

Life history perspectives on pest insects: What's the use?

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Abstract In his seminal 1954 paper on the 'population consequences of life history phenomena', Cole noted that 'these computations may have practical value in dealing with valuable or noxious species'. In the present paper, the question is asked: 'is research based on evolutionary perspectives in general, and life history theory specifically, really useful for dealing with insect pests?' Perhaps such theory-based research is rather a luxury: time and resources would be better spent on entirely applied aspects of the problem. The conclusion of the present discussion is that having an evolutionary perspective guiding research is actually a very cost-effective way of dealing with applied problems, as it provides a clear basis for interpretations, generalizations and predictions. Life history theory is a very central and necessary part of both population ecology and general evolutionary theory, and its specific usefulness in pest forecasting and management are discussed. Nevertheless, our ability to predict insect population dynamics is still limited, and so is our ability to make use of an insect's life history traits to predict its propensity to become a pest. I suggest that the former shortcoming is largely due to poor understanding of insect life history plasticity. This, in turn, may partly be due to a paucity of studies where reaction norms are investigated as putative adaptations. I suggest that the latter shortcoming is due to problems inherent with studying life history traits as adaptations, for example the lack of an independent fitness model and the fact that life histories tend to form syndromes of coadapted traits. These points are illustrated with examples from my own work on non-pest butterflies and from insect–*Eucalyptus* systems.

Key words: demography, IPM, life history theory, optimality, outbreak forecasting, pest insects, phenotypic plasticity.

INTRODUCTION

In 1954 Cole published a seminal paper entitled 'The population consequences of life history phenomena'. Cole outlined, as had others before him, how population growth is critically affected by even the slightest variation in demographic parameters such as fecundity, survival to reproductive age and age at first reproduction. However, Cole took this several steps further. He noted that evolutionary fitness must be equally strongly affected by such variation, leading on to a discussion, from a theoretical standpoint, of which types of life cycles we should expect to find in nature. He stressed that life history traits should be viewed as putative adaptations to specific environments, and it is in this sense that Cole's paper marks the start of modern life history theory.

Cole also noted that 'these computations may have practical value in dealing with valuable or noxious species'. In the present paper, I examine this statement critically. I ask the question 'if research based on evolutionary theory in general, and on life history perspectives specifically, really is useful for dealing with insect pests?'. Is not such research rather a luxury, interesting in its own right, but not really what is critically needed? Isn't it the case that time and resources

are better spent directly on entirely applied aspects of the problem, such as quantifying pest numbers, finding resistant plants or ways of avoiding or dealing with pest outbreaks? I deal with this question in a way that presumes no prior knowledge of life history theory.

I will also discuss the reasons for our limited ability to forecast pest population dynamics, and our limited understanding of the relationship between traits of insects and their propensity to become pests.

WHAT IS LIFE HISTORY THEORY?

Life history traits

Before attempting to answer the questions put forward in the introduction, I must clarify what I mean by life history theory. First, what are life history traits, really? We are all familiar with some other types of traits of organisms; usually they are divided into morphological, physiological and behavioural traits. Life history traits are elusive in that they do not fit well into any of these categories, but have aspects of all three.

A list of life history traits would typically include those having to do with reproduction and development, such as number of offspring, offspring mass, age and mass at first reproduction, number of reproductive events and the intervals between them. Often other

major aspects of the life cycle are added to the list, such as adaptations for diapause and migration, and patterns of senescence and life span. What these traits all have in common is that they describe the life cycle of the organism rather than how the organism is shaped, how it works internally, or how it behaves. Although life history traits are always influenced by or even determined by morphological, physiological or behavioural traits, these dimensions are not the primary focus in life history theory. Perhaps the best definition of life history traits is that they are traits quantitatively describing transitions between different parts of the life cycle.

Two things determine the probability of transferring from one part of the life cycle to the next: life history traits and the chances of survival. The frequency of surviving individuals (or the reverse: rates of mortality) is not in itself a life history trait because it is not intrinsic to the organism (except perhaps at old age). However, these percentages are often strongly affected by variation in life history traits such as patterns of reproduction (e.g. Tatar *et al.* 1993; Blanckenhorn 1994). The reverse is also true: variation in the chances of survival is believed to be one of the most important aspects of the environment when it comes to shaping adaptive life histories (Cole 1954; Stearns 1976; Southwood 1977). Therefore, survival patterns are important parts of life history without being life history traits per se.

Total life span is a somewhat special case. It is totally determined by mortality rates summed up over the life cycle, yet it has often been treated as a life history trait in its own right (see Rose (1991) for references). This often reflects a belief that life span is at least partly determined by an intrinsic factor or factors causing senescence and increased rates of mortality at old age.

Three theories in one

'Life history theory' can actually be seen as at least three separate but interacting bodies of theory (Fig. 1).

1. Theory regarding demography and population dynamics

The rate of increase of a population can be directly determined from a life table summarizing age-specific reproduction and survival to these ages. Hence, the study of life history traits is always an integral part of population ecology (Begon *et al.* 1996).

2. Theory regarding fitness and optimality

The relative fitness of a certain trait (e.g. a morphological trait) will be strongly influenced by the life histories of individuals carrying this trait. If a green-coloured genetic variety of beetles produces more eggs than another brown variety, then the green beetles will

soon entirely replace the brown ones, unless they have another advantage such as shorter generation times. This is true to the extent that most models of fitness (e.g. the intrinsic rate of increase or lifetime reproductive success) are composed entirely of life history traits, together with probabilities of surviving different transitions in the life cycle. Most models of fitness are really models of population growth: the higher the capacity for growth, the higher the fitness. This is based on an assumption (often implicit) that at least occasionally there will be some room for increases in population size. The genetic variety with the highest capacity to exploit such opportunities will tend to increase in frequency in the population.

Models of fitness are necessary for approaches in evolutionary biology where predictions regarding what 'should' be the observed traits of organisms are

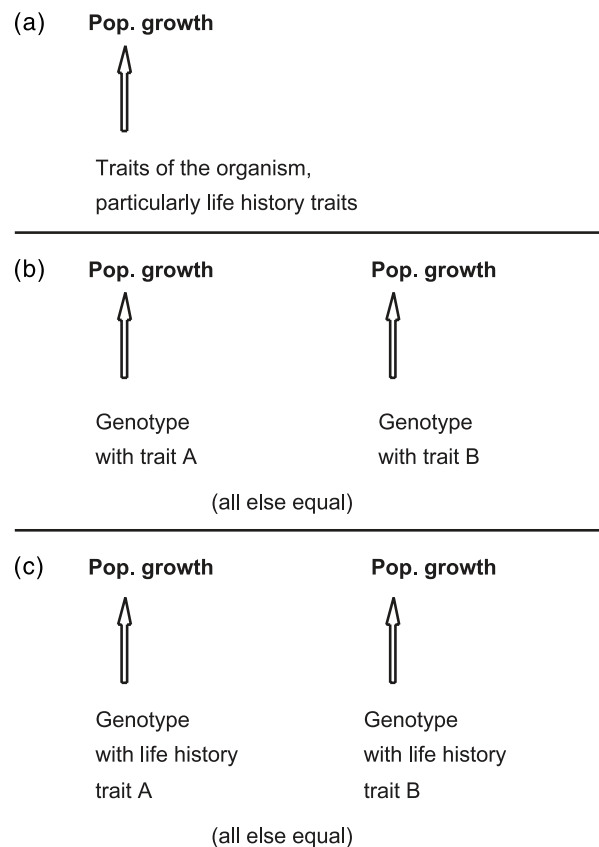


Fig. 1. The three bodies of life history theory and how they are interrelated. (a) Theory for demography and population dynamics. Variation in life history traits determines the potential for population growth, and can hence potentially explain much of population dynamics. (b) Theory for fitness and optimality. The potential for population growth is used as a model of evolutionary fitness. From optimality, we are most likely to observe the genetically determined trait that results in the most rapid increase in numbers. (c) Theory for life cycles and life history adaptation. The aforementioned principle is also applied to the life history traits themselves, in an attempt to view the life cycle as an adaptation to the environment.

made, based on some kind of evolutionary reasoning (Stearns 1982; Grafen 1988; Kozłowski & Janczur 1994). In the following, I make no distinction between 'true' optimality theory (finding the genotype that maximizes fitness) and approaches aimed more at finding evolutionarily stable strategies that cannot be invaded by competing genotypes (see also Kozłowski & Janczur 1994). Rather, for the present purposes, I include both under the general label of 'optimality reasoning'.

3. Theory of life cycles and life history adaptations

We have seen above that life history traits largely determine population fluctuations as well as fitness, but ultimately we want to understand what determines the life history traits and the shape of the life cycles themselves. This is the third body of 'life history theory' (Horn 1978; Roff 1992; Stearns 1992).

THEORY OF DEMOGRAPHY AND POPULATION DYNAMICS

Do we need forecasting for pests?

Few can doubt the importance of population forecasting for pest management, and therefore the usefulness of the first body of life history theory, the one dealing with population dynamics. Integrated pest management (IPM; Cate & Hinkle 1994) typically involves monitoring insect numbers and environmental conditions, with the use of pesticides only if absolutely necessary. In IPM, decisions are based on expectations of future population levels. The only alternative to IPM would be to wait and see if damage levels become high and then always apply chemicals (other types of control are not likely to be feasible at this late stage). Such a practice is not sustainable, not only because of the potential environmental hazards but also because insects evolve resistance at a faster rate than we can invent new pesticides (Mallet 1989). To use chemicals as seldom as possible will slow this process, perhaps even to a level where it is countered by fitness advantages in non-resistant insects, hence avoiding the evolution of resistance. Pest forecasting in itself does not necessarily involve evolutionary reasoning. It can be a strictly mechanistic practice of mapping the essential environmental determinants of fluctuations in insect numbers.

Fluctuations in *Eucalyptus* pests

There have been few attempts at explaining fluctuations in the numbers of *Eucalyptus* pests, but some examples are reviewed in Carne and Taylor (1978) and Ohmart and Edwards (1991). One concerns outbreaks of the giant phasmatids *Didymuria*, discussed by Readshaw (1965). An important factor in determining when these

outbreaks will occur is evidently variation in temperature, which in turn affects the frequency of individuals entering egg diapause and hence whether the life cycle will last for 1 or 2 years (Readshaw & Bedford 1971). In life history terms, when diapause is averted in a large fraction of individuals, the average age at first reproduction is drastically lower, generation times are shorter and there is a larger capacity for population increase. It is also important to study the rest of the community; mortality from insectivorous birds and insect parasites may be of great importance in this system (but see also Campbell (1974)). Hughes and Westoby (1992) showed that the eggs of many phasmatids seem to be specially adapted for promoting the removal and burial of eggs by ants. The eggs have a 'capitulum', similar to the elaiosomes of ant-dispersed seeds. As expected, only species that drop their eggs freely onto litter have these egg adaptations, not those that bury the eggs themselves or conceal them by gluing them to vegetation. However, *Didymuria* eggs apparently lack capitula, although females drop eggs, and although burial of seeds reduces parasitism by wasps in *Didymuria violescens* (Hughes & Westoby 1992). In other words, there may be more opportunity for wasps to cause egg mortality in this system than in many other phasmatids. Not only the abundance of wasps, but also the details of wasp search behaviour may be important in determining whether wasps can dampen the fluctuations in *Didymuria* populations.

Another *Eucalyptus* pest insect that has been studied in some detail is the psyllid *Cardiaspina albitextura*, which has been studied by Clark (1964, 1975). The interpretation suggested by Clark involves a population normally kept in check by predators and parasites (*Psyllaephagus*), but with the parasites in turn being attacked by hyperparasites (other species of *Psyllaephagus* and *Echthroplexis psyllae*). In the study area, there are two generations per year plus a partial third generation, resulting in a large capacity for yearly increase. Low temperature evidently reduces the percentage parasitism of the psyllids, leading to the realization of some of this capacity for population increase. This takes the population to a level where hyperparasites are attracted, which reduce parasitism even more. The population increase is eventually stopped by damage to foliage (lack of good oviposition sites) and reduced fecundity of females (apparently this is a plastic life history trait). The extent of the decrease is dependent on predation patterns and foliage shedding by the trees. The population can increase again to cause a new outbreak if the number of psyllids (and their parasites) is still high enough to attract hyperparasites.

The life system

From these examples, it may sound as if the population dynamics are ultimately determined by fluctuations in

the environment, particularly in weather and natural enemies. This view is not uncommon (e.g. Berryman (1996)). However, the life histories of the insects are equally important. Development time and patterns of reproduction will determine how populations respond to environmental fluctuations, if at all (see also Tammaru & Haukioja (1996)). Interestingly, Clark (1964) noted specifically that the insect's traits are as important as the environment, and he suggested the term 'life system' for this kind of interaction between species and environment. The term 'life system' is still in use (Kennedy & Storer 2000).

From these examples we can see another very common theme in insect population dynamics: the importance of overall life cycle regulation, especially diapause control. Long-term forecasting must ultimately be based on knowledge of the major aspects of the pest insect's life cycle, and of how it is regulated. How many generations are there per year? How long is each generation? In what developmental stage does diapause occur (if at all)? How is diapause induced and broken? Are there further complications such as extra instars induced under some circumstances? Is there a migratory phase and, if so, how is it induced? Without this basic knowledge to guide data collection and interpretation, forecasting will be impossible or very short term at best.

I think it is fair to say that our understanding of insect population dynamics is still limited. It may be possible to forecast a few weeks ahead, but even this type of forecasting is often erratic. Predicting year-to-year fluctuations is typically beyond our capabilities, and even understanding them with the benefit of hindsight is very difficult. The reason for this is of course the sheer complexity of the problem. How would we go about tracking the effects of an independent variable such as weather, which has strong direct and indirect effects on insect life history and population dynamics? We need to understand not only the life cycle of the insect, how it is affected by weather and by host plant quality, but also how the host plant quality is affected by weather, and by the insect! We need to know if there are alternative host plants, and if so how they are affected, and how they are ranked by ovipositing females. We need to know something about natural enemies and important competing species: how they are affected by weather, by variation in plant characteristics, and by their own enemies. The list can go on. Clearly, we need some guidance in this search for explanations.

THEORY OF FITNESS AND OPTIMALITY

Understanding the life system

Rabb and Guthrie (1970) wrote that 'pest management is the reduction of pest problems by actions *selected*

after the life systems of the pests are understood and the ecological as well as economic consequences of these actions have been predicted, as accurately as possible, to be in the best interest of mankind' (italics are mine).

How can we 'understand' the life system of the pest? To be able to do this we need a unifying theory on which to base explanations, generalizations and predictions. Because nature is a product of evolution, evolutionary theory can provide this theoretical base. Furthermore, if we believe that processes of adaptation in current or previous environments have shaped organisms, we can use optimality reasoning. We can ask ourselves what the traits of an organism will be like if traits resulting in higher evolutionary fitness are typically those that will be observed.

Note that it is not necessary to believe in the extremes of 'adaptationism' (Orzack & Sober 1994) in order to make use of optimality reasoning. It is enough to believe that natural selection is a powerful process, resulting in some degree of adaptation. It may well be that many traits of organisms are not perfectly adapted to the environment (especially not the current one), because there are many constraints to evolution by natural selection (Wanntorp 1983). However, it is not very fruitful to base predictions on such constraints, at least not without a backdrop of expectations from optimality (e.g. Futuyma *et al.* 1993; Price 1994). We may not always be able to understand or predict the pattern in exact quantitative detail. This is true when the observed pattern is not entirely due to adaptation, or when adaptive processes other than the one under study are partly responsible for shaping it (in reality, many so-called 'constraints' are of this type). However, it is still possible to make qualitative predictions from optimality concerning, for example, how species, populations or genotypes are expected to differ (Nylin 1994; Gotthard & Nylin 1995).

To make predictions from optimality reasoning, or even to interpret observed patterns and generalize to other organisms, we need models of fitness. We do not really *know* which traits result in the highest fitness unless we have followed the population for generations (and if we have, explanations based on optimality would be entirely circular). What is needed is a fitness model that is independent of the studied trait (Stearns 1982). As noted previously, the relationship between fitness, population dynamics and life history is so strong that most fitness models are really models of population growth, composed of life history traits and patterns of survival/mortality (Fig. 1).

Evolutionary studies of pest insects

There are many examples of research areas that are essential for pest management and which have gained greatly from evolutionary theory. Among them could be mentioned the study of animal behaviour in general,

but also the study of natural enemies and biological control (Luck 1990), insect learning (Prokopy & Lewis 1993), sexual selection (Boake *et al.* 1996) and the study of insect–host plant relationships (Bernays & Chapman 1994). Patterns observed empirically are often explained as adaptations in these fields, but when dealing with pest insects there are rather few attempts at making predictions based on optimality.

The study of seasonal adaptations is another such research area that is of particular importance in the present context (Tauber *et al.* 1986). It covers many important aspects of the life cycle regulation of insects, such as regulation of development, diapause, migration and seasonally occurring forms of the insect, by photoperiod and other seasonal cues. Life cycle regulation in insects is often facultative, in other words an example of phenotypic plasticity (Nylin & Gotthard 1998). The individual insect will either enter diapause or develop directly to sexual maturation (and produce a generation of offspring the same season) according to, for example, photoperiod at a sensitive stage in the life cycle. As mentioned previously, this type of knowledge is crucial for forecasting and hence for pest management.

One source of erratic forecasting may be that the importance of low-level plasticity, within rather than among developmental pathways, is not appreciated enough (Nylin & Gotthard 1998). We can attempt to calculate if the population will enter diapause or not by simply summing up the effects of the (expected) temperature on growth. Will the sensitive stage in the life cycle be reached before or after the photoperiodic threshold has passed? However, the insect may well have quantitative responses to photoperiod in addition to the qualitative (threshold) response. It may speed up growth and development in response to photoperiods signalling a late date, having time for another generation although simple calculations say that it should not. There can also be complex interactions between temperature and photoperiod (see subsequent discussion). Similarly, host plant quality affects growth directly ('non-adaptively' in the case of poor quality host plants) but can also be a seasonal cue, as well as an indicator of future conditions in itself (Wedell *et al.* 1997). Poor host plant quality today suggests poor quality in the future, and hence that another generation may not be possible. Growth rates can then be reduced adaptively rather than non-adaptively, presuming that high growth rates carry costs such as increased risks of starvation or predation and hence should be avoided if possible (Gotthard *et al.* 1994).

Understanding plasticity: examples from butterflies

As we have seen, understanding phenotypic plasticity (in pests, plants, enemies and competitors) is at the

heart of understanding insect population dynamics. Understanding plasticity amounts to understanding the evolution of reaction norms, that is, the range of phenotypes displayed by a single genotype over a range of environments experienced during ontogeny (Nylin 1994; Gotthard & Nylin 1995). By way of illustrating many of the aforementioned points and those mentioned in the Discussion section, I will briefly delineate some results from my own research group, which studied the evolution of seasonal plasticity with butterflies as model insects. In particular, this section should serve to show how optimality reasoning gives us the means to interpret and explain, to generalize and to predict.

1. Photoperiodic thresholds for diapause induction have been observed to show latitudinal variation among populations in relatively stationary insects (Danilevskii 1965). This can be easily explained in adaptive terms, and for this reason it is possible to generalize to other insects under similar circumstances and thus predict similar patterns. Latitudinal variation was indeed found in, for example, *Polygonia c-album* (Nylin 1989) and *Pararge aegeria* (Nylin *et al.* 1995b).
2. Variation in photoperiodic thresholds within populations has seen comparatively little study. Ignorance of this type of variation may be one source of erratic forecasting and of difficulties with explanations using hindsight. It could be expected that often some proportion of the population will follow a life cycle with a smaller number of generations per year than the average. This is because in some very poor years, only these individuals will succeed in giving rise to offspring that reproduce the next year. This reasoning was used to explain such a pattern in *Pieris napi* (Wiklund *et al.* 1991), but to my knowledge, predictive studies are lacking.
3. Males often enter the reproductive population before females, a phenomenon known as protandry. When monitoring insects for pest management it is important to be aware of such temporal patterns. The pattern itself can be explained by sexual selection theory (Wiklund & Fagerström 1977), which can also be used to predict exceptions, as was done in a comparative study of two populations of *Pararge aegeria* (Nylin *et al.* 1993). From protandry theory, males can also be *predicted* to be more prone to enter diapause than females under near-critical conditions, that is, the sexes should differ in photoperiodic thresholds (Wiklund *et al.* 1992). This was indeed found in several species of butterfly, and was also used to explain the same pattern in another butterfly, which was not studied by us (Nylin *et al.* 1995a).
4. In crickets it has been observed that development time becomes progressively shorter as the day-lengths used for rearing become shorter (Masaki 1978). This was given the adaptive explanation that

it serves to ensure that all individuals reach the developmental stage suited for diapause in time for winter, because in autumn shorter daylengths signal later dates. When similar reaction norms were observed in *P. aegeria*, we could generalize from crickets to butterflies to provide an adaptive explanation (Nylin *et al.* 1989). In this case, reaction norms with shorter development times in shorter daylengths were observed both in a range of long daylengths (inducing direct development) and in a range of short daylengths (inducing diapause). Thus, we also generalized between developmental pathways, reasoning that under direct development a shorter daylength means less time to produce another generation, and hence still a need for a shorter development time.

5. For a more critical test of the adaptive hypothesis, we performed a series of true experiments on this and related satyrine butterflies. First, we compared reaction norms in *P. aegeria* from different latitudes, predicting steeper reaction norms relating development time to daylength in the north (where the seasonal amplitude in daylength variation is highest); this pattern was indeed found (Nylin *et al.* 1995b). Second, we compared two closely related species of *Lasiommata* butterflies differing in the stage used for hibernation. In one species individuals spend the winter as half-grown larvae, so that late-instar larvae occur before summer solstice when daylengths are increasing. In the other species, hibernation is in the pupal stage, so that late-instar larvae occur in the autumn when daylengths are decreasing. Hence, short daylengths should signal the need to complete development rapidly in the latter species, but the reverse should be true in the former. This prediction held true, as demonstrated by reaction norms with opposite slopes (Nylin *et al.* 1996a). Next, we compared reaction norms before and after hibernation in two species that spend the winter in the larval stage, so that daylengths in the field are decreasing in early instars and increasing in late instars. Generalizing from the previous late-instar results in these and other species, we predicted that opposite reaction norms would be displayed by the same larvae in early instars, and this was what we found (Gotthard *et al.* 1999). Finally, we investigated how temperature interacts with photoperiod and the developmental stage of the larvae in one of these species. We reasoned that in autumn (prehibernation larvae) high temperatures should be used to speed up growth and development in short daylengths, because they signal a late date. The effect should not be equally strong in long daylengths, which signal plenty of time left in the season. The opposite should be true in the spring (posthibernation larvae). These interactions were exactly

what we found; in fact, temperature had negligible effects on larval growth rates when daylengths suggested that there was ample time for completing development (Gotthard *et al.* 2000a). Such results graphically illustrate the need for more plasticity studies based on optimality reasoning and life history analysis.

Preference and performance

Another research area that is central to pest management is the study of pest performance on different plants, and of how plant preferences of ovipositing females correlate to the performance of their offspring on these plants (Thompson 1988). In the following, 'plant' can refer to species, plant parts, developmental stages, genotypes or chemical forms.

The study of performance variation provides many clear examples of the importance of studying life history plasticity for improved pest forecasting. For instance, Ohmart *et al.* (1987) and Ohmart (1991) investigated the effects of *Eucalyptus* leaf toughness and nitrogen content on life history, and hence population dynamics, of the chrysomelid beetle *Paropsis atomaria*. They showed how drought, in this particular system, is likely to decrease the risk of outbreaks because of its adverse effects on *Eucalyptus* and hence on *Paropsis* (only old foliage present, resulting in low fecundity and poor growth and survival). See Ohmart and Edwards (1991) for other examples from *Eucalyptus* and Larsson *et al.* (2000) for a theoretical treatment of how plant quality affects population dynamics through its effects on individual life histories.

Moving on to preference–performance correlation studies, some kind of optimality reasoning is the norm in this field, in contrast to most of the research areas already mentioned. When doing such a study, the a priori assumption is generally that females should prefer the plants on which their offspring perform best, in other words the ones resulting in highest offspring fitness. To continue the example of paropsine chrysomelids just given, Steinbauer *et al.* (1998) tested the prediction that the age of foliage is more important than the specific *Eucalyptus* species or genotype for the oviposition preference of such beetles. In this case there was ample background knowledge of performance on which to base explicit predictions. However, in many studies the optimality reasoning is only implicit, the investigators may not even be aware that they are in fact making predictions from optimality. If so, too little thought may be given to choosing an appropriate fitness model, that is, the most relevant performance variables may not be measured (Nylin *et al.* 1996b). For instance, a high growth rate may be very important for an insect with several generations per year, whereas for a univoltine insect with plenty of time to

reach the hibernating stage, it can be more important to determine if the host plant affects mating success or winter mortality.

Often correlations are weak or absent. This may be because the wrong performance measures were taken, or it may be because evolutionary constraints lead to non-adaptive female oviposition behaviour (Nylin *et al.* 1996b). Alternatively, it may reflect the fact that field characteristics of the plant, such as associated natural enemies (often excluded or changed in the experiment), are important for offspring fitness. It can also be a result of strong selection for increased female fecundity. After all, the fitness of an ovipositing female is determined not only by average offspring fitness but also by the total number of offspring (Nylin & Janz 1996).

The reason why this type of study is important to pest management is that it provides the necessary background knowledge regarding exactly how the insect relates to the plant. This knowledge can be used directly to guide management practices, or to suggest further research. If we do find a reasonable correlation between preference and laboratory performance, then we have some understanding of the basis for the decision of a female whether to oviposit or not. This knowledge can be used when planning how and when to plant and manage the area. Good preference–performance correlations can also suggest candidates for selection of resistant plants.

If we find a poor correlation, although female preference does vary significantly among plants, this can be explored in other ways. It may suggest plants that can strongly attract female oviposition, but cause reduced fitness in their offspring. This can be due to a chemical similarity to ancestral hosts for example. Such plants could be planted together with the economically important plant, deflecting oviposition and controlling the population increase at the same time. The reverse pattern, low preference for a high-performance plant, could suggest that these species are associated with natural enemies in the field, in other words a place to search for candidates for biological control.

When correlations are weak because of a lack of clear preference patterns, this is more indicative of a generalized oviposition pattern in the females. In such insects the fitness of females is evidently higher (at least under natural conditions) if they oviposit rather indiscriminately, than if they spend time searching for the best plants or plant parts. This can be the case in, for example, short-lived insects (Larsson & Ekblom 1995) and in relatively polyphagous insects with high larval mobility (Tammara *et al.* 1995). Again, we need this kind of knowledge when developing forecasting and management practices. In indiscriminate insects, realized fecundity and hence the number of eggs or early juveniles observed will not be very strongly affected by environmental variation in space and time. However, the fitness and population growth of offspring

may still be very strongly affected because they will later grow under very variable and often suboptimal circumstances. The reverse is true for more discriminating insects. In other words, monitoring techniques and the way this information is input into forecasting schemes and strategies regarding planting and management must all differ depending on where the insect fits in the spectrum from strong to weak correlations.

THEORY OF LIFE CYCLES AND LIFE HISTORY ADAPTATIONS

The last body of life history theory is concerned with understanding the evolution of life cycles and life histories themselves. Using the optimality approach, the variations in life history traits among organisms are viewed as adaptations to different types of environments (Cole 1954; Roff 1992; Stearns 1992; Fig. 1). These life history adaptations, in turn, will have consequences for population dynamics and fitness as described previously.

If it were possible to classify insects into different classes according to their life histories, in a manner that reflects their adaptive evolution, this would strongly increase the chances that these classes of species are in some sense real. Such a classification could be very useful for pest control. For instance, many new species find their way to Australia every year. If a screening of some essential life history traits could tell which of these insects are most likely to be invasive, border control of these species could be given top priority. Similarly, which of all insects found feeding on *Eucalyptus* are most likely to have outbreaks and become serious pests? Which of them do we have to keep a close eye on and where should research efforts be directed?

The most well known attempt at classifying life histories evolutionarily is the r/K scheme. MacArthur and Wilson (1967) suggested that a population experiences very different forms of selection in the early and late phases of colonization. Early on, there are plenty of resources and mortality is often density-independent. Genotypes favouring short generation times and high fecundity will increase in frequency. In other words, an appropriate fitness model could be r (the intrinsic rate of population increase). In later phases, resources will be scarce and much of the mortality will be density-dependent. The rate of increase in numbers will level off toward a more or less stable level called K, which can be thought of as the carrying capacity of the environment given this set of traits (see Cole (1954) for historical references to demographic theory). It may now be more important to grow and live slowly to make efficient use of resources and not to reproduce until offspring can be given a good start in life. Traits favouring a high K will have a greater chance of persisting in

the population, so K now becomes a better fitness model. This is one of the few examples of a fitness model stressing long-time persistence of a genotype, rather than population growth as a model of individual reproductive success.

Later, other authors (Pianka 1970; Horn 1978) suggested that species and races should also differ according to which of these types of selection has been most important during their evolution, so that they can be placed along an r - K continuum. This approach has been criticised and resurrected several times over the years (Boyce 1984) and it remains influential. If used with caution, it can undoubtedly give some hints regarding what to expect from immigrants or newly discovered insects on economically important plants. An r -strategist should be more likely to be both invasive and to produce outbreaks, everything else being equal (Southwood & Comins 1976; Wallner 1987). However, everything else is seldom equal. The diversity of actual life histories is too great to fit comfortably into this or other simple schemes.

Some other attempts have been made to specifically identify traits that predispose an insect to become a pest. Price (1994) suggested a link to preference-performance correlations. Strong preference-performance correlations suggest that females discriminate strongly between oviposition sites. Realized fecundity will drop when most good sites are taken and/or the performance of offspring will drop when poor sites have to be used. This density-dependence will stabilize the population levels and such insects are less likely to become pests than species with poorer preference-performance correlations.

A related point was made by Tammaru and Haukioja (1996). They noted that, among the Lepidoptera, pest species typically do not feed much (or at all) as adults. These insects are capital breeders (reproduction is based almost only on resources acquired in the larval stage) as opposed to income breeders (with significant adult feeding). The authors suggested that capital breeders are more likely to have outbreaks because the amount of reproduction is not very strongly determined by environmental variation, instead it is largely determined by female size. This situation selects for heavier females and eventually for the extreme syndrome of flightlessness and hence indiscriminate females that do not feed, commonly seen in lepidopteran pests.

Although these ideas are clearly interesting and should be investigated further, this particular body of life history theory is presently the least directly useful one when it comes to applications in pest identification and control. See Steinbauer (1999) for an attempt to apply these concepts to a *Eucalyptus*-feeding insect and a discussion of the difficulties. This is just a special case of the general situation; life history adaptations are undoubtedly the least understood type of adaptation. We know a good deal regarding why organisms display

certain behavioural, morphological or physiological traits in a particular environment or situation, whereas adaptive explanations for particular life history traits are much more uncertain. This may seem paradoxical considering that life history traits are so closely related to fitness, but I suggest that this close relationship is exactly the reason for the elusiveness of life history adaptation. We lack an independent fitness model, on which to base optimality reasoning (Fig. 1). For instance, it is clearly reasonable to say that females should often prefer to oviposit on host plants that result in good growth and survival. It is harder to say if females should lay a single egg or a whole batch on each plant, because we have no idea what this does to fitness; this sort of statement cannot be made without simultaneously considering the entire life history.

Another way to put this is to consider again the relationships between population dynamics, fitness and life history adaptations, using the example of an insect that we can think of as an r -strategist. This insect will have traits such as a short generation time, indiscriminate oviposition, rapid growth and high fecundity, coupled with population dynamics characterized by fluctuations. Is it the combination of life history (and other) traits that creates the fluctuations, or is it the fluctuations that have selected for these traits, fitness in this case being approximated by r ? Clearly, it works both ways. Life history traits create their own selective regimes, and for this reason life histories often form entire 'syndromes' of coadapted traits, including also traits of behaviour, morphology and physiology. These syndromes are made even tighter by trade-offs and positive correlations among different life history traits. The problem for adaptive explanations is to tease apart these syndromes in order to understand at least something of evolutionary causality. This has proven difficult, but there are ways to succeed.

The traditional method is to compare closely related species (or populations of the same species) differing in traits or in habitat in only one or a few respects, so that the effects of these differences can be studied. Examples of trait differences were given previously. As an example of a habitat difference, in several studies we compared populations of *P. aegeria* from Sweden (strongly seasonal habitat, discrete generations) and Madeira (almost non-seasonal, generations overlap, butterflies fly all year). As already mentioned, we predicted and found a lack of protandry in Madeira (Nylin *et al.* 1993). Furthermore, the lack of a selective premium on a long life for Swedish males seems to have resulted in shorter life spans (Gotthard *et al.* 2000b).

A promising avenue of research for the future is the increased use of phylogenetic methods, because this is the only way to test hypotheses of causality critically. The hypothesis is not supported if the presumed evolutionary cause (e.g. characteristics of the host plant) appears later in the phylogeny than the trait that was

supposedly explained by it (i.e. the plant was recently colonized).

DISCUSSION

I began with the question of whether life history theory is useful, in a practical sense, when it comes to managing pest insects. By now, it should be clear that my conclusion would be that it is. The most straightforward application of life history analysis is that it helps us predict what will happen to population numbers (necessary in IPM), but it also gives us evolutionary fitness models for optimality reasoning. It can also eventually give us an idea of what types of insects are most likely to become serious pests, although results in this area must still be described as provisional.

I noted previously that our understanding of insect population dynamics is limited, which also limits the timespan over which we can forecast with any confidence. I believe that progress in this area is hampered by several hierarchical layers of complexity. First, the dynamics of a pest are not determined only by its own traits but by those of the entire community (e.g. Wallner 1987; Berryman 1996). Second, the most important pest traits in this context are life history traits, and they are notoriously difficult to interpret adaptively. Hence, generalization is also difficult. Third, the life history traits of pest insects and other community members are not fixed in the way that most models of population dynamics implicitly assume. They respond plastically to variation in the environment, in ways that are poorly understood. These problems only highlight the need for guidance in research, and evolutionary theory can provide at least some guidance. For instance, one reason for the poor understanding of phenotypic plasticity in animals may be that it is not until recently that serious attempts have been made to interpret *all* types of plasticity as being adaptive in some sense. Even plasticity typically dismissed as 'non-adaptive', such as slower growth on poor host plants or in low temperatures, can show adaptive variation. We have not yet seen how far applying optimality reasoning to such variation can take us (Gotthard & Nylin 1995; Nylin & Gotthard 1998).

Applied entomology is often non-evolutionary, aimed at understanding proximate mechanisms and using this understanding to predict and control pest outbreaks. However, it is wrong to see evolutionary studies as purely 'academic' luxuries, contributing little of direct practical use. In fact, the search for proximate explanations works best when guided by reasoning based on evolutionary theory. In the present paper, I have stressed one particular kind, optimality reasoning in the broadest sense, because I believe that it has the most power to generate predictions. Evolutionary theory

is not the only body of theory that can be used to generate predictions (biological theory can be entirely mechanistic; e.g. Rausher 1985), but it is the most universally powerful one when it comes to living organisms. As I have shown by the examples given above, evolutionary theory gives us the means to interpret observed patterns, to generalize to other organisms and hence to predict patterns without extensive knowledge of mechanisms particular to certain systems. We frequently need 'educated guesses' in applied biology, and evolutionary theory can provide them.

Predictions are a very good thing to have in research. Certainly, searching empirically for explanations, more or less at random, can sometimes lead to unexpected discoveries. With time and perseverance, we may also be able to understand a few pest life systems this way, if they are simple enough. However, a much more cost-efficient way of going about any research problem is to study the available background theory, make predictions from it and then test the predictions. This process of hypothesis testing helps ensure that research is done in the light of existing knowledge. It also increases the chances that all observations that will be needed for later interpretation are really made, and decreases the risk of spending time and money on observations that may prove to have no great value. Finally, the general consequences of these observations (i.e. whether they support existing theory or not) are immediately apparent, so that they can be spread to others without too much delay. Basing research on theory is not a luxury activity, but to do otherwise can be.

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