REVIEW

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Towards a general theory of host acceptance by aphid parasitoids

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Abstract. I present the thesis that the most effective means of developing a unified theory of host exploitation by aphidophagous insects would be through a rational, first-principles approach. This approach entails the use of life history theory wherein host acceptance "decisions" are evaluated on the basis of contribution to current and future lifetime reproductive success wherein future success is discounted by life expectancy. A simple example involving egg load and host discrimination demonstrates the value of dynamic life history theory as a means of structuring experimental and empirically based research programs. Finally, I argue that a unified theory of host acceptance for aphidophagous insects must consider: (1) spatial distribution of hosts (2) hyperparasitoids and (3) population dynamics of telescoping generations of hosts.

INTRODUCTION

Aphids and their natural enemies constitute one of the most complex groups of organisms in terms of lifestyle, life-history and population dynamics. For example, aphid life-cycles can be holocyclic or anholocyclic (Dixon, 1985). This great variance among aphid species is exemplified by an equally bewildering array of traits that can be attributed to their natural enemies. For example, the longevity of aphid parasitoids can vary from just a few days to several weeks (Starý, 1970). Taken together, any attemps to develop a general theory that explains the oviposition-related behaviours of aphidophagous parasitoids must somehow deal with this tremendous diversity. In doing so however, one faces the perennial problem of "missing the forest for the trees". In this paper I hope to show how one can retain the view of the trees without losing sight of the forest.

Biological theories can take many forms, but there are essentially two quite different routes through which theories are developed. In the first, empirical data is collected and then analyzed (using statistical procedures) in the hopes that some sort of theory will emerge that explains the relationships between the various parameters and their effects. This kind of science-by-induction may not be productive because one can not decide, a priori, what kinds of data and over what ranges of conditions those data should be gathered (Gale, 1979). In the second, theory is derived from first principles that specifically address those factors that mediate the interactions between (in this case) a parasitoid and its host. As a result, critical questions and appropriate experimental designs emerge. Here, I concentrate on the second approach, while freely admitting that few of us ever practice either approach (1) or (2) in their strictest sense.

The first step in the development of an aphidophagous parasitoid oviposition theory requires some attempt to clarify the form of the biological phenomenon that we wish to understand. Though I will argue later that we must also consider issues relating to emigration, for the time being, let us assume that the primary problem lies in understanding why some hosts are sometimes readily accepted for oviposition (by the same parasitoid) and other times not. I will argue that the key to resolving this issue lies in replacing the simple currently popular stimulus-response concept with one of dynamic response thresholds (Mangel & Roitberg, 1993). These thresholds are generated by the interaction between parasitoid physiology and environmental conditions. Thus, a parasitoid harbouring a particular eggload while foraging in habitat where hosts are common might have a high response threshold whereas that same individual might possess a low response threshold when foraging in habitats where hosts are rare. As a result, encounters with the same host under each of those scenarios will frequently lead to contrasting expressions of host acceptance.

Miller & Strickler (1984) used similar terminology to describe the relationship between insect herbivores and stimuli that signal food plant quality. In their discussion they related an individual's response to a see-saw that sits on a moving fulcrum. On the one side of the fulcrum lie external excitatory inputs while external inhibitory inputs occupy the other side of the see-saw. The position of the fulcrum is determined by internal inhibitory and excitatory inputs. Thus, the likelihood of host acceptance is determined by both the strengths of the external stimuli and the position of the fulcrum. The theory I wish to develop is in the spirit of the Miller/Strickler model but as such I hope to define an internal theory for the fulcrum i.e. why is it that the fulcrum shifts a particular distance when, for example, eggloads vary in size.

Asking questions about the WHY of response profiles (i.e. a particular set of responses to a given stimulus under various conditions) necessarily requires examining such responses from an evolutionary perspective. As such, it is mandatory for the theory to explain how and why such profiles evolve in nature and thus avoid the dangers of employing a too-narrow (e.g. functional or causal alone) perspective (Roitberg, 1992).

FIRST PRINCIPLES

I begin development of a parasitoid host response theory by asking the following questions: "How would parasitoid host-acceptance response profiles evolve in habitats that differ in terms of resource structure and availability?" In order for response profiles to evolve the following conditions must be met (see Endler, 1986):

(i) Phenotypic variation (i.e. response profiles varying among parasitoid individuals) must be present within parasitoid populations.

(ii) This phenotypic variation must have a heritable basis.

(iii) There must be consistent co-variance betwen phenotypic expression and fitness (i.e. contribution to gene pools).

(iv) Genetic correlations must not constrain evolution (e.g. selection for expression of behavior x must not select against expression of behavior y).

(v) For habitat-specific responses to evolve there must be limited gene-pool exchange between populations inhabiting the various environments (Carriere & Roitberg, in prep.)

For the remainder of the paper I will concentrate on condition (iii) while acknowledging the importance of the other conditions.

Condition (iii) specifies that different variants will contribute differentially to the gene pool and as such only then can their representation in the population change over time Population biologists generally use surrogates of fitness to estimate contributions, the most popular candidates being lifetime reproductive success. I will employ a similar measure while acknowledging current discussions on such measures (e.g. Yoshimura & Clark, 1991; Koslowski, 1993). In addition, I will define lifetime reproductive success as: the number of adult offspring produced by a parasitoid in its lifetime (the reason for this restriction will become clear later).

In addition to the above, I suggest that a general theory of parasitoid host response incorporate several other biological features/assumptions:

(i) The world is not deterministic. Thus, certain biological events only occur with some probability. When such events are mutually exclusive, the sum of those probabilities equals one (Mangel & Clark, 1988).

(ii) Parasitoids produce their eggs either proovigenically or synovigenically.

(iii) Hosts are encountered sequentially i.e. not simultaneously.

The key to developing a life history theory of parasitoid host exploitation lies in characterising both the parasitoid and its environment. A simple starting point would be to employ a single parameter, egg state, as a physiological descriptor and another parameter, host encounter rate, as an environmental descriptor. In addition, one would include expectation of life as a further parameter to desribe the discounting of future success by the likelihood of being alive. Assuming that hosts of different qualities can be found in the habitat, a host acceptance theory should predict the circumstances (physiological and environmental states) under which particular hosts would be accepted.

Mangel & Clark (1988) show how the above assumptions and parameters can be employed in Dynamic Life History models [a special application of Stochastic Dynamic Programming (Bellman, 1957)] that can be used to calculate the consequences for acceptance of lower-than-best quality hosts. I do not intend to reinvent their theory here but rather to point out that these kinds of theories are highly appropriate for our purposes because they: (1) are sensitive to physiological and ecological parameters (e.g. Roitberg et al., 1992; 1993) and (2) seek behaviours that are responsive to stochastic worlds.

As an example of how such theories can be applied, consider a proovigenic parasitoid that encounters two different kinds of hosts in an environment where host density can be estimated through odour cues. Employing a Dynamic State Variable Model of the type described above, one can calculate the conditions under which hosts will be accepted. Figure 1 shows such a relationship. An important feature of this figure is not just the fact that host acceptance is predicted to be sensitive to eggload but that there is a function that describes this relationship and this relationship is based upon first principles from life history theory. This in turn suggests that wasps with different life histories should have different sensitivities to eggload: this, in fact, appears to be the case (e.g. Bai, 1991).

Of course, not all wasps are proovigenic and so one can ask whether a whole new theory must be developed to describe synovigenic animals given that the dynamics of eggload constitute a very different biological process. The answer is that the general theory can be used but, in so doing, we are forced to look in more detail at the process that

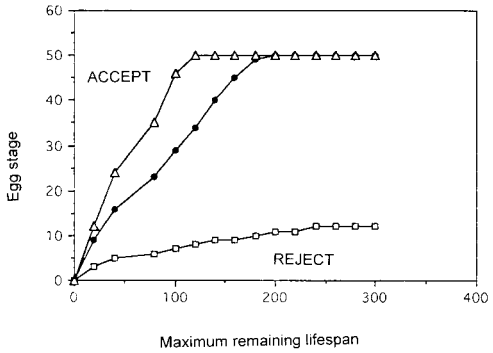

Fig. 1. Acceptance and rejection regions of hypothetical proovigenic parasitoids for hosts of intermediate quality as a function of eggload and time. The region above each line is the minimum egg state below which rejection of the low quality host will always occur. Notice that the accept region near the origin (i.e. near the end of life) is very large (i.e. is insensitive) to egg load. The difference in height between the three lines (i.e. the rejection spaces below each line) indicates that parasitoids become more choosey as good hosts become more common: good hosts make up 0.1 (open square), 0.5 (closed circle) and 0.9 (open triangle) of the total population.

determines egg availability. Now, it becomes necessary to employ two physiological state variables: mature and immature eggs. Figure 2 takes a single point from Figure 1 and extends it into the aforementioned second egg state dimension. Again, the theory should be most useful in that it can be used in development of experimental design for a broad range of parasitoids.

Finally, a question that emerges from this discussion is: is it necessary to develop a separate theory for aphidophagous parasitoids or would current models suffice? Put another way: do aphidophagous parasitoids present unique systems? I suggest that these systems are nearly unique (or require a unique approach) because of the following combination of characteristics:

(i) spatial distribution of hosts
(ii) hyperparasitoids
(iii) population

SPATIAL ASPECTS

As noted at the outset, the shapes, sizes and densities of aphid colonies vary dramatically both within and across species. As a result, the foraging success of individual

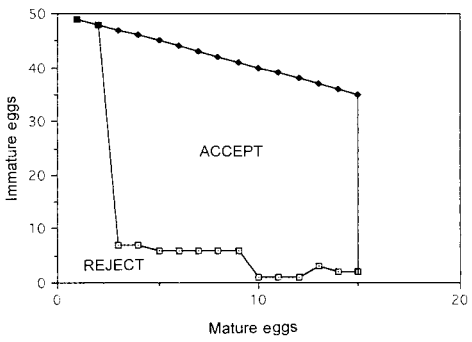

Fig. 2. Acceptance and rejection regions of hypothetical synovigenic parasitoids for hosts of intermediate quality as a function of mature and immature eggs at a single point in time (150 time units from the maximum expectation of life from birth). As in Fig. 1, the animal produces up to a maximum of 50 eggs in its lifetime. The upper line has a negative slope beause of the 50 egg lifetime. Thus, mature and immature eggs must total 50 or less.

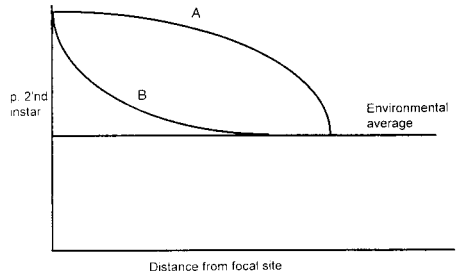

Fig. 3. Host availability curves for two different degrees (A & B) of aphid clumping where the curves show the rate at which the probability of locating a second instar aphid drops off (toward the environmental average) at varying distances from a second instar that a parasitoid has just encountered.

parasitoids depends upon their response to such variation. Unfortunately, most current parasitoid oviposition-response theories assume that hosts are contained within patches that have no spatial structure (e.g. Ayal & Green, 1993). Clearly, this is an oversimplification that could impede the likelihood of deriving testable hypotheses regarding host acceptance if such responses are sensitive to patch structure. Recently, Mangel (1994) and I (Roitberg, 1992) have attempted to incorporate variance in spatial structure into theories of host acceptance for tephritid fruit flies. The key to these new theories lies in incorporation of what Mangel (1994) calls "structure functions". These functions describe the relationship between the availibility and quality of hosts at one position in space and the values for the same parameters at other positions relative to the one of interest. For example, imagine that the two slopes shown in Fig. 3 are generated by degrees of aphid clumping wherein the curves define the rate at which the probability of a parasitoid locating a second instar aphid drops off (toward the environmental average) at varying distances from a second instar that a parasitoid has just encountered. Both curves shown are reasonable descriptors of what one might find in nature but they represent two different degrees of clumping. When these curves are incorporated into a general host acceptance theory they could generate predictions of different acceptance responses to encounters with low quality hosts. The important issue that this consideration raises is: we can't talk about host acceptance and patch leaving decisions as being separate; they are part of the same "package " and given the variation in patch structure of aphid colonies, inclusion of structure functions seems necessary.

In addition to the innate tendency for aphids to develop colonies of particular size and structure, there is the effect of plant architecture (Lawton, 1983). This would seem to be of greatest importance for parasitoids that exploit polyphagous aphids that infest plants of varying architecture. Recently, Li et al. (1993) developed methods to elucidate the effect of architecture and scale on the expression and impact of host acceptance in aphid-parasitoid systems.

HYPERPARASITOIDS

Hyperparasitoids are thought to be important agents of mortality in aphid-parasitoid systems (ref. e.g. Ayal & Green, 1993). The issue, however, from a perspective of host acceptance theory is not whether hyperparasitoids kill parasitoids but rather whether there exists a relationship between patterns of egglaying by parasitoids and likelihood of

hyperparasitism. If for example, the probability of hyperparasitism increases with increasing number of parasitized aphids, at a given site, then a function must be included in the theory that would discount the evolutionary payoff for high numbers of eggs laid at particular sites (see Weisser, 1993) (similarly, if perception of hyperparasite odour gives an indication of higher-than-average hyperparasitoid threat then similar effect should occur e.g. Höller et al., 1993). This discounting would generally lead to predictions of parasites abandoning sites more quickly than one might expect otherwise (e.g. Ayal & Green, 1993). A life history theory that includes this discounting factor could make explicit predictions based upon the lifehistory parameters and their values. Once again the first-principles approach shows the potential for theory to direct research i.e. it tells us what we should be looking at with regard to hyperparasitism (i.e. the situations in which hyperparasitoids are likely to have an evolutionary impact on parasitoid behaviour).

REPRODUCTION PATTERNS AND GENETICS OF TELESCOPING GENERATIONS

The main issue that I raise here is that the population dynamics that we observe are the result of interactions across at least three trophic levels and at one trophic level (the host aphid) we deal with animals that reproduce asexually during the time of year that many parasites are present. As a result, the evolutionary and population dynamic impact of parasite (and selection for response by aphids) is not as clear cut as it is for sexual organisms that reproduce through discrete generations. For example, in our work on altruism in aphids (McAllister & Roitberg, 1987; McAllister et al., 1990), it is clear that the payoffs for particular behaviours cannot simply be measured in terms of immediate offspring production but rather through some measure of reproductive potential such as the intrinsic rate of natural increase (e.g. Kindlmann & Dixon, 1989).

Second, what are the evolutionary implications of interactions between parasites and their hosts? How might aphid clones respond to the evolutionary pressures they face from parasitoids and how might such response affect parasite behaviour? I suggest that aphids are not the passive, static organisms that they are generally portrayed to be. Recently, Andrade & Roitberg (submitted) demonstrated: (1) considerable within-clone variability in response to disturbance and (2) rapid, strong within-clone responses to selection (apparently through maternal effect). Thus, even asexual hosts can respond rapidly to changing environments. Finally, one should also be aware that aphid behaviour is also likely to be state dependent and so expression of escape behaviours and emigration might also differ under different exogenous and endogenous states and this will surely complicate the situation (e.g. Stadler et al., 1993).

CONCLUSION

During the past century biological control has been an inexact science at best (van Lenteren, 1980). Part of the reason for the general lack of scientific rigour can be attributed to the lack of a general unifed theory that can predict variability in behaviour and links that variability to population level processes (Luck, 1990). Recent attempts to develop bridge laws that link individual processes to population-level phenomena are a step in the right direction (DeAngelis & Gross, 1992). Equally important is development of theory that helps us understand both how and why individuals do vary so greatly in nature. The kinds of approaches that I have outlined above should steed us well in our search for an

aphidophagous insect exploitation theory. It has never been more crucial than now, however, that the more-empirically oriented scientists learn the theory, question its structure and use it to guide their own research programs.

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