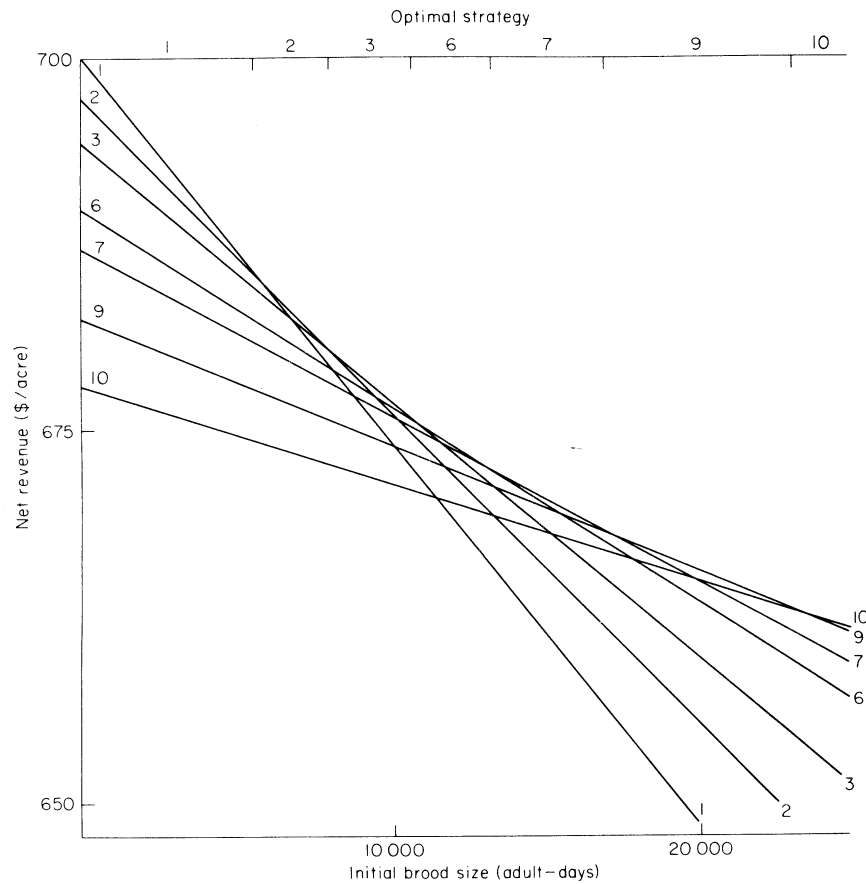
A set of net revenue lines can then be produced for different sizes of pest population, using information from the cost and damage function (Fig. 15.12). Each spraying strategy is rational when its revenue line is above that of the no-spraying strategy (1) and the most efficient strategy at each population level is the highest revenue line. The optimal control for the range of possible population sizes is given by the curve made up of the segments of revenue lines representing the most efficient strategies.

The froghopper, however, passes through four broods in a year. Clearly if there is no density dependent relationship between the broods then the problem of control remains relatively straightforward:

Table 15.4. Optimal application times for ten spraying strategies directed against a single froghopper brood. (From Conway *et al.*, 1975.)

Strategy	Time from first adult emergence (days)																		Percentage of adult-days removed
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
1																			0·0
2											NR								19·3
3									NR					NR					32·7
4										R									37·6
5					NR										R				42·8
6								NR		R									49·0
7							NR			NR	NR		R						57·2
8							R					R				NR			60·9
9							R			R									67·4
10				R												R			74·9

R = residual spray; NR = non-residual spray.

Optimal strategy

Fig. 15.12. Optimal spraying strategies (see Table 15.4) against a single brood of froghoppers. Net revenue is measured in Trinidad and Tobago dollars. (After Conway *et al.*, 1975.)

the size of all four broods is a function of the level of control of the first and the procedure, described above, for determining the best strategy is adequate. This would be true, for example, of the rice brown planthopper described in Table 15.1 which has a *b* value of approximately o. However, if density dependent regulation is present, as for example in the green leafhopper which has a *b* value of approximately equal to 1·0, the dynamics make the finding of an optimal control solution more complex.

Density dependence can be represented by an equation of the form

described by eq. (3.3), that is

$$A_{t+1} = \lambda A_t^{1-b} \qquad (15.3)$$

Here A_{t+1}, A_t are the numbers of adult days at time t and $t+1$; λ is the net rate of increase (as discussed in chapters 2 and 3); and b is a measure of density dependence (with the characteristic return time $T_R = 1/b$). In the case of the sugar cane froghopper we do not know the value of b but it is possible to derive an optimal control solution for different likely values of b, using the technique of dynamic programming (Shoemaker, 1973). Table 15.5 shows the results using the initial range of control strategies described in Table 15.4. As can be seen, with b equal to 0·5 (i.e. undercompensation) the spraying becomes concentrated in the second brood and with $b = 1·25$ (i.e. overcompensation) it becomes concentrated in the second and third broods.

Table 15.5. Optimal spraying strategies (see Table 15.4) for four froghopper broods with different degress of density dependence between the broods (After Conway *et al.*, 1975).

Initial size of 1st brood	Density dependence (value of b)											
	$b = 0$				$b = 0.5$				$b = 1.25$			
	Brood strategy				Brood strategy				Brood strategy			
	1st	2nd	3rd	4th	1st	2nd	3rd	4th	1st	2nd	3rd	4th
1000	2	2	1	1	1	9	2	1	1	10	10	1
5000	10	5	1	1	6	10	3	1	1	9	10	1
10000	10	10	1	1	10	10	3	1	2	9	10	1

15.4.2 *Resistance costs*

The remaining question is whether these solutions remain optimal if we take pesticide resistance into consideration. Comins (1977b) has extended his simple resistance model to tackle this problem. Underlying his approach is the notion that pesticide susceptibility in pest populations is an irreplaceable natural resource. It is essentially a free resource in the short term but, once lost, high costs are incurred in switching control to a usually more expensive substitute.

Comins makes two important approximations. The first is that the survival of the susceptible individuals is related to pesticide dosage by a

simple 'random search' equation, so that

$$S_i = \exp(-C_i/A_i)$$

or

$$C_i = A_i \ln S_i. \tag{15.4}$$

Here C_i is the cost of control of the ith pest generation; A_i is a 'cost parameter' specified separately for each generation; and S_i is the proportional survival of susceptibles from pesticide application for the ith generation. The value of A_i can be estimated from the results of field experiments. The second approximation is that the effective dominance of resistance stays the same regardless of pesticide dose. These assumptions do not appear to invalidate the results except, perhaps, for very low or very high pesticide application rates.

This model demonstrates very clearly that strategies which lead to a reduction in long term resistance costs are simply the optimal strategies which result when resistance is ignored, but the cost of applying insecticide is assumed to be somewhat larger than it actually is. Thus the cost parameter A_i for the control of each pest generation is increased by a constant amount Q,

$$A_i \rightarrow A_i' = A_i + Q, \tag{15.5}$$

where Q is the 'effective cost of resistance'.

The parameter Q represents the equivalent present cost of future resistance, evaluated in terms of the characteristic time for resistance to develop to the particular pesticide. Estimation of this time component implicitly takes into account the degree of dominance and initial gene frequency. In practice, values in the range of 4–12 years are probably reasonable (assuming that no cross resistance is anticipated). Values for Q can then be estimated using a standard discount formula and a range of values for the cost of switching to new pesticides once resistance has developed. Finally, the optimal value of Q can be determined graphically.

In the case of the sugar cane froghopper, Comins assumed a characteristic resistance time of four and a half years and that the cost of pesticide would be doubled once resistance to the present compound is established. The optimal strategies are the same as those when resistance is not considered but the effective prices are increased. As can be seen from Table 15.6, where density dependence is undercompensating the

resistance cost becomes large when there is a large initial population, reflecting the much heavier pesticide treatment which is required for successful control. But the case of overcompensating density dependence is more complicated, since a large initial population produces a smaller second brood and a larger third brood.

Table 15.6. Effect of resistance on the cost of optimal spraying strategies for the froghopper. (After Comins, 1977b.)

Density dependence	Initial size of 1st brood (Adult-days)	Total cost ($)	
		No resistance	resistance
$b = 0.5$	2000	59	59
	5000	73	77
	10000	84	99
$b = 1.25$	2000	90	98
	5000	95	100
	10000	104	109
$b = 0$	2000	35	35
	5000	49	53
	10000	60	75

15.4.3 *Resilient pest management*

So far I have considered the situation of a single pest species on a crop, where accurate population estimates are possible and the farmer is aiming at a mathematically precise profit maximization. The real world is more complicated.

In most situations one knows only the probability of an approximate level of pest attack. Here the problem is best approached by the use of Bayesian decision matrix (Halter and Dean, 1972; Norton, 1976b). This approach is also useful where profit maximization is no longer the goal. Profit maximizers are assumed to be risk neutral; in other words they value each successive increment in income in the same way. But many, particularly smaller, farmers can be classified as risk averse. They value initial increases in income far higher than later increases. For example, a farmer who has just started farming and has little capital available will set his primary goal as the achievement of a

certain minimum level of income. Such a situation will be particularly true of subsistence farmers in developing countries who will put a much higher value on achieving, each year, the necessary level of subsistence than on each increment of income above that level.

Most farmers also have to cope with an assortment of pests on a variety of crops. The control techniques which seem, on the previous analysis, to be most appropriate for a particular pest now have to be modified in the light of the other pest problems. Many of the pioneer integrated control programmes were expressely designed to cope with situations of this kind. For instance in the early 1960's, in northern Borneo, an integrated control programme was designed (see Table 15.2) for a complex of half a dozen pests on cocoa (Conway, 1971b). Most of these pests were intermediate pests, although close to the r-end of the spectrum. In their natural habitat of primary or secondary forest, they were regulated by a variety of natural enemies, but heavy spraying with organochlorine insecticides had apparently destroyed these enemies resulting in severe pest outbreaks on the cocoa. As a first step the use of organochlorine insecticides was stopped and within a few months several of the major pest species came under natural parasite control, reverting to levels which caused little damage to the cocoa. However, two pests remained and these had to be controlled in a manner which did not upset the balance, so recently re-established for the other species. One of these two pests was the tree borer *Endoclita hosei*, referred to earlier in the chapter as a typical K-pest. This was successfully controlled by combining injection with insecticide of any borings found and the destruction of the secondary forest tree species which was the primary host of the borer in the vicinity of the cocoa. The second pest, a bagworm (Psychidae), which showed a high reproductive rate characteristic of r-pests, was knocked down by a selective insecticide and then came under parasite control.

In such a situation, and indeed for the great majority of pest control problems, aiming for a precise mathematically optimum control is unrealistic. The farmer is more interested in having guidelines or decision rules, derived from a mixture of empirical studies and mathematical models, which provide a reasonably satisfactory level of control which is both durable and resilient to changing circumstances. At the outset much of the seemingly necessary biological information the farmer requires may be too difficult, too costly or too time consuming to obtain. In the long run crucial biological parameters may change, for example due to the evolution of resistance, and there may be major

fluctuations in prices of products or the costs of control. The farmer requires a system of pest management which is able to cope with this considerable uncertainty.

Recently a study focussed on this problem has been carried out for the cattle tick *Boophilus microplus* in Australia (Sutherst *et al.*, 1979). The life cycle of this pest is relatively simple: eggs are laid on the pasture and the larvae are eventually picked up by passing cattle. The adult ticks cause serious damage to the cattle hides. Several broods a year are produced and the dynamics can be well represented by a Leslie matrix model (Leslie, 1945; Usher, 1972) of the form

$$n_{t+1} = An_t \qquad (15.5)$$

where n_{t+1} and n_t are population vectors and A is a transition matrix representing fecundity, survival and development. The crucial dynamic feature of the life cycle, however, is the degree of density dependent competition between larvae for a place on the cows' hide, and the matrix model is modified to incorporate this using an equation of the form of eq. (3.3).

The model was used initially to obtain optimum strategies for the traditional means of control, which is dipping the cattle in an acaricide. The results of the simulations showed that the best strategy was to
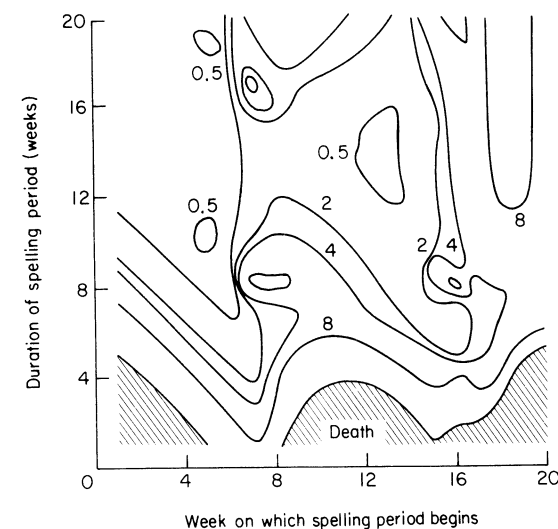

Fig. 15.13. Nomogram for single spelling and dipping of the cattle tick, showing the effect of spelling time and duration on beef losses (Australian \$/head/annum). (After Sutherst *et al.*, 1979.)

dip five times at three-weekly intervals early in the season. This strategy appears surprisingly robust. Even quite large changes in the initial population density, egg and larval survival and the density dependence relationship require only the addition or subtraction of a single dipping. It is also robust to management errors, such as incomplete mustering of the cattle or mistiming of the dipping, and to changes in the price of beef.

However, cattle ticks are becoming increasingly resistant to acaricides and so the model was used to examine alternative methods of control, in particular the spelling of cattle. This entails the removal of cattle from an infested pasture for a period long enough that the tick population dies out. Various patterns of spelling, both alone and combined with dipping, were examined and a highly robust solution was found to be a single spelling period each year, with a dipping at its beginning and end (Fig. 15.13).

This strategy can be even further improved by the use of tick resistant breeds of cattle, on which there is much stronger density dependent competition between the tick larvae, and by carefully controlled high individual doses of acaricide which will, in this situation, effectively delay acaricide resistance. Such a strategy copes well with the existing known dynamics and promises to provide the flexibility which will permit adaptive changes to the unforeseen events of the future.

16
Bioeconomics

COLIN W. CLARK

16.1   Introduction

The term 'bioeconomics' is used in this chapter simply as a shortened term for 'biological resource economics'. The possible alternative meaning of the term (sometimes further reduced to 'bionomics'—see chapter 3) to describe the strategies of organisms or populations to maximize ecological fitness, will thus not be intended here.

The main problems of bioeconomics as a subject of study concern the way in which biological systems and economic systems interact with one another. These interactions are obviously of vital importance to human welfare, since virtually all of our food, much of our clothing, and many other fundamental human needs are met by biological resources. Because biological resources are so important, it is not surprising to find severe *conflicts of interest* dominating many of the problems of resource management. Any useful theory of resource economics (biological or other) must take cognizance of these conflicts of interest and their consequences. Broadly speaking, bioeconomics thus impinges on many fields besides biology and economics, including law, political science, ethics, and so on.

In classical economics, conflicts of interest between competitive producers is recognized as a 'good thing' for society—the 'invisible hand' of Adam Smith. It is important to keep in mind, however, that the classical notion of competition refers to *marketplace* competition: the most successful competitors are those that can place goods that people desire on the market at the lowest prices. Clearly such competition is often socially beneficial.

In resource economics, on the other hand, it turns out that competitive exploitation of resources is almost invariably a 'bad thing' for human welfare. Competitive resource use results in overexploitation, or depletion, of renewable resource stocks, and in extreme cases may lead to the actual extinction of populations or species. A successful