Current Problems in Host-specificity Screening

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Abstract

The interpretation of equivocal results on plant species closely-related to the target weed has become the most important issue in host-specificity studies, particularly with increased concern over possible effects on native species. The two main problems are the determination of natural behaviour from experimental studies and the assessment of the ultimate consequences for non-target species in a new environment. Current experimental procedures vary in their value for predicting natural behaviour. Assessing the eventual effect requires consideration of the temporal and spatial distribution of non-target species, their density and the environmental diversity. Finally, a mechanism for decision-making is required.

Introduction

The subject of host-specificity screening continues to provoke discussion and concern, though with a gradually changing emphasis. Currently, the problem is twofold: first, that of measuring host-specificity behaviour in a meaningful manner in an experimental situation, as described by Dunn (1978); and second, the interpretation of such results to predict the effect of an introduction on non-target species. Harris (1983) considered the possible effects on rare as against common species, while Lawton (1985) has treated the whole problem from a more general, theoretical viewpoint. In addition, both Turner (1985) and Andres (1985) considered known effects on non-target species in their discussion of conflict-of-interest situations. The purpose of this account is to review briefly both problem areas, to try to identify where progress has been made in a practical sense and where the major gaps in theory and knowledge still occur.

For the behavioural scientist, an insect’s host range may be defined usefully as those plants on which an insect completes normal development in nature (Hanson 1983). This is only partially relevant to biological control, where the concern is with damage, predicting it in a new environment and with evaluating its significance, but Hanson’s emphasis on normal development in nature is vital to current approaches in this field. What is often measured are those plants on which it is possible for an insect to develop; i.e., the physiological host range. Over this are laid two networks of further restrictions, or sieves: a behavioural sieve (encompassing those visual, chemical and tactile stimuli, the response to which has been evolved by the insect to exploit the resource efficiently and which at the same time ensures the insect’s restriction to a limited range of species); and an ecological sieve (covering spatial and temporal coincidence). It is these two sieves and our progress in defining them which is the major concern. However, there still persist areas of misunderstanding and debate in the conduct and interpretation of classical starvation tests, and it is important to first ensure that the basic starting point is defined adequately.

Non-choice Testing and the Physiological Host range

Non-choice or starvation tests are often ridiculed because they tend to give unhelpful results. Nevertheless, they can be done under laboratory conditions, in quarantine, and they do delimit a host range, which therefore allows the rejection of a large number of plant species irrelevant to further consideration. Clearly also, it might be easier to show that first instar larvae cannot develop in various species by a starvation test in the laboratory, than to study
the oviposition behaviour of a free flying adult under conditions where its behaviour is natural. Bearing in mind the basic importance of these tests, it therefore seems profitable to summarise a few salient points, without referring to the detail of individual techniques.

Adult Feeding

If an adult cannot mature its eggs or complete the rest of its development on a non-target plant species, there is a tendency to discount any feeding which does occur. However, the risk may not be negligible if large numbers are present. Under such conditions, damage to non-hosts by adults leaving their normal host (secondary wandering) would clearly be limited to areas within the normal range of movement from the normal host, but the risk needs to be defined, especially for the Hemiptera. Aphids in particular represent a special case in that minor exploratory feeding could result in virus transmission and quite sophisticated experiments may be necessary to quantify the risk (Briese 1988).

Oviposition

Oviposition is very rarely a damaging act in itself. It has to be linked to subsequent larval development; i.e., of young larvae. It can be related closely to adult feeding and where egg development is dependant on satisfactory nutrition, tests must allow adequate time for the expression of this possibility. There is often no discrimination observed between host and non-host when oviposition is tested in a cage, eggs being laid indiscriminately. This should be recognised as evidence that this is an unsuitable means of showing discriminating behaviour, not a demonstration that it does not exist.

First Instar Larvae

Testing the reaction of first instar larvae by placing them directly on plants is appropriate either when there is a possibility that in nature they might wander to a non-host (even if oviposition was on the normal host), or when it has not been possible to demonstrate a restriction of oviposition to only the normal host-plant. In terms of predicting natural behaviour it is of questionable value for those species with a specialised oviposition restricted to the host or its close relatives, combined with direct larval entry (e.g., weevils which lay in plant stems or developing seed heads).

Late Instar Larvae

For boring, gall-forming and some mining species, this stage is clearly not tested separately from the first instar, though if acceptable to the first instar, the net result is effectively to test the later instar also. There are cases where the plant has proved unsuitable at this stage, often because of physical limitations such as the test plant being too small (e.g., Dialectica scalariella [Zeller] [Lepidoptera: Gracillariidae]) in the leaves of several Boraginaceae (Delfosse and Cullen 1985), or Cochylis atricapitana Sr. (Lepidoptera: Cochylidae) and Platypilla isodactyla Zeller [Lepidoptera: Pterophoridae] in the stems of Senecio spp. (Asteraceae) (Cullen, unpublished data).

The real importance of testing this stage is for free-ranging larvae which might leave the host plant and possibly cause temporary damage. Where secondary wandering is a possibility, the probability of such damage under different circumstances needs to be assessed.

Conclusions from this Testing

Three points need to be kept in mind when assessing the data derived from such basic studies. First, negative results are valuable in that they determine the plant species on which development is not possible and therefore may be rejected from further consideration. Positive results indicate those plant species requiring further consideration. Second, the
categories are not independent of each other: the relevance of some being entirely dependant on the results obtained in others. Third, the ability to complete development is not an absolute criterion. Damage from secondary wandering needs to be taken into consideration.

Whether or not development is completed is important in that a priori it determines whether the agent can exist in the absence of the main host plant species. It should therefore be examined in some detail.

During host-specificity testing of *Longitarsus flavicornis* (Stephens) (Coleoptera: Chrysomelidae), an agent studied for the control of ragwort, *Senecio jacobaea* L. (Asteraceae), adults were confined with several native Australian *Senecio* spp. in turn. Their performance varied with the test species, but feeding and oviposition occurred. In the best case, oviposition was at a rate 50% of that on *S. jacobaea* (Cullen 1979). Further studies showed that some larval development was possible and in a large experiment, four adults were obtained from 385 larvae under ideal conditions (Cullen, unpublished data). Assuming 100% of these were fertile and using the figures of 175 obtained for fecundity, 1.04% for larva to adult survival, and a sex ratio of 1:1, the rate of increase was less than 1.0 under the best conditions. There was an extremely low probability of *L. flavicornis* surviving on this plant species in the field.

So although the capacity to complete development is an important criterion, damage can occur without it, and that it is possible does not necessarily mean that damage will or is even likely to occur. In such cases, it is clearly important to quantify results accurately. If feeding and/or oviposition is less than on the normal host, by how much?

If development can occur on a species other than the normal host, this can introduce another factor into the experimental procedure, in that in some species the developmental experience of the parent or more commonly, the immediate prior experience of a feeding adult or larva, has been shown to influence the subsequent choice or acceptance of hosts (Hovanitz 1969, Jermy *et al.* 1968). Parental experience has not been investigated in the testing procedure for any biological control agent up to now and would rarely be necessary. Sufficient development on an important non-target species for this to be considered a real risk, has normally led to rejection of the agent from further consideration in any case. This situation could change and therefore this possibility may need to be considered further in the future. The effect of the prior feeding experience of an insect is also seldom significant for similar reasons; i.e., feeding on a non-target species sufficient to justify maintaining a population on this species as an alternative to its normal host, prior to testing, would normally preclude the agent from further consideration. Alternatively, the common practice of maintaining newly hatched larvae on test species for considerable periods (or until death) effectively tests the possibility of conditioning. In general, these considerations are more relevant at a level of host restriction below that normally required for biological control agents.

Where the immediate prior experience of a mobile adult or larva can be relevant is in the influence of contact with non-hosts and less-preferred hosts during searching behaviour, which is a characteristic of an insect’s natural environment. It is this more natural situation, which should be considered at this stage if further progress is to be made, particularly with regard to any positive results obtained.

**Choice**

While still subject to the constraints of the laboratory system, considerable benefit can be obtained from the introduction of the principal element more typical of natural systems, that of choice. Choice tests also have the advantage of often being feasible under laboratory conditions and are therefore frequently utilised. Amid varying designs, the common principle is the presence of the normal host plant at the same time as the test species. Choice tests will almost always allow a closer definition of the likely host range, but the presence of non-hosts or less preferred hosts in the insect’s experimental environment, while mimicking the natural situation more effectively, introduces a further factor. Some insects have been demonstrated to have the capacity to learn from prior experience (Traynier 1979). Their ability to distinguish between hosts and non-hosts may well be reinforced by exposure to non-hosts
over a period of time. On the one hand, this could produce a variation in response with time of exposure to a range of hosts of varying acceptability, and on the other, the presence of completely unrelated non-hosts may influence the degree of distinction between real hosts and related partial hosts. The former effect was tested for in the study of L. flavicornis in the presence of native Australian Senecio spp. (Cullen 1979), with no significant difference in behaviour noted over time, but the latter effect has never been a feature of laboratory choice experiments though it is the normal situation in the field.

A choice test may not be appropriate in all situations. Where the normal host is scarce or has been removed (e.g., many cases of secondary wandering), the real choice in nature is between feeding on a non host and wandering on, with the risk of starvation. The element of choice is fundamental to an insect's behaviour under natural conditions, but it is often not possible to reproduce the form of that choice under controlled laboratory conditions.

Field testing

When an insect searches for and accepts a host plant in the field, the behavioural sequence is mediated by a chain of responses to stimuli from the environment, from colour and plant structure, from a plant's chemical composition and often its surface texture (May and Ahmad 1983). Any restriction on the testing environment will remove a number of stimuli, the result being not to block a behavioural sequence, but to remove the selection process normally applied at that point, leading to an increased host range as determined by the testing environment. The only method of ensuring there are no such restrictions and of predicting behaviour under natural conditions is clearly to study the behaviour under such conditions. When the number of plants remaining to be tested has been reduced to a reasonable number, it should not be too difficult to do so, but this area has not been pursued as vigourously as it might.

To examine the reaction of a candidate agent to the presence of a test plant in the agent's normal environment, a choice test is often the most appropriate and having located a population of the insect on its host plant, the only modification usually required is to interplant the test species among the host plant population (e.g., Harley 1969). Slightly more formalised variations include the planting of host and non host in a set design; e.g., a Latin square or randomised block design, adjacent to a natural population. These need not preclude the inclusion of other "weedy" non-host species and both open and weedy formal designs have recently been used in the field by Cullen (1989).

However, there are again some situations where a choice test may not be the most appropriate. If the adults or larvae are likely to find themselves without the host, maintenance of specificity should be tested under such conditions. A form of this was advocated by Dunn (1978), involving killing the host in the field after establishment of the agent on it, the host plant being surrounded by test plants. Cullen (1988) carried out a similar test by placing adult Pachymerus cordiner Germer (Coleoptera: Curculionidae) on small stands of non hosts some distance away from any host. These are effectively field starvation tests, giving the insect the choice of accepting a non-host or of wandering away at the risk of dying.

Practical Problems with Natural Conditions

Despite the obvious desirability of carrying out studies under natural field conditions, there are often good reasons why this is not possible, principally concerned with either low insect density or quarantine considerations. If the prevailing normal insect density in the field is too low to obtain meaningful results, it may be possible to build it up for limited periods, though this may involve some behavioural disturbance by capture and release. Also, this is clearly not possible for many flying insects. However, it is already an instructive result if the normal insect density in the presence of an equilibrium population level of the target weed is too low to record any damage to a test species.
Another problem is whether the required test plants are permitted to be grown in the field, in the country of origin of the insect. Where only crop plants are involved, most of which are fairly universal, it may not be too difficult, though some countries will not permit the introduction of cultivars not already present in the country. However for native species, it is clearly impossible to simply plant them out in an overseas country, where there is always the risk that they may themselves establish and become weeds. Nevertheless, it is sometimes possible to do the next best thing and use potted plants under careful supervision; obviously not producing seed, without any root contact with the soil and either being destroyed or taken back to quarantine afterwards. European thistle and knapweed insects have been tested against North American Cirsium spp. (Asteraceae) in this way for the first time in the open in Italy (Rizza et al. 1988, Dunn pers. comm.) and in Greece (Sobhian pers. comm.) while Cullen (1989) has recently tested P. cordiger against Australian native Boraginaceae in Greece.

A final option is the possibility of carrying out such tests in the country of introduction, as suggested by Dunn (1978). Normally this would be absolutely impossible with an as yet foreign insect, but it may be possible to use insects treated in some way so as to be sterile, or to use them in environments where they could be killed afterwards or die naturally. This has not been undertaken anywhere yet, but the possibility should not be overlooked.

When Natural Conditions are Unattainable

When it proves impossible to carry out studies on the unfettered insect, freely finding and rejecting plants under natural conditions, restrictions on the insect's host finding behaviour have to be imposed, but need to be recognised and kept to the minimum.

The first and major restriction is often a cage; to confine the agent and to increase its density. If this is the only problem, it may still be possible to carry out the work in the field (Harley 1969) and for some species valid and valuable results may be obtained. For others it is more difficult; e.g., many Diptera. The size of a cage is possibly an important factor in many cases, though contact with any barrier, regardless of distance moved, is sometimes known to disrupt behaviour. One compromise was suggested by Dunn (1978), the partial cage, which served to concentrate insects initially, but to allow them to escape and disperse if the plant was rejected.

However, the very object of a cage is to confine, the more so in a laboratory or a quarantine building and hence a major restriction has been placed on the insect's behaviour. It is important to accept as few more as possible. If the behaviour of a species is studied over a period of years, it may be possible to define those stimuli that control host location and acceptance and ensure that these are present. Otherwise the cage environment should be kept as natural as possible. For an active, wandering adult or larva, space is likely to be important so this should be maximised. Other conditions (e.g., light, temperature and R.H.) may also be important. For oviposition and development of larvae, the size and stage of growth of the plant is often important.

During host-specificity studies of P. cordiger, dramatic differences in behaviour were found when the adults were given as close to natural conditions as possible compared with standard laboratory conditions. Precautions taken included as large a cage as practicable, of the least obstructive structure as possible, positioned in full sunlight, with plants hardened off outside, arranged so as to be growing through an open, dry, sandy soil surface on the base of the cage. Choice tests under these conditions showed very clear feeding and oviposition preferences compared with meaningless results obtained with similar tests under much more artificial conditions (Cullen 1989). An additional feature of this study was the inclusion of a test species in the same genus as the target weed, which was normally clearly distinguished and avoided in the field in the country of origin. This served as a control for the effect of cage conditions and some feeding on it did show that the insect's behaviour was still not completely comparable to that under field conditions, prompting further experimentation without any cages.
In another study, the complete area of a 3 x 4 m quarantine room was converted to resemble a field area with plants of *Chondrilla juncea* L. (Asteraceae) and lettuce, *Lactuca sativa* L. (Asteraceae) arranged in a set pattern. Partially developed larvae of the moth *Opoplopsamma weverheimsteini* (Lepidoptera: Phycitidae) had been shown to be able to occasionally complete development on lettuce roots, though this had not been observed in the field and first instars were unable to develop on any species other than the normal host, *C. juncea* (Hasan and Wapshere 1977). To test the possibility of damage from secondary wandering following the death of their host, larvae were established on *C. juncea* rosettes in the middle of the experimental area. These host plants were to be killed later, the larvae being forced to leave. In one direction, they could move into an area of mixed host and test plants and then an area of tests plants, while in the other direction there was a metre of bare ground before reaching an area of solely test plants. This experiment had to be terminated before completion, but some host plants had already died and examination of lettuce plants showed occasional nibbles, but no establishment or significant damage, even in the semi starvation situation one metre away.

This brief review of testing procedures serves to reinforce the truism that the better the knowledge of the agent and of the questions which need to be asked, the more relevant and valuable are likely to be the results.

Given the best set of experimental data obtainable under the circumstances, it must then be put into its environmental context to assess what is likely to be the real significance of any sort of damage observed on a non-target species.

**The Ecological Sieve**

*Defining the Problem*

There are a number of ecological questions which need to be asked so as to better define the circumstances and probability of any risk suggested from the testing results.

*Spatial distribution.* Three spatially-related questions are most important:

1. Is the agent likely to maintain itself indefinitely on a non-target species or will it be dependant on the presence of the target weed - even if, as in the example quoted of *L. flavicornis*, it is possible to develop completely on another species? This clearly determines whether the agent could potentially damage a non-target over all its range or whether its distribution will be confined to the weed, in which case the extent to which this is sympatric with the non-target species can be assessed.

2. Are there any known ecological or physiological limits on the agent; e.g., temperature or moisture limits, other environmental requirements, soil types, symbiotic species, nutrient requirements of the plant, etc., which may determine the limits of its distributions? The prediction of an insect or any other agent's distribution from a combination of physiological and climatic data is rarely possible with the necessary precision at the pre-introduction stage: though with the benefit of hindsight, explanations of eventual distribution are commonly invoked on such grounds after the event; e.g., *Agasticles hygrophilus* Selman & Vogt (Coleoptera: Chrysomelidae), *Perapion antiquum* (Gyllenhal) (Coleoptera: Curculionidae), *Coleophora parthenica* Meyrick (Lepidoptera: Coleophoridae), *Apion fasciostre* F. (Coleoptera: Apionidae), *Chrysolina quadrigemina* Saffuan (Coleoptera: Chrysomelidae) (Julien 1987). A comparison of an agent's known native climatic range with the climate of the area of introduction is a more feasible, readily applicable method and this can be formalised in a computerised form; e.g., Climex (Sutherst and Maywald 1985), though predictions about where an agent will not occur must still be made with caution.

3. Are there geographic boundaries which would restrict distribution to certain regions where the species may be released, such as oceans, deserts or mountains? Large water masses are accepted as barriers between countries and continents, mountain ranges are known to be effective barriers, and in Australia, inland desert regions are recognised as effective.
Temporal distribution. Does the phenology of a non-target species coincide with the agent's period of activity? For example, for the weevil *P. cordiger*, a living rootstock in summer is necessary, i.e. a perennial, or a summer annual species like its host. One of the genera tested, *Myosotis* (Boraginaceae), only has winter annual species. It was enormously difficult to even maintain such plants for tests carried out in summer, and the fact that oviposition does occur and larval development can be obtained on this species is meaningless as the plants will be dying when insects emerge.

Performance on non-target host species. If the results from the testing procedure have been appropriately quantified, it should be possible to suggest whether, all things being equal, the damage will be the same as on the host, 50% of it or perhaps only 10%. Is it only likely to occur when agent populations are high?

Consideration of each of these factors should yield a more precise estimate as to what extent, when and under what circumstances, if any, damage can be expected.

Assessing the Significance of Damage

Does damage of a particular type on a non-target species, at for example 50% of the level which is expected to decrease the target weed population, necessarily mean a significant reduction of that species? This is the type of question which is relevant at this point and clearly concerns ecological prediction. The development of this area of plant-agent interaction in plant population dynamics is still in its infancy and as yet only fairly general guidelines are available. It is convenient to distinguish between non-target economic plants and native species. For economic species, effects are easier to quantify because the value is precisely defined. It is an artificial, manipulable environment, probably with a known tendency to pest attack and most importantly, may well have control measures which would take account of any newcomers. Any loss or increased cost is a matter of economics and estimates can be made and entered on the debit side of the ledger.

The situation is nowhere near as clear with native species, where, in a complex and variable natural environment, the concern is about aesthetics, decline in numbers, possible extinction and decrease of the genetic pool.

Density Dependence

A particularly important consideration for native species is that of density. The target weed is a problem because of an unnaturally high density and the aim is to achieve a lower, natural density, typical of its equilibrium level in its country of origin. At such a level, further decline is not expected; the weed becomes too difficult to find, the agent is far more dispersed, etc. Thus there should not be too much impact on another species already in equilibrium with its environment, including its own suite of specialised natural enemies. While the target weed is still at a high density; i.e., until the population of the new agent has equilibrated, a greater level of damage might be sustained on a non-target species, in the vicinity. Once equilibrium is attained, or in areas away from the target weed, little effect might be expected on the population level of an endemic species, as its density is lower; and the lower the density, the lower the probability of an effect. Thus it also follows that if there is to be an effect on a native species, it is more likely on a common species and least likely on a sparsely distributed or endangered species (Harris 1985).

It is important to keep in mind that it is specialist agents, stenophagous species, which are under discussion. It is not difficult to find examples of generalist species introduced into new environments and having an effect on native species, but there are very few examples of specialists. This might be seen as being in conflict with successful attempts at biological control of native species by the introduction of exotic natural enemies. However, the extent to which such native species are still at a natural equilibrium level is questionable. They have often become weeds because of an increased density brought about by changes in the environment. The control of *Opuntia* spp. (Cactaceae) on Santa Cruz Island (Goeden et al. 1967) may well fall in this category, aided by a not too precise specialisation of the agent used.
Diversity

In a consideration of the probability of damage to a native species in disturbed versus native environments, environmental diversity is an important factor. Host plants are more difficult to find in more complex and diverse environments (Root 1973). The effect is more pronounced with specialists, for whom it is a matter of locating a small host patch size in a mass of non-hosts. With decreasing specialisation, a greater proportion of plants become acceptable, host patch size increases and there are less non-hosts to confuse host finding behaviour (Stanton 1983).

These considerations of density and diversity both point to a lesser effect on a native species in a native environment; i.e., a greater effect is to be expected on a native species where it is at a high density, in a simplified and/or changed environment; e.g., agricultural areas, than in the native habitat, which is normally the area of greater concern.

However, while data are scarce, there are some cases known of development on, and damage by introduced agents on some native species. These have all been in North America and have involved Voglia malloi Pastrana (Lepidoptera: Pyralidae), introduced for control of alligator weed, Alternanthera phyloexoides (Mart.) Griseb. (Amaranthaceae) developing on Philoxerus vermicularis (L.) R.Br. (Amaranthaceae), Rhinocyllus conicus Froelich (Coleoptera: Curculionidae) for control of various thistles, developing on native Cirsium spp. (Asteraceae), Agrilus hyperici (Creutzer) (Coleoptera: Buprestidae), C. quadrigemina, Zeuxidiplosis giardi Kieffer (Diptera: Cecidomyiidae), all for control of Hypericum perforatum L. (Clusiaceae) developing on Hypericum concinnum Benth. (Clusiaceae) and Microlarinus spp. (Coleoptera: Curculionidae) introduced against Tribulus terrestris L. (Zygophyllaceae) developing on native Kallstroemia spp. (Zygophyllaceae) (Turner 1985).

Utilisation of the native species by V. malloi and Microlarinus spp. has been quite low (Turner 1985) and impact therefore negligible. On the native Cirsium spp., utilisation by R. conicus has varied from low in Montana (Rees 1977) to high in California (Turner 1985) and the degree of impact is still under study. H. concinnun has apparently been reduced in size in some areas by C. quadrigemina and A. hyperici and the latter may also shorten the life span or kill plants. However, H. concinnun remains a common element in the communities to which it is native (Andres 1985). We are clearly a long way from a state of biological pollution as suggested by Howarth (1983), but such cases need careful documentation and study. Interestingly, two other North American Hypericum spp. sympatric with H. perforatum over part of its range and also fed on by C. quadrigemina under experimental conditions, have not been recorded as hosts in the field, probably due to quite slight habitat differences (Andres 1985).

A Matter of Judgement

Having assessed the information as best one can, the final question is one of judgement, for which the key elements are not only good information, but also a mechanism for assessment and decision making. It may be that some harm to native species, particularly if its limits can be quantified in some way, could be accepted, rather than reflexly rejected, when balanced against a greater overall benefit, if there is a mechanism for objective and informed assessment. This is where the relevant systems in several countries are still feeling their way.

An extremely significant decision was made recently in Australia, where permission was given to release a moth, Euclasta whalleyi Popescu-Gorj (Lepidoptera: Pyralidae) to attack rubber vine, Cryptostegia grandiflora R.Br. (Asclepiadaceae), in the knowledge that it will develop on two native species (McFadyen and Turnour 1987). One of these was considered not being at risk due to geographical isolation, while possible damage to the other was assessed as posing no risk to its gene pool and physically limited by its lower density compared with that of the target weed. Most importantly however, any damage to the native species by E. whalleyi was considered a much smaller risk than that posed by the target weed, which is invading the habitat of the native species.

There are almost certainly some decisions which are going to cause more problems than this one and clear mechanisms for discussion, mediation and authoritative decision (Turner 1985)
will become crucial. Australia has the *Biological Control Act 1984* (Commonwealth of Australia 1984) a legal mechanism, including a formal public inquiry, but the aim is really to avert litigation by giving legal authority to a decision to release. This is of necessity a time-, money- and energy-consuming process and should really only be considered as a last resort.

Conclusions

This account started by considering the relatively straightforward laboratory experimentation which has formed the basis of host-specificity studies for as long biological control has been practised. The shortcomings of this approach and the subsequent emphasis on trying to predict behaviour and its ecological consequences in nature and on the problems of administrative decision-making should not be seen as diminishing the value of the traditional approach. It is necessary to retain the use of the standard non-choice and choice testing. Not only is it sometimes difficult to do otherwise, but it does remove a large number of plant species from further consideration. It is for those remaining that the use of more natural conditions needs to be pursued. When this is not possible, a combination of as much knowledge of the agent's biology and behaviour as possible, a certain amount of experimental improvisation and careful interpretation must be relied on.

In many respects therefore we are still doing the experiment first and may have to ask whether it is meaningful afterwards. This is not only because it may be all that is possible, but more importantly, because decisions on meaningfulness and responsibility for those decisions, remains a very difficult and inadequately researched area.

References


Traynier, R.M.M. 1979. Long-term changes in the oviposition behaviour of the cabbage butterfly, Pieris rapae, induced by contact with plants. Physiol. Ent. 4:87-96.