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The Population and Community Ecology of Invading Insects [and Discussion]

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The population and community ecology of invading insects

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Theory is equivocal about invasion success, implicating various combinations of r, a population's intrinsic rate of increase, K, its 'carrying capacity', enemy-imposed death rates and the coefficient of variation in population numbers as determinants of establishment. Data for a wide variety of organisms, both vertebrates and invertebrates (including insects), accidentally or deliberately introduced by man into the British Isles, appear to show that the probability of establishment of an invader is positively correlated with body size. These data are consistent with the idea that the amplitude of population fluctuations is the main determinant of invasion success, but not with theoretically expected effects of r or K (because populations of small organisms generally fluctuate more than populations of large organisms, but both r and K decrease with increasing body size). However, data for various insect orders introduced into Britain show exactly the opposite trend, with probability of establishment decreasing with increasing body size, and hence possibly with decreasing r and/or K. Possible reasons for these contradictory results, including biases in the data, are discussed. Finally, data from a variety of sources, including insects released as biological control agents, show that enemies (parasitoids and predators) are often a cause of failure to establish particular species of introduced insects. These data add further to the uncertainty about the main determinants of invasion ability. The only clear conclusion to emerge from a combination of theoretical and empirical studies is that r alone is not obviously the main, or even an important determinant of invasion success.

INTRODUCTION

There is considerably more theory than hard data on what makes a species a 'good invader'. This paper is neither a comprehensive review of theory, nor an exhaustive summary of available data on insects as invading species. Rather, it has as its general theme the importance of r, the intrinsic rate of population increase, as a predictor of invasion ability, with insects as the main examples. The notion that a high value for r favours colonization of new habitats by organisms is extremely well established in the literature, and can probably be traced to a number of sources, not least to Pianka's seminal paper on r- and K-selection (Pianka 1970). Insects are usually regarded as classically 'r-selected' organisms.

The terms r- and K-selection were coined by MacArthur & Wilson (1967). Among the many theoretical and empirical observations on the characteristics of invading species contained in this book, three are particularly pertinent to this paper:

(i) The chance of an invading species (formally, a hypothetical single individual propagule) establishing in an area scales *not* as r, but as r/λ, where $r = \lambda - \mu$. Here, r is the intrinsic rate of increase of the organism in its new environment, and λ and μ are *per capita* birth and death rates respectively. In their model, it is the ratio λ/μ, rather than $r = \lambda - \mu$, which contributes most to successful invasion. In other words 'the good colonizer has a large r, which is achieved by a low mortality rate rather than a high birth rate'.

(ii) Persistence of the invader in the community is also aided by a high 'carrying capacity', K. Indeed, for particular combinations of λ and μ there is a 'take-off' value of K above which extinction is extremely unlikely.

(iii) 'A community can be closed to a species (i.e. invasion is impossible) in ways that are often both difficult to predict and surprising in their consequences'. MacArthur & Wilson discuss several mechanisms of exclusion, one of which is 'too many' predators. It is this mechanism that we wish to consider here, rather than more traditional processes involving classical interspecific competition. We do so not because predation is necessarily more important, but because it is more neglected, both theoretically and experimentally, as an exclusion mechanism. As we will show later, predators and other types of natural enemy can override any advantage potentially accruing to an invader from a high value of r.

We have included prediction (i) and (ii) from MacArthur & Wilson mainly for historical reasons, because their model, and later developments (see, for example, Richter-Dyn & Goel (1972)) do not lend themselves readily to testing in the field. This is because the main cause of population fluctuations driving extinction in these models is demographic stochasticity (Shaffer 1981; Leigh 1981; Nisbet & Gurney 1982; Wilcox & Murphy 1985). Real populations live buffeted by the vagaries of the environment, and (except under controlled laboratory conditions) environmental stochasticity is usually a far more important cause of population fluctuations than demographic stochasticity. Leigh (1981) models the effects of density-independent perturbations on populations (environmental stochasticity) via the coefficient of variation in numbers from one generation to the next. One of his most important predictions is:

(iv) For a population founded by a hypothetical single individual, 'the relative amplitude (coefficient of variation) of a population's fluctuations is the single most decisive variable affecting the average lifetime of that population', more important, in fact, than r or K. However, in his models, high r and high K certainly reduce the chances of extinction in founding populations.

Leigh does not split r into birth and death rates; hence his predictions are not exactly comparable with MacArthur & Wilson's. Moreover, Leigh uses finite difference equations, and MacArthur & Wilson use differential equations, further adding to the difficulties of direct comparison. But in general terms, all these models leave little room to doubt that r alone should not be a good predictor of invasion ability.

How well do predictions (iii) and (iv) help in understanding the invasion and establishment of insects into ecological communities? And to what extent do insect data support or refute these predictions? We review two main classes of data. First, information about the success and failure of insects introduced into Britain is brought together, comparing insects with other major taxa, and then looking at selected orders of insects. Secondly, we examine some of the reasons why phytophagous insects introduced in biological control programmes against weeds in several parts of the world failed to establish, in particular developing the theme that the impact of natural enemies (predators, parasites, parasitoids and diseases) can be a cause of failure. Similar evidence is also sought from natural invasions by phytophagous insects, and examples briefly reviewed. As part of this second theme, we also draw attention to recent theoretical studies on the role of enemies in limiting species establishment in communities (Holt, 1977, 1984). We have chosen to restrict examples in the second part of the paper to phytophagous insects because these are the organisms we know best; they are also the most species-rich group of animals in world, and hence cannot be regarded as somehow 'atypical' (Strong *et al.* 1984).

Anticipating the conclusions of the paper, we find that empirical tests of theory are equivocal. In part this is because the data are often difficult to interpret; but problems also arise because appropriate theory is far from well developed. It is not clear what makes an insect species a good invader.

Establishment of introduced insects in Britain

Extensive data now exist on the probability of establishment by species deliberately or accidentally introduced into the British Isles by man, i.e. excluding natural vagrants (Brown 1985; Williamson & Brown, this symposium). We have used part of this large data set to calculate the probability of establishment of insects as a whole, for comparison with other major taxa, and then examined selected orders of insects. In both cases body size has been used as the basis for comparison, because r is inversely correlated with body size in comparison from bacteria to elephants (Pianka 1970; Southwood 1981), and because average population densities and presumably therefore 'carrying capacities', K, (Peters 1983) decrease with increasing body size. Of course, size varies widely within taxa (see, for example, Hemmingsen (1934)), but providing the difference between groups is large relative to variation within a group, the data should be sufficiently robust to reveal recognizable patterns.

Insects compared with other taxa

There is a significant, albeit noisy, positive correlation between mean body size and the probability of establishment of introduced taxa in Britain (figure 1). Insects lie reasonably close to the overall regression line. A positive correlation is totally unexpected if r and K are the main determinants of establishment, but is consistent with Leigh's argument that the coefficient of variation of population size is the most important factor determining the persistence of a founding population. In general, smaller animals vary much more in population density from generation to generation than populations of large animals (Williamson 1972; Hassell *et al.* 1976); this variation is measured either by the standard deviation of the logarithm of the population size, or, equivalently, by the coefficient of variation.

However, it is also possible that the pattern revealed by figure 1 is an artefact. Possible errors could work in two ways. Taxonomic prejudice among Britain's army of amateur naturalists is towards larger, more easily identified groups. Since amateur observers played a significant part in gathering the data on which the analyses are based, there may have been a greater tendency to overlook unsuccessful introductions of small species, because unsuccessful invasions are harder to detect, and to observe mainly successful establishment by small species. If proportionately more unsuccessful invasions of larger, more 'fashionable' taxa are noted, the effect will be to generate artificially high rates of establishment as species become smaller. If this is the principal bias in the data it will tend to oppose the trend in figure 1 and suggests that the pattern therein is real. However, it also seems likely that smaller organisms are more easily introduced accidentally, carried in soil or on plants, for example. Hence a much higher proportion of introductions of smaller organisms may fail because they are climatically, or in other ways, unsuited to life in Britain. Deliberate introductions of vertebrates should involve species more carefully matched to their adopted environment. In other words, the pattern

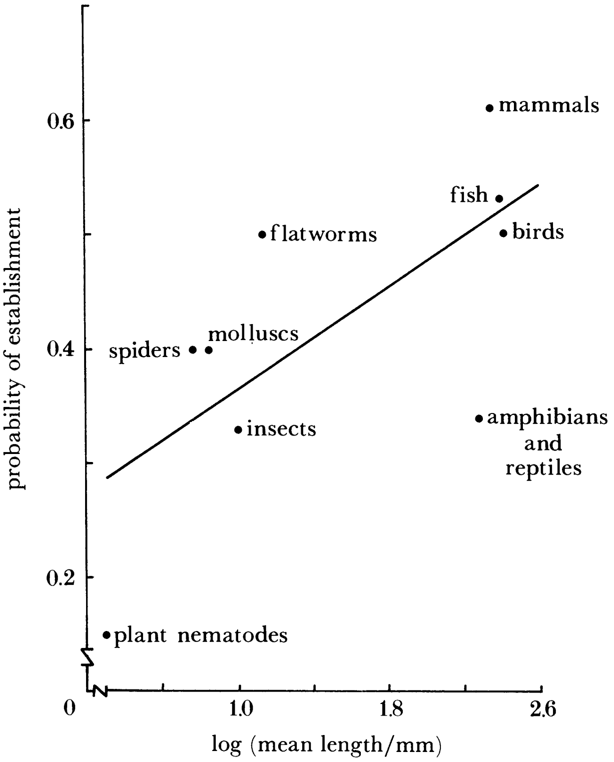

FIGURE 1. Probability of establishment of various taxa, deliberately or accidentally introduced by man into the British Isles, as a function of average body size (from data in Brown (1985)). The probability of establishment is the number of species with established populations at more than one site in Britain divided by the total number of species introduced. Estimates of body size are geometric means of every fifth entry for particular taxa in standard European keys and field guides. Sizes are not, therefore, the mean sizes of the species that were actually introduced, because many of these sizes are not recorded in the literature; estimated sizes should, however, provide correct relative rankings for the introduced species. The fitted regression is: $y = 0.11x+0.25$, $r = 0.69$, $0.05 > p > 0.02$. Establishment at two or more sites was used as a criterion to reduce errors arising from marginally and doubtfully established species.

shown in figure 1 may simply measure how carefully introductions have been matched to the British climate and its habitats, and may have nothing to do with extinctions caused by amplitude of population fluctuations in the manner invisaged by Leigh (1981). On the evidence currently available, we are unable to decide between these alternatives. Hence the data in figure 1 provide only weak support for prediction (iv).

Carefully controlled introductions of vertebrates and invertebrates would help to resolve these problems. One such experiment, unique as far as we know, was carried out by Levins & Heatwole (1973) on Palomintos Island, Puerto Rico. All the introductions failed, for various reasons, namely predation (on one of the introduced species of lizard), interspecific competition (a second species of lizard and an ant), or unsuitable habitat and climate (a frog, a snail and a *Drosophila*). However, what is interesting in the present context is that the population persisting for the greatest length of time and for which evidence of breeding occurred was a lizard, *Anolis pulchellus*. On these extremely limited data, therefore, one of the vertebrates was the best colonist. This is at least consistent with figure 1.

Comparisons between orders of insects

The pattern revealed by figure 1 is reversed when orders of insects are compared (figure 2). Good colonists are smaller taxa, possibly with higher rates of population growth and higher *K*. Of course, insect orders differ in all sorts of ways other than average body size, but we know of no natural history characteristics of different orders, other than *r* and *K*, that might contribute to probability of establishment and which are correlated with body size in the manner revealed by figure 2. Unfortunately, for insects, we do not actually know if *r* is inversely correlated with body size; hence the biological processes underpinning figure 2 are entirely speculative.

There are two ways to interpret these data. By concentrating on one group of organisms, insects, we may have reduced the range of variation encountered in the amplitude of population fluctuations, making *r* or *K* or both, rather than the coefficient of variation in population size, the most important determinant of population establishment. In other words, figure 2 could still be consistent with Leigh's predictions. We require more detailed population data than are currently available to test Leigh's predictions quantitatively rather than qualitatively, and hence explore this possibility further. Alternatively, restricting comparisons to insects may eliminate ecologically trivial reasons for variation in the probability of establishment, revealing effects hidden in figure 1. Our guess is that the truth includes elements from both explanations.

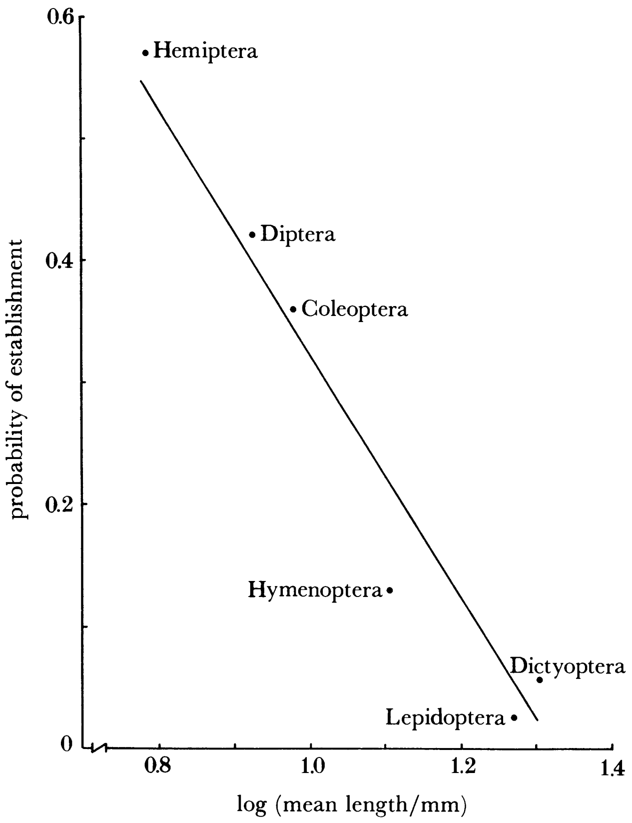

FIGURE 2. Probability of establishment of species in different orders of insects introduced by man into the British Isles, as a function of average body size. (See figure 1 for details.) The fitted regression is: $y = -1.06x + 1.39$, $r = 0.98$, $p < 0.001$.

THE EFFECT OF ENEMIES

Theoretical considerations

The most surprising thing about figure 2 is the unequivocal nature of the correlation between probability of establishment and body size, and hence possibly r or K or both. It is surprising because theoretical arguments suggest that other parameters can strongly influence probability of establishment by an invading species, not least the impact of enemies (Holt 1977, 1984). Not only may there be 'too many' predators, in MacArthur & Wilson's words, but also too many parasitoids, parasites and diseases, all ready to take their toll of the invader, with similar general consequences.

Holt used Lotka–Volterra models of enemy–victim interactions to derive the conditions for invasion and successful establishment of a species into a community, when the invader is subject to attack by resident natural enemies. For successful invasion:

$$r > aP,$$

where r is again the intrinsic rate of increase of the invading species, a is the attack rate of enemies already present in the community upon the invader, and P is the density of resident enemies.

In other words, the potential rate of increase of the victim population must be greater than the rate at which resident enemies find and kill them. Other things being equal, invasion will be more difficult not only when r for the invading species is small, but also if invaders are particularly vulnerable to attack by resident enemies (high a), and if the population of resident enemies is large. Clearly, in these models at least, r is not the arbiter of invasion success.

Holt also discusses the conditions for sustained coexistence of species in a community after invasion. Imagine populations of two victim species, A and B, and population of shared enemies. Suppose initially that only A and the enemy live in stable equilibrium. Now let B invade, ($r_B > a_b P$; subscripts define the species, and P in this case refers to the population size of the enemy coexisting with A alone). Once B invades, the total population of victims, n_{A+B}, increases, and the enemy population also increases because it has more food. As Holt shows, the net effect on A is to reduce its equilibrium numbers, possibility to extinction. In his terminology there is 'apparent competition' between A and B through their shared enemy, or competition for 'enemy-free space' in the terminology of Jeffries & Lawton (1984).

The outcome (which species coexist and which are eliminated) in this community of three or more species depends, among other things, on the relative values of the intrinsic rates of increase (r_j) of victim species and on enemy attack rates upon victims (a_j) (Holt 1977). It also depends upon the degree of separation and rates of enemy movement between spatial niches supporting different victim species (Holt 1984). Moreover, as enemies become more polyphagous (Holt 1977), or less choosy in their spatial foraging niche (Holt 1984), the permissible variance in the ratio $r_j : a_j$ for stable coexistence of victim species declines. Under these conditions, coexistence is favoured by all species (invader and resident) having similar values of r and a, *or* by wide variation in values of a_j and appropriate tuning of r_j. This makes qualitative testing of Holt's arguments very difficult. It also makes it seem very unlikely that invasion and stable coexistence of species will depend in any simple way upon r, although invasion is always easier when r is high.

Field data

What evidence is there that polyphagous enemies ever prevent establishment of potential invaders in the manner envisaged by Holt? A variety of data involving many different taxa have been reviewed by Holt himself (1977, 1984), and by Mitchell (1971), Jeffries & Lawton (1984), Gilbert (1984) and Lawton (1986) among others, and will not be dealt with in detail here. They suggest that enemies could be a frequent cause of failure for invading species, although detailed population dynamics data are lacking, and it is usually impossible to tell how well particular examples conform to the assumption of Holt's models. Some of the best studied examples come from the failure of phytophagous insects to establish themselves when introduced in biological control programmes against weeds (Goeden & Louda 1976). For example, the net rate of increase ($r-aP$) of *Bactra truculenta*, an olethreutid moth introduced into Hawaii for control of purple nutsedge (*Cyperus rotundus*), was severely curtailed by attacks from a polyphagous hymenopterous egg parasitoid, *Trichogramma minutum*, and two other unspecified parasitoids, although in this case the parasitoids did not prevent establishment. Indeed in none of the cases reviewed by Goeden & Louda did parasitoids prevent establishment, whereas predators did. Cinnabar moth, *Tyria jacobaeae*, failed to establish both in Australia and in New Zealand when released as a biological control agent against ragwort, *Senecio jacobaea*, because of attacks from birds and a variety of polyphagous invertebrate predators.

There are several other possible examples, not involving biological control agents but explicitly invoking parasitoids as the cause of failures to invade by phytophagous insects. Samways (1979) reported that adults of the sphingid moth *Erinnyis ello* naturally invaded an isolated experimental plot of cassava, but the eggs and caterpillars were so heavily parasitized that no larvae reached the final instar. Eggs were particularly heavily attacked by *Trichogramma fasciatum*, which was probably present in the crop before *Erinnyis* arrived, because it also attacks a variety of other hosts. Similarly, Zwölfer (1979; personal communication) found that experimental colonies of the dipterous thistle gallfly, *Urophora cardui*, could be established on their normal host plant, *Cirsium arvense*, growing beyond the limits of the natural European range of *U. cardui*. However, some of these colonies were then exterminated by the hymenopteran *Eurytoma robusta*, a widespread and important parasitoid of *Urophora* spp. with large populations sustained on alternative hosts.

The obverse prediction, that invasion will be easier for species immune to attack by resident parasitoids, is a more feeble, but still interesting, test of theory. Crawley (this symposium) reviews the invasion of the cynipid *Andricus quercuscalicis* into Britain. The galls of this species have no morphological close counterparts on native oaks in this country, and its rapid and successful invasion may be due, at least in part, to a virtual absence of attack by parasitoids.

Predation has also been implicated as an agent preventing natural invasion and establishment of phytophagous insects on new host-plants. Examples all involve butterflies that appear to avoid potentially suitable species of plants as food for their larvae. Although these plants are nutritionally satisfactory, their use as food plants may be precluded by resident predators, for example ants (Singer 1971; Benson 1978; Smiley 1978).

In some cases, however, the role of ants is very different, and provides unexpected support for theory, based on a comparison of the host-plant ranges of lycaenid butterflies that do and do not enter into mutualistic associations with ants. The association is generally regarded as a protection against larval and pupal enemies of the butterflies, particularly parasitoids (Atsatt

1981; Pierce & Mead 1981). In a comparative study of 282 species of lycaenids from Australia, South Africa and North America, Pierce & Elgar (1985) found that, in general, ant-attended species use a wider variety of host-plants than do non-myrmecophilous species. Many species of lycaenids also appear to have 'host-shifted' (i.e. invaded and established themselves on a new host plant) in ways that cannot be understood from either the chemistry or the taxonomy of the plants, a feature of their biology that Atsatt (1981) again attributes to protection by ants from natural enemies. The inference must therefore be that enemies often prevent the invasion of otherwise suitable species of plants by Lepidoptera that do not enjoy the protection of ants.

These and similar examples are certainly consistent with the view that enemies can play an important role in limiting or totally preventing the invasion of otherwise suitable habitats by victim species. Unfortunately in no case that we are aware of for insect invaders do we know all, or even most, of the parameters thought to be important from population models of the invasion process. Hence the links between theory and data are at best tenuous, and critical tests of the models non-existent.

Conclusions

It is little wonder we find it difficult to predict whether or not a particular species of insect (or indeed any other organism) will successfully invade a new habitat (Robinson & Dickerson 1984). Even in biological control, where introduction of agents is of considerable economic importance, rates of successful establishment are often low and very poorly understood (see, or example, Beirne (1985)). Holt's models suggest that *a priori* predictions of success or failure will at least require detailed knowledge of the abundances of potential enemies of the invader, together with estimates of attack rates, and the rate of increase of the colonist. Moreover, there are often likely to be effects of direct competitors on species trying to enter a new community. (To keep the manuscript within reasonable bounds, we have ignored 'conventional' competitive exclusion of invaders, but there is no reason to believe that this process is any more or less important than predation.) The result of taking all these possible processes into consideration is a 'snowstorm' of parameters to be estimated before invasion success can be predicted for particular cases. Even if we could gain all this knowledge, real population systems are stochastic, not deterministic, and real populations are subject to density-independent perturbations that are the focus of Leigh's (1981) analysis. Hence we see little prospect of ever having enough information to predict with any degree of confidence the success or failure of particular introductions or natural invasions.

Against this generally gloomy picture, figure 2 stands out as a clear and apparently unequivocal pattern, strongly implicating body size, and hence possibly some combination of r and K (both of which are correlated with body size), as the key determinants of invasion success, within one reasonably tightly constrained taxonomic group of organisms, namely insects. However this is an *average* picture, summed over a large number of individual cases. In other words, it appears to be much easier to understand what makes a successful invader, on average and after the event, than it is to predict the outcome of particular cases. This may seem an obvious point, but we often seem to assume that general understanding will aid detailed prediction; the complexities outlined here should be enough to convince us that this is not the case for invading organisms, or indeed for many other areas of ecological endeavour. In order to predict we must first have a good idea of what the ground rules are; however, this is merely the first step in a long and difficult process leading to accurate predictions.

The trouble is that, for insect invaders, we are not yet convinced that the ground rules are even known. First, the probability of successful establishment of insects in Britain appears to be dependent on r or K, or perhaps both, or at least is correlated with body size in a way that implicates r and K (figure 2). However, current theory does not lead us to expect such a clear effect. Leigh's model rather emphasizes the amplitude of population fluctuations as the main determinant of invasion success, not r or K, and Holt's models implicate enemies. Nor do the data in figure 2 permit a decision about whether it is r or K that actually influences establishment, as both decline with body size. Secondly, we do not yet know if a population's response to environmental stochasticity, reflected in the coefficient of variation in population size, really enters into the picture at all, although Leigh's models make intuitive sense and figure 1 is consistent with his predictions. Unfortunately, it is difficult to be sure that the pattern revealed by figure 1 is not due to biases in the data that are correlated with taxonomy; certainly the difference between figure 1 and figure 2 is very worrying. Finally, sufficient field data exist to suggest that enemies sometimes prevent invasion and establishment in the manner envisaged by Holt and hinted at by MacArthur & Wilson. These field data make us wary of expecting any simple relationship between species characteristics (r, K, or the amplitude of their population fluctuations) and the probability of successful invasion.

The only solution to this empirical and theoretical uncertainty is more, and better, theory, linked to carefully planned field experiments on invading species. Currently, the only certainty is that there are neither theoretical nor empirical grounds for believing that r alone is the principal, or necessarily even an important, arbiter of invasion ability.

We are grateful to Mark Williamson for valuable discussions and for the invitation to take part in this meeting. Joy Bergelson, Phil. Heads and Brad. Hawkins read, and made very helpful comments on, the manuscript, and prevented the invasion of a number of errors.

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Discussion

M. J. CRAWLEY (*Department of Pure and Applied Biology, Imperial College, London, U.K.*). To what degree did host–plant incompatibility limit the success of establishment of introduced herbivorous insects?

J. H. LAWTON. Phytophagous insects may be unable to use many or even most of the plants in their environment for a variety of reasons, including problems of timing, various physical defences (trichomes, waxy cuticles etc.) and plant chemistry, all of which fall under the term ‘host incompatibility’. It does not actually tell us very much, and I did not wish to discuss all the many and varied reasons why colonization by phytophagous insects may fail. As I explained in the paper, I chose to discuss the effects of enemies on colonization not because I think they are necessarily more important than other processes, but because enemies have been relatively ignored.

M. J. CRAWLEY. How is your correlation between invasion success and body size influenced by the well-known positive correlation between body size and breadth of diet (or degree of polyphagy)?

J. H. LAWTON. I do not know. If anything, I would guess that larger, more polyphagous species should find it easier to colonize because they have a greater variety of potential foods. For the insects at least this is not what we see, though figure 2 is based on data from such different taxa of insects that I doubt whether anything sensible can be said about degrees of polyphagy at different positions on the graph.

M. J. Way (*Imperial College, Silwood Park, Ascot, Berks., U.K.*). World distribution patterns are likely also to be important. One would expect widely distributed species to be better invaders. Such widely dispersed species are often small, like aphids.

J. H. Lawton. Two of the most widely distributed birds (naturally distributed, that is) are barn owls and moorhens. The latter is an island colonist: the former is not. I doubt if small size is a factor here!

M. W. Holdgate (*Department of the Environment, 2 Marsham Street, London, U.K.*). Some years ago I analysed the fauna established on Tristan da Cunha islands and pointed out that, as with other oceanic island groups, there were similarities between its makeup and that of 'aerial plankton' caught in nets trailed by aircraft or at sea. However, although dispersal may be size-related, other factors are clearly also involved in establishment.

R. M. May, F.R.S. (*Department of Biology, Princeton University, New Jersey, U.S.A.*). Does the correlation between size of organism and invasion success remain if one leaves the nematodes out of the calculation?

J. H. Lawton. Yes, but weakly. There are a number of odd features about that graph.

Sir Richard Southwood, F.R.S. (*Department of Zoology, South Parks Road, Oxford, U.K.*). There are, as I think Dr Lawton recognizes, several other explanations for his figure 1. In particular I am thinking of those features that relate to an organism's tolerance of variations in its habitat. His 'large organisms' are either mammals and birds, which are warm blooded and therefore less susceptible to weather differences than insects, or fish. One notes that aquatic habitats show less fluctuation than terrestrial environments. Again, larger organisms are in general more polyphagous than smaller ones; therefore, the chances of their establishment would be less dependent on finding exactly the 'right food'.

J. H. Lawton. Actually, the data for larger organisms in figure 1 include mammals, birds, fish, amphibians and reptiles. Fish are apparently intermediate between birds and mammals. However, given the nature of the data and the many possible errors that they could contain, I think it would be foolish to read too much into them. All I would say is that larger organisms are probably better 'buffered' against environmental fluctuations, and this may be one reason why their populations fluctuate less. If, as Sir Richard suggests, they are also more polyphagous, as I have replied to Dr Crawley, this might indeed facilitate colonization.

Sir Richard Southwood, F.R.S. There is another point about predation. Vertebrates tend not to have so many generalized predators as invertebrates.

R. J. O'Connor (*British Trust for Ornithology, Beech Grove, Station Road, Tring, Herts, U.K.*). Some successful recolonists of Britain are species that formerly had man as a major predator, but no longer do so.