A Variable-Response Model for Parasitoid Foraging Behavior

L. E. M. Vet,[1] W. J. Lewis,[2] D. R. Papaj,[1] and J. C. van Lenteren[1]

An important factor inducing variability in foraging behavior in parasitic wasps is experience gained by the insect. Together with the insect's genetic constitution and physiological state, experience ultimately defines the behavioral repertoire under specified environmental circumstances. We present a conceptual variable-response model based on several major observations of a foraging parasitoid's responses to stimuli involved in the host-finding process. These major observations are that (1) different stimuli evoke different responses or levels of response, (2) strong responses are less variable than weak ones, (3) learning can change response levels, (4) learning increases originally low responses more than originally high responses, and (5) host-derived stimuli serve as rewards in associative learning of other stimuli. The model specifies how the intrinsic variability of a response will depend on the magnitude of the response and predicts when and how learning will modify the insect's behavior. Additional hypotheses related to the model concern how experience with a stimulus modifies behavioral responses to other stimuli, how animals respond in multistimulus situations, which stimuli act to reinforce behavioral responses to other stimuli in the learning process, and finally, how generalist and specialist species differ in their behavioral plasticity. We postulate that insight into behavioral variability in the foraging behavior of natural enemies may be a help, if not a prerequisite, for the efficient application of parasitoids in pest management.

[1] Department of Entomology, Wageningen Agricultural University, P.O. Box 8031, 6700 EH Wageningen, The Netherlands.
[2] Insect Biology and Population Management Research Laboratory, USDA-ARS, Tifton, Georgia 31793.

INTRODUCTION

Insect behavior is no longer considered to be fixed and predictable, but rather it varies in response to the insect's physiological condition and genetic composition as well as to environmental factors. However, the quest for factors inducing variability in parasitoid foraging behavior has largely centered on the influence of learning. Experience in either preadult or adult stages modifies adult behavior (see below). Learning may be loosely defined as ''any change in behaviour with experience'' (for a discussion of the definition of learning, see Papaj and Prokopy, 1989). It can impinge on every phase of parasitoid foraging from habitat location to host acceptance. Associative learning (defined as the establishment through experience of an association between two stimuli or between a stimulus and a response) has now been demonstrated in several parasitoid species (Lewis and Tumlinson, 1988; Turlings *et al.*, 1989; Vet, 1988; Vet and Groenewold, 1990), and it appears to be a general phenomenon in the Hymenoptera.

Studies on sources of variability in parasitoid behavior other than learning (including both genetic and nongenetic sources) are still rare (Lewis *et al.*, 1990). Prévost and Lewis (1990) demonstrated genetic variability in responses to host-plant odors and studies by Mollema (1988) point to genetic variability in host selection behavior. The animal's physiological state will specify its responsiveness to stimuli, especially to those related to essential resources (Tinbergen, 1951; Nishida, 1956; Herrebout, 1969; Herrebout and van der Veer, 1969; Gould and Marler, 1984; Dicke *et al.*, 1986).

Apart from the interest in behavioral variation from a theoretical standpoint [where we ask whether plasticity in behavior is adaptive or if such plasticity affects the evolution of other behaviors (Papaj and Prokopy, 1989)], there is an applied side to understanding the mechanisms that generate behavioral variation. Ultimately, the effectiveness of natural enemies in controlling populations of insect pests is in part associated with this variability. Understanding its nature may result in its manipulation to our benefit (see, e.g., Gross *et al.*, 1975; Wardle and Borden, 1986) and thus insight into behavioral variability is a help, if not a prerequisite, for the efficient application of biological control agents (Lewis *et al.*, 1990).

In this paper, we argue that certain key stimuli evoke absolute responses that are conservative to change in both an ontogenetic and an evolutionary sense. As such they act as an ''anchor'' by which responses to other stimuli are altered freely in a reliable manner. Other key stimuli arise through association with the original key stimuli and act to accelerate learning of new stimuli. Even for insects of a given genetic constitution, physiological state, and degree of experience, a behavioral response to a given stimulus varies both among individuals

and over repeated observations of the same individual. Variability in a response
will depend on the magnitude of the response. The impact of learning will relate
to the magnitude and variability of behavioral responses. These ideas are pre-
sented in a conceptual variable-response model based on several major obser-
vations of a foraging parasitoid's responses to assorted host or host microhabitat
stimuli.

OBSERVATIONS UNDERPINNING THE MODEL

Five observations made in our collective studies of parasitoid foraging
behavior inspired the model: (1) different stimuli evoke different responses or
levels of response; (2) strong responses are less variable than weak ones; (3)
learning can change response levels; (4) learning increases originally low
responses more than originally high responses; and (5) for naive females, host-
derived stimuli serve as key stimuli (rewards) in associative learning of other
stimuli.

Different Stimuli Evoke Different Responses or Levels of Response

A naive female parasitoid searching for hosts in which to lay eggs encoun-
ters a variety of environmental stimuli. Consequently foraging typically involves
a sequence of responses to some of these stimuli, first to the long-range cues
(usually for locating and selecting proper habitats) and then to close-range cues
(usually for detecting and selecting hosts). The stimuli and motor patterns
evoked by them are diverse and include a variety of plant and host chemicals
such as volatiles toward which the parasitoid walks or flies and nonvolatiles to
which the parasitoid is arrested, antennates, or probes with her ovipositor. Stim-
uli may also be physical in nature, including light, which induces migratory
flight behavior, and sound or mechanical vibrations, which elicit orientation
responses to hosts (see Vinson, 1976, 1981, 1984; Lewis *et al.*, 1975; van
Alphen and Vet, 1986).

Let it be assumed that natural selection has set the strength of the response
to each of the stimuli involved. The outcome of this selection will not be with-
out some developmental constraint, but naive animals would nevertheless be
expected to show the highest responses to those stimuli that, in evolutionary
time, are predictably correlated with high reproductive success. Support for this
functional argument is found in work with parasitoids of *Drosophila* larvae,
where differential responses to odors from different host food substrates or from
substrates in different stages of decay is adaptive (Vet, 1983; Vet *et al.*, 1984;
Vet and Janse, 1984). Differential responses (with or without plausible adaptive
functions) are reported not only for several species attacking Drosophilidae (Vet

et al., 1984; Vet, 1985) but also for parasitoids of other host types (e.g., Drost *et al.*, 1988; Sheehan and Shelton, 1989; see also references given by Vinson, 1976, 1981, 1984; Lewis *et al.*, 1975; van Alphen and Vet, 1986).

It is not surprising to observe that parasitoids do not respond to each possible stimulus with the same response intensity, as it is this mechanism that incites the expression of preferences, a phenomenon with an obvious function for each animal living in a complex environment where it has to make choices among the "bad, good, better, or best."

Strong Responses Are Less Variable than Weak Ones

Many investigators of parasitoid behavior have undoubtedly made the observation that the more strongly parasitoids respond to a stimulus, the less sensitive they are to all manner of disturbance. The stronger the response, the more predictable its occurrence as can be quantified by calculating its coefficient of variation (CV) (Sokal and Rohlf, 1981). Table I shows data sets for three *Leptopilina* species. Females were allowed to search on a standard patch of host food substrate until they decided to leave. Animals with the same type of for-

Table I. Comparison of the Variability (CV as %; See Text) of Responses (Average Search Times; s) of Animals with the Same Level of Experience Responding to Different but Comparable Stimuli[a]

Experience on	Searching on	Average search time	CV
A. None (naive)	M	211	58.8
None (naive)	AY	102	87.3
M	M	810	55.6
M	AY	179	83.2
AY	AY	569	62.7
AY	M	393	69.7
B. B	B	589	49.9
B	AY	97	87.1
AY	AY	247	83.4
AY	B	584	56.9
C. M	M + kairomone	415	39.6
M	M − kairomone	179	85.8

[a] (A) *L. heterotoma* with three different experience treatments [naive; oviposition experience on mushroom (M) or on apple/yeast (AY) substrate]. Comparison of average search times on M and AY substrate patches. (B) *L. fimbriata* (specialist on decaying plant material) with two different experience treatments [oviposition experience on decaying beet leaves (B) or on AY]. Comparison of search times on B and AY substrate patches. (C) *L. clavipes* with oviposition experience on mushroom. Comparison of average search times on mushroom patches with and without host kairomone. A partly from Vet and Schoonman, 1988; B from Vet, Poolman Simons, and Suverkropp, unpublished data; C from Vet, 1985.

aging experience can be compared in their response to two different substrate types. The response to the substrate stimulus is expressed as the search duration. Within each pair, the longest search time corresponds to the lowest CV, or in other words, strong responses are less variable than weak ones. There may be good physiological reasons for expecting this pattern in variability. When a response to a given stimulus is strong, it is less likely to be deflected by responses to other stimuli, as the insect is more liable to filter out and thus ignore sensory inputs from other stimuli that may evoke motor patterns different from that of the stimulus under investigation. This explanation appeals to the importance of allothetic mechanisms in the control of behavioral output (i.e., control by external information; see Visser, 1988). Additionally, motor patterns under strong allothetic control may be less susceptible to alteration by idiothetic mechanisms (i.e., under control by internal information).

Learning Can Change Response Levels

Studies on the influence of experience on foraging behavior in parasitoids focus on changes in what the animals respond to and/or changes in the strength of these responses, rather than the (probably less likely) modifications of the form of the motor patterns involved.

Preadult Experience

Parasitoids develop in and emerge from hosts. This specific environment can influence behavioral responses by the adult (e.g., Thorpe and Jones, 1937; Vinson *et al.*, 1977; Smith and Cornell, 1978; Vet, 1983; Sheehan and Shelton, 1989). The adult parasitoid's response is most likely modified prior to or during eclosion through a chemical legacy from previous developmental stages (Vet, 1983, 1985; Corbet, 1985). Elegant experiments by Hérard *et al.* (1988) with *Microplitis demolitor* females suggested that the cocoon is a potential source of information learned by the parasitoid during or just after emergence. A clear distinction between preadult and adult effects of experience on adult behavior is difficult to make (Vet and Groenewold, 1990). "Naive" insects have had the least possible experience with the stimuli to which they will respond. We define a naive insect not as an insect without any experience, but as one which has had no experience beyond that which occurred during development within and eclosion from the host.

Adult Experience

Experience during the adult stage has more impact on subsequent behavioral responses than experience during development (Vinson *et al.*, 1977; Jaenike, 1983; Vet, 1983; Drost *et al.*, 1988; Sheehan and Shelton, 1989). In the

case of parasitoids, hosts or host products serve as *key stimuli (rewards)* in association with which insects either (1) learn to respond to stimuli that previously evoked no overt response (e.g., Vinson *et al.*, 1977; Lewis and Tumlinson, 1988; Vet and Groenewold, 1990) or (2) increase a preexisting but weak overt response to a stimulus (i.e., so-called "alpha conditioning"; see Carew *et al.*, 1984; Gould and Marler, 1984).

In *Drosophila* parasitoids, responses to microhabitat odors are strongly influenced by alpha conditioning (Vet, 1983, 1985, 1988; Vet and van Opzeeland, 1984; Papaj and Vet, 1990). *Leptopilina heterotoma* females dramatically increase their responses to stimuli after having encountered them in association with oviposition in host larvae. Females experienced with apple-yeast substrate respond significantly more strongly to the odor of an apple-yeast substrate than naive females or females experienced with another substrate [in olfactometers (e.g., Vet, 1988) and in mark-recapture experiments (e.g., Papaj and Vet, 1990)]. Similar response increases to stimuli associated with hosts, and in some cases with host by-products only, have been demonstrated in several other parasitoid species including other eucoilids (Vet, 1983; Vet *et al.*, in preparation), braconids (Vinson *et al.*, 1977; Drost *et al.*, 1986, 1988; Turlings *et al.*, 1989), tachinids (Monteith, 1963), ichneumonids (Arthur, 1966, 1971), aphidiidids (Sheehan and Shelton, 1989), and trichogrammatids (Kaiser *et al.*, 1989). Various types of stimuli can be involved in these learning processes. There are reports in the literature of parasitoid species learning odors, colors, and shapes.

Learning Increases Originally Low Responses More than Originally High Responses

With flies and parasitic insects it has been observed that responses to less preferred stimuli are influenced more by learning than responses to more preferred stimuli (Jaenike, 1982, 1983, 1988; Prokopy *et al.*, 1982; Vet and van Opzeeland, 1984; Kaiser *et al.*, 1989; Sheehan and Shelton, 1989; Vet *et al.*, in preparation). These observations may possibly account for the remarks of some colleagues working only with highly preferred stimuli, that "their" species do not seem to learn. In some studies it is partly the method by which the behavioral response is measured that limits how much a response changes with experience. When responses are measured in terms of choice situations or percentages—and so the behavioral measure has an upper bound of 100%—there may be little scope for learning. For example, in *Asobara* species, the preference for odors of originally less preferred host substrates is increased markedly by an oviposition experience on these substrates. No such measurable effect occurs with substrate odors that are originally more preferred, as an increase in preference for these odors is barely possible (Vet and van Opzeeland, 1984; see also Drost *et al.*, 1986, 1988).

In conclusion, experimental data with parasitoids and flies suggest that this lower effect of learning on responses that are initially high is (although sometimes a methodological feature), a true behavioral phenomenon. It may reflect the existence of a maximum response to a stimulus as set by physiological constraints.

For Naive Females, Host-Derived Stimuli Serve as Key Stimuli (Rewards) in Associative Learning of Other Stimuli

As stated earlier, associative learning seems to be a major source of behavioral plasticity in parasitoids and other insects. Responses to stimuli can be acquired or enhanced by linking these stimuli to a key stimulus (reward). However, what is the nature of these reinforcing stimuli for parasitoids? Naive insects foraging for food use stimuli unambiguously associated with feeding (e.g., sugars) as key stimuli (Papaj and Prokopy, 1989). It is no accident that these stimuli are most frequently used in conditioning paradigms. They elicit responses which are strong and consistent. By analogy, we expect naive parasitoids foraging for hosts to use stimuli unambiguously associated with oviposition as key stimuli, and not, for example, stimuli associated with finding the host habitat. This is in fact what is observed, for example, in *L. heterotoma*, which does not link a novel odor to the presence of a substrate, but to the presence of hosts (Vet and Groenewold, 1990).

Current knowledge indicates that the key stimuli used by naive parasitoids in associative learning are always host derived. These stimuli themselves generally elicit strong and predictable responses in naive animals.

THE MODEL

A simple conceptual model embraces these initial observations. It encompasses that: First, parasitoids do not respond to each possible stimulus in the same way or to the same extent. Second, strong responses are less variable than weak ones. Third, learning can change response levels. Fourth, the extent to which experience alters a response depends on its original level and that learning increases weak responses more than strong ones. Fifth, in naive individuals, stimuli that evoke high and predictable responses such as those derived from the host are most likely to function as a key stimulus to condition other stimuli.

Response Potential

We first postulate a unique *response potential* for each stimulus perceived by a parasitoid. Note that we are speaking of *potential* and not realized behavior. The response potential is a way of assigning all incoming stimuli a relative

value in common units regardless of whether those stimuli evoke fundamentally different responses. If, for example, the odor of a host substrate stimulates upwind anemotaxis in a parasitoid, any differences in the insect's walking speed in different odor plumes reflect differences in response potentials among the odors. However, for stimuli that evoke different behaviors (e.g., ovipositor probing vs flying in the presence of odor), response potentials cannot be compared readily by external observation alone.

We assume that a maximum response potential exists for a naive individual of a given physiological state, developmental history, and genetic composition. This maximum is set by constraints on the motor patterns elicited by stimuli, e.g., a maximal walking speed or a maximum ovipositor-probing frequency.

Ranking of Stimuli

In Fig. 1 all stimuli perceived by the insect are ranked according to the strength of their response potential in the naive insect. Each stimulus occupies a unique ''slot'' along the response potential continuum. Stimulus S_1 has the highest response potential and the response potentials to the different stimuli decrease along the abscissa.

The sigmoidal shape of the distribution is based on the assumption that the distribution is actually composed of two types of stimuli: those with responses maintained by natural selection and those with responses maintained by constraint. The first group of stimuli (i.e., those maintained by natural selection) involves some stimuli that are essential in the host-location process of the parasitoid and that evoke very high, adaptive responses in the naive insect. We can think of indispensible host-derived stimuli that are used in the location or acceptance of a highly suitable host. They are situated on the left of the curve and show high response potential levels. Stimuli in the tail of the sigmoid involve
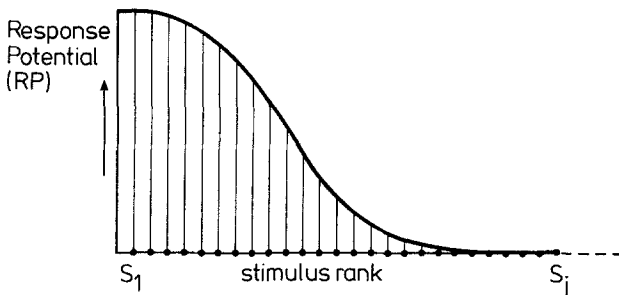
Fig. 1. Diagram of a female parasitoid's potential behavioral response to a variety of environmental stimuli. All stimuli perceived by the insect are ranked according to their response potential in the naive insect. Stimuli beyond S_j are outside the range of sensory perception of the animal.

stimuli that evoke very weak, behaviorally neutral responses that are maintained by some constraint. Some of the latter stimuli may be components of, or may overlap with, the more important stimuli. It may not be cost effective or even possible to reduce these responses to zero. It may be that these behaviorally neutral responses act as a reference library which the animal employs as needed during associative learning. The part of the curve in between the stimuli with high and those with low response potentials are stimuli of intermediate value. "Stimuli" $S > j$ are beyond the range of sensory perception of the animal. As these stimuli cannot be perceived, they can never be learned. This distinguishes them from other behaviorally neutral stimuli to which responses can be induced through learning.

Experience

We next assume that experience can change the response potential of a stimulus, and when it does so, it moves this stimulus from one slot to another. Since a given slot can hold one and only one stimulus, this change always causes some other stimuli along the continuum to be displaced as well.

Variability

We further assume that there is always some variability when we actually measure the *overt* behavioral response to a certain stimulus, even if the response potential remains constant. So given an insect of a particular genetic composition, physiological state, and level of experience, the overt response can be predicted only with a certain error, as shown by the shaded area in Fig. 2. The magnitude of variability is assumed to depend on the strength of the response
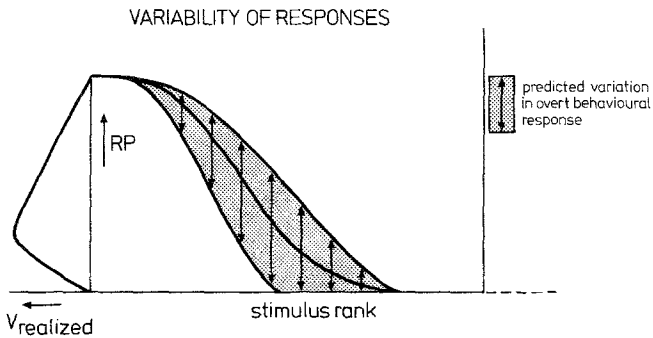
Fig. 2. Relationship between response potential level and variation in *overt* behavoural response. For each stimulus the predicted variation is given by the height of the shaded area. The resulting pattern of variability in actual responses over the range of response potentials is given by the V_{realized} curve. See text for additional explanation.

potential. When response potentials are high, they show low variability within the individual. Although this assumption is mainly empirically derived, it may be based on a plausible physiological reason (see Strong Responses Are Less Variable than Weak Ones, above). Furthermore, between individuals we expect little variation when responses to stimuli on the left-hand side of the abscissa are measured. Natural selection not only has led to these response potentials being inherently high but also has probably reduced differences in the maximal level of these response potentials between individuals of a population, which again reduces the variability in responses measured. So when response potentials are high, actual responses appear constant and predictable, and when response potentials are lower, actual responses are assumed to show more variability within and between individuals. These responses vary over successive measurements in an unpredictable manner. When response potentials are very low, there is in reality less and less room for variability in the actual response, simply because responses cannot be lower than zero. Thus, extremely low mean responses may actually be associated with reduced variability than occurs with slightly higher mean responses. The resulting pattern of variability in actual responses over the range of response potentials is portrayed by the curve of realized variability ($V_{realized}$) positioned vertically on the left-hand side in Fig. 2.

Key Stimuli

Finally, we assume that whether a stimulus can serve as a key stimulus (reward) for another stimulus in associative learning depends on the position of the two stimuli on the response potential continuum. Specifically, stimuli with the higher response potentials will be most likely to condition responses to stimuli with lower response potentials in associative learning. Moreover, we assume that the higher the response potential of the key stimulus, the greater the behavioral change it induces.

Synopsis

Figure 3 presents a flow diagram of the major concepts of the model. The central idea is the response potential. The lines indicate an influence or determination of one factor upon another, the arrows specifying the direction in which this occurs. This system is couched within the internal and external environment of the parasitoid.

HYPOTHESES RELATED TO THE MODEL

We can easily see that the model embraces each of our initial observations, but furthermore, it enables us to formulate various testable hypotheses.
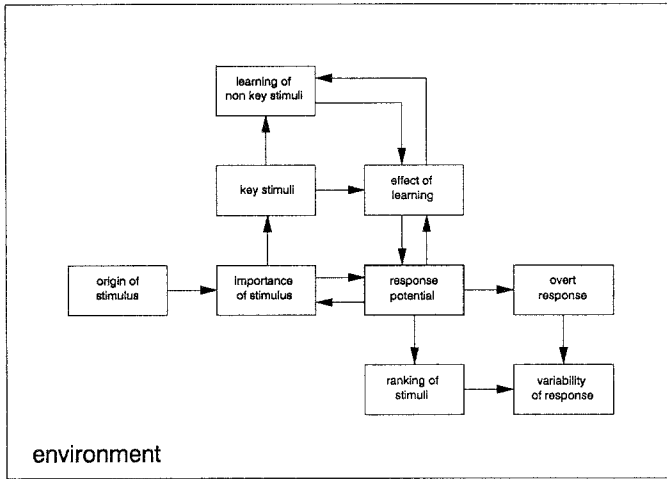
Fig. 3. Flow diagram of the major concepts of the variable-response model.
For explanation see text.

When Learning Changes the Response to a Stimulus, It Should Change the Variability of that Response Accordingly

Since learning usually increases the response to a stimulus, it should also reduce the variability of that response. Thus in general, the responses of naive individuals should be more variable than those of experienced individuals. Several examples suggest this to be the case. Naive and experienced *L. heterotoma* females differ in their variability (CV) in the time spent searching on two substrates (Table II). After an oviposition on a substrate the time spent searching on that substrate increases and becomes less variable. Similarly, *Trichogramma evanescens* responds to a sex pheromone of its host, *Mamestra brassicae*, in a

Table II. Comparison of the Variability (CV as %; See Text) of Responses (Average Search Times; s) of *L. heterotoma* Females with Different Levels of Experience (Either No Oviposition Experience or Oviposition Experience on Beet (B) or Apply/Yeast (AY) Substrate) Responding to the Same Stimulus[a]

Experience on	Searching on	Average search time	CV
None	B	458	101.1
B	B	2657	69.5
None	AY	376	71.8
AY	AY	1366	41.3

[a] From Vet and de Moed, unpublished data.
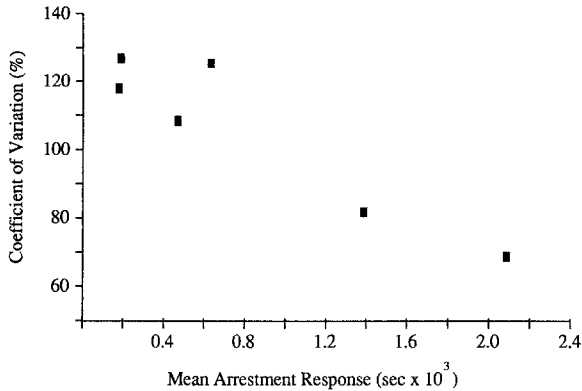
Fig. 4. Relationship between mean response (arrestment response as s) and variability of this response (coefficient of variation = SD × mean^{-1} × 100%) for *Trichogramma evanescens* in an odor plume of host sex pheromone. Each square represents females within a particular experience treatment (e.g., oviposition experience, experience with sex pheromone, no experience). See text for additional information. Data from Noldus *et al.* (in preparation).

wind tunnel, i.e., uses it as a kairomone (Noldus, 1988; Noldus *et al.*, 1988). The respnse is expressed as the duration of arrestment on a platform in the odor plume. Different experiences influence the mean duration (Noldus *et al.*, in preparation) which correlates with a significant decrease in variability (Fig. 4). Finally, *Exeristes roborator*, an ichneumonid parasitoid, was exposed to one of three conditioning treatments: (1) a natural host and habitat, (2) no exposure (naive), or (3) conditioning to a factitious host in an artificial habitat [Table III; based on Wardle and Borden (1986)]. Its response to a natural host was then measured. The responses of the naives varied more than those of females experienced on the natural host. Experience with the "wrong" host and habitat

Table III. Comparison of the Variability (CV as %; See Text) of Responses to *Rhyacionia buoliana*-Infested Scots Pine by the Parasitoid *Exeristes roborator* in Three Experience Groups: I, Oviposition in *R. buoliana* in Scots Pine; II, Naive; III, Oviposition in *Galleria mellonella* in Egg Cups[a]

Experience group	Average time/female spent probing (min)	CV
I	23.3	83.7
II	18.2	98.9
III	3.4	205.9

[a]Based on data from Wardle and Borden (1986).

significantly reduces its response to natural hosts and simultaneously increases the response's variability.

The Magnitude of the Change in Response for a Given Stimulus with a Given Experience Depends on the Level of the Original Response

If a given experience increases a stimulus' rank order with a certain number of steps, the change in its response potential will depend on its original position in the rank order. If it was ranked either low or high, then its response potential will change relatively little. If it was of intermediate rank, then the change will be larger (Fig. 2). This may explain the observations by Lewis and Tumlinson (1988) in which *M. croceipes* rapidly learned some plant odors but exhibited more limited learning of other odors, e.g., vanilla (which is originally behaviorally neutral and so situated on the far right of the stimulus rank axis).

A number of stimuli with high response potentials will even evoke responses that are not variable and not subject to modification by experience. These stimuli include those that trigger motor responses known as "fixed-action patterns" (Manning, 1972; Alcock, 1984).

A Change in Response to a Stimulus Exerted by Experience Can Change Responses to Other Stimuli

When experience increases the response potential of a stimulus, i.e., increases its rank order, other stimuli will be displaced and their rank order (response potential) will decrease. Furthermore, the response potential of several stimuli may increase in concert due to experience. This phenomenon has been shown for parasitoids (Vet and van Opzeeland, 1984; Drost *et al.*, 1988; Turlings *et al.*, 1989; Eller *et al.*, in preparation). Note that by increasing the rank order of one stimulus, the response potentials of some stimuli will change while those of others remain unaffected. This pattern, in which experience with a given stimulus affects the response to other stimuli *to differing degrees* [= cross-induction of Papaj and Prokopy (1986)], has been shown for saprophagous and frugivorous insects (Jaenike, 1983; Papaj and Prokopy, 1986; Papaj *et al.*, 1989). Such cross-induction may be a selectively neutral but physiologically unavoidable side effect of other response modifications that are adaptive. It remains to be examined in parasitoids.

The Response Pattern Exhibited in a Choice Situation Will Be Dictated by the Rank Order of the Stimuli Involved

If animals are faced with comparable stimuli (such as odors from different host plants), they should prefer the stimulus with the highest response potential. If the response potential is modified sufficiently through experience, learning

may reverse the preference. For example, if *L. clavipes*, a parasitoid of mushroom-feeding *Drosophila*, is reared on a yeast substrate, its response to yeast odor increases but the increase is insufficient to displace the response to mushroom odor. However, if it oviposits in hosts on yeast, it prefers yeast odors to those of mushroom (Vet, 1983).

Key Stimuli Are Expected Most Often to Be Those that Evoke Strong Responses in Naive Individuals, but Any Stimulus Whether or Not It Evokes a Strong Response in a Naive Individual Can Potentially Act as a Key Stimulus for Other Stimuli

If we look at animals other than parasitoids, the stimuli (sugar, shock, poisons, etc.) most frequently used in conditioning paradigms are exactly those that elicit strong and consistent responses. In parasitoid foraging, oviposition-related stimuli and, generally speaking, host-derived products elicit the least variable of all responses in the naive female (Zanen *et al.*, in preparation), and to the best of our knowledge, it is these stimuli that function as key stimuli in associative learning. The model assumes that the key stimulus with the highest response potential will give the strongest reinforcement. Such high-response stimuli are likely to be closely and reliably linked with the material presence of a host and its suitability for larval survival. By using such stimuli as the predominant reinforcers in associative learning processes, the insect can freely increase its responses to stimuli which are not reliable predictors of host presence and suitability in the long term (i.e., over evolutionary time) but which happen to be predictors of host presence and suitability in the short term (i.e., over the lifetime of the insect).

The idea that any stimulus can *potentially* act as a key stimulus may account for the phenomenon of second-order conditioning. Second-order conditioning occurs when a stimulus that has been conditioned by a key stimulus becomes itself a key stimulus (Sahley, 1984). As the response potential of this conditioned stimulus increases in our paradigm, it displaces increasingly more other stimuli and is increasingly likely to be effective as a key stimulus for other stimuli. Second-order conditioning has been found in a variety of vertebrates and invertebrates (Sahley, 1984), including bees (Menzel, 1983), but has never been investigated in parasitoids.

Therefore one of the major insights of our model is perhaps this implication that many more types of stimuli can act as key stimuli than has been previously assumed, including stimuli that originally elicit little or no overt behavioral response in the naive insect. Our model suggests that the number of key stimuli used by a parasitoid in learning will increase as increasingly more stimuli are "confirmed" to be reliable predictors of host presence and suitability. Through this second-order conditioning, the insect effectively constructs a hierarchy of

biologically meaningful causal relationships over the course of its foraging life. Acquiring a large and reliable set of key stimuli may increase the rate at which the insect learns. If this faster learning confers some reproductive benefit upon the individual, the accumulation of key stimuli should have some selective advantage.

The Shape of the Response Potential Curve Will Differ Among Species and Will Reflect the Ecological Circumstances Within Which the Species Operates

Much attention has been devoted to the differences in foraging strategies between generalist and specialist species (e.g., Waage, 1979) and, in particular, to the possible correlation between niche breadth and learning ability (Arthur, 1971; Cornell, 1976; Daly *et al.*, 1980; Gould and Marler, 1984; Vet and van Opzeeland, 1984; van Alphen and Vet, 1986; Papaj and Prokopy, 1989). It is usually postulated that generalist species (because of their more variable environment) will more ably learn than specialist species. For insects the evidence for this is conflicting (Papaj and Prokopy, 1989). Perhaps we can add some "food for thought" from the viewpoint of this variable-response model. The shape of the response curve itself can be expected to differ among species and to reflect the ecological circumstances within which each species operates. If the area under the response curve is constrained and remains relatively constant across—related?—species, we might expect that generalist species have a flatter distribution of response potentials than specialists (Fig. 5). As a general rule based on our model, we expect specialists to show less variability in their responses than generalists, with regard to the stimuli which they are specialist or generalist for. In addition, we can argue that as the fraction of intermediate response potentials is greater in generalists than specialists, the breadth of what can be learned is expected to be greater in generalist species. For parasitoids there is some evidence that both generalists (e.g., Arthur, 1966; Vet and
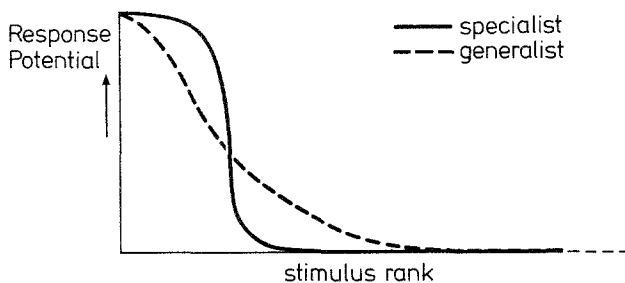
Fig. 5. Differences in response potential curves between specialist and generalist parasitoid species. See text for additional explanation.

Schoonman, 1988; Turlings *et al.*, 1989) and specialists (e.g., Arthur, 1971; Vet, 1983; Vet and van Opzeeland, 1984; Sheehan and Shelton, 1989) can learn but not enough data exist to make a meaningful comparison of their relative learning ability. Present data include work on only distantly related species. Any comparison would risk erroneously attributing differences in learning to differences in diet breadth when in fact they are due to other factors, for example, differences in phylogeny (Papaj and Prokopy, 1989). We suggest that the lack of consensus with regard to the learning abilities of specialists and generalists may be due in part to the failure to test enough stimuli over the possible range of response levels.

CONCLUDING REMARKS

The effect of experience on the mean and variability (and thus predictability) of behavioral responses has interesting implications for the use of parasitoids in biological control. An improved predictability of natural enemy behavior will stimulate application of biological control (Lewis *et al.*, 1990). Unpredictable behavior can hamper the development of reliable introduction schemes, can lead to disinterest in the biological control method, and can result in the release of exorbitantly high numbers of animals, leading to high control costs. The postrelease migration behavior of parasitoids away from the target area is considered a special problem (e.g., Ridgway *et al.*, 1981; Keller *et al.*, 1985). Increasing the mean and reducing the variability of the response to target stimuli through experience could considerably alleviate this problem.

Although our model implies that all learning in parasitoids can be reduced to simple associative processes where a reinforcement increases the response to some other stimulus, it easily includes other effects of experience where an obvious reinforcement is lacking (e.g., sensitization and habituation).

A behavioral repertoire is a complex process, influenced by genes, environment, physiology, and experience. Being aware of this complexity, we merely present a tool to simplify and clarify the effect of experience on behavioral responses and variability in those responses. The simplicity of the model enables us to formulate clear and testable hypotheses bearing on the desired or unavoidable manipulation of natural enemies, interspecific differences in behavioral plasticity, and learning mechanisms. Many of the above-mentioned hypotheses remain to be tested for foraging parasitoids as well as for other animals. For our own research the heuristic value of the model is already clear. Previously anecdotal behavioral data with several different species are now within a conceptual framework which is open to experimental testing.

ACKNOWLEDGMENTS

REFERENCES

Alcock, J. (1984). *Animal Behavior: An Evolutionary Approach*, 3rd ed., Sinauer, Sunderland, Mass.

Arthur, A. P. (1966). Associative learning in *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). *Can. Entomol.* **98:** 213–223.

Arthur, A. P. (1971). Associative learning by *Nemeritis canescens* (Hymenoptera: Ichneumonidae). *Can. Entomol.* **103:** 1137–1141.

Carew, T. J., Abrams, T. W., Hawkins, R. D., and Kandel, E. R. (1984). The use of simple invertebrate systems to explore psychological issues related to associative learning. In Alkon, D. L., and Farley, J. (eds.), *Primary Neural Substrates of Learning and Behavioural Change*, Cambridge University Press, Cambridge, pp. 169–184.

Corbet, S. A. (1985). Insect chemosensory responses: A chemical legacy hypothesis. *Ecol. Entomol.* **10:** 143–153.

Cornell, H. (1976). Search strategies and the adaptive significance of switching in some general predators. *Am. Nat.* **110:** 317–320.

Daly, M., Rauschenberger, J., and Behrends, P. (1980). Food-aversion learning in kangaroo rats: a specialist-generalist comparison. *Anim. Learn. Behav.* **10:** 314–320.

Dicke, M., Sabelis, M. W., and Groeneveld, A. (1986). Vitamin A deficiency modifies response of predatory mite *Amblyseius potentillae* to volatile kairomone of two-spotted spider mite. *J. Chem. Ecol.* **12:** 1389–1396.

Drost, Y. C., Lewis, W. J., Zanen, P. O., and Keller, M. A. (1986). Beneficial arthropod behavior mediated by airborne semiochemicals. I. Flight behavior and influence of preflight handling of *Microplitis croceipes* (Cresson). *J. Chem. Ecol.* **12:** 1247–1262.

Drost, Y. C., Lewis, W. J., and Tumlinson, J. H. (1988). Beneficial arthropod behavior mediated by airborne semiochemicals. V. Influence of rearing method, host plant and adult experience on host-searching behavior of *Microplitis croceipes* (Cresson), a larval parasitoid of *Heliothis*. *J. Chem. Ecol.* **14:** 1607–1616.

Gould, J. L., and Marler, P. (1984). Ethology and the natural history of learning. In Marler, P., and Terrace, H. S. (eds.), *The Biology of Learning*, pp. 47–74. Springer-Verlag, New York.

Gross, H. R., Lewis, W. J., Jones, R. L., and Nordlund, D. A. (1975). Kairomones and their use for the management of entomophagous insects. III. Stimulation of *Trichogramma achaeae, T.*

pretiosum and *Microplitis croceipes* with host seeking stimuli at the time of release to improve their efficiency. *J. Chem. Ecol.* **1:** 431–438.

Hérard, F., Keller, M. A., Lewis, W. J., and Tumlinson, J. H. (1988). Beneficial arthropod behavior mediated by airborne semiochemicals. IV. Influence of host diet on host-oriented flight chamber responses of *Microplitis demolitor* Wilkinson. *J. Chem. Ecol.* **14:** 1597–1606.

Herrebout, W. M. (1969). Habitat selection in *Eucarcelia rutilla* Vill. (Diptera: Tachinidae). II. Experiments with females of known age. *Z. ang. Ent.* **63:** 336–349.

Herrebout, W. M. and van der Veer, J. (1969). Habitat selection in *Eucarcelia rutilla* Vill. (Diptera: Tachinidae). III. Preliminary results of olfactometer experiments with females of known age. *Z. ang. Ent.* **64:** 55–61.

Jaenike, J. (1982). Environmental modification of oviposition behavior in *Drosophila. Am. Nat.* **119:** 784–802.

Jaenike, J. (1983). Induction of host preference in *Drosophila melanogaster. Oecologia* **58:** 320–325.

Jaenike, J. (1988). Effects of early adult experience on host selection in insects: Some experimental and theoretical results. *J. Insect Behav.* **1:** 3–15.

Keller, M. A., Lewis, W. J., and Stinner, R. E. (1985). Biological and practical significance of movement by *Trichogramma* species: A review. *Southwest. Entomol. Suppl.* **8:** 138–155.

Lewis, W. J., and Tumlinson, J. H. (1988). Host detection by chemically mediated associative learning in a parasitic wasp. *Nature* **331:** 257–259.

Lewis, W. J., Jones, R. L., Gross, H. R., and Nordlund, D. A. (1976). The role of kairomones and other behavioral chemicals in host finding by parasitic insects. *Behav. Biol.* **16:** 267–289.

Lewis, W. J., Vet, L. E. M., Tumlinson, J. H., van Lenteren, J. C., and Papaj, D. R. (1990). Variations in parasitoid foraging behavior: Essential element of a sound biological control theory. *Environ. Entomol.* (in press).

Manning, A. (1972). *An Introduction to Animal Behaviour*, Edward Arnold, London.

Menzel, R. (1983). Neurobiology of learning and memory: The honeybee as a model system. *Naturwissenschaften* **70:** 504–511.

Mollema, C. (1988). Heritability of host selection behaviour of *Asobara tabida*. In *Genetical Aspects of Resistance in a Host-Parasitoid Interaction*, Ph.D. thesis, University of Leiden, Leiden, The Netherlands, pp. 99–107.

Monteith, L. G. (1963). Habituation and associative learning in *Drino bohemica* Mesn. (Diptera: Tachinidae). *Can. Entomol.* **95:** 418–426.

Nishida, T. (1956). An experimental study of the ovipositional behavior of Opius fletcheri Silvestri (Hymenoptera: Braconidae), a parasite of the melon fly. *Proc. Haw. Entomol. Soc.* **16:** 126–134.

Noldus, L. P. J. J. (1988). Response of the egg parasitoid *Trichogramma pretiosum* to the sex pheromone of its host *Heliothis zea. Entomol. Exp. Appl.* **48:** 293–300.

Noldus, L. P. J. J., Lewis, W. J., Tumlinson, J. H., and van Lenteren, J. C. (1988). Olfactometer and windtunnel experiments on the role of sex pheromones of noctuid moths in the foraging behaviour of *Trichogramma* spp. In Voegel, J., Waage, J. K., and van Lenteren, J. C. (eds.), *Trichogramma and Other Egg Parasites*, Colloq. INRA 43, INRA, Paris, pp. 223–238.

Papaj, D. R., and Prokopy, R. J. (1986). Phytochemical basis of learning in *Rhagoletis pomonella* and other herbivorous insects. *J. Chem. Ecol.* **12:** 1125–1143.

Papaj, D. R., and Prokopy, R. J. (1989). Ecological and evolutionary aspects of learning in phytophagous insects. *Annu. Rev. Entomol.* **34:** 315–350.

Papaj, D. R., and Rausher, M. D. (1983). Individual variation in host location by phytophagous insects. In Ahmad, S. (ed.), *Hebivorous Insects: Host-Seeking Behavior and Mechanisms*, Academic Press, New York.

Papaj, D. R., and Vet, L. E. M. (1990). Odor learning and foraging success in the parasitoid, *Leptopilina heterotoma. J. Chem. Ecol.* **16**(11) (in press).

Papaj, D. R., Opp, S. B., Prokopy, R. J., and Wong, T. T. Y. (1989). Cross-induction of host fruit acceptance in medfly: The role of fruit size and chemistry. *J. Insect Behav.* **2:** 241–254.

Prévost, G., and Lewis, W. J. (1990). Genetic differences in the response of *Microplitis croceipes* to volatile semiochemicals. *J. Insect Behav.* **3:**277–287.

Prokopy, R. J., Averill, A. L., Cooley, S. S., and Roitberg, C. A. (1982). Associative learning in egglaying site selection by apple maggot flies. *Science* **218:** 76–77.

Ridgway, R. L., Ables, J. R., Goodpasture, C., and Hartstack, A. W. (1981). *Trichogramma* and its utilization for crop protection in the U.S.A. In *Proceedings Joint American-Soviet Conference, "Use of Beneficial Organisms in the Control of Crop Pests,"* Washington, D.C., pp. 41–48.

Sahley, C. L. (1984). Behavior theory and invertebrate learning. In Marler, P., and Terrace, H. S. (eds.), *The Biology of Learning*, Springer-Verlag, New York, pp. 181–196.

Sheehan, W., and Shelton, A. M. (1989). The role of experience in plant foraging by the aphid parasitoid *Diaretiella rapae* (Hymenoptera: Aphidiidae). *J. Insect Behav.* **2:** 743–759.

Smith, M. A., and Cornell, H. V. (1978). Hopkins host-selection in *Nasonia vitripennis* and its implications for sympatric speciation. *Anim. Behav.* **27:** 365–370.

Sokal, R. R., and Rohlf, F. J. (1981). *Biometry*, Freeman, New York.

Thorpe, W. H., and Jones, F. G. W. (1937). Olfactory conditioning in a parasitic insect and its relation to the problem of host selection. *Proc. R. Soc. Ser. B* **124:** 56–81.

Tinbergen, N. (1951). *The Study of Instinct*, Oxford University Press, London.

Turlings, T. C. J., Tumlinson, J. H., Lewis, W. J., and Vet, L. E. M. (1989). Beneficial arthropod behavior mediated by airborne semiochemicals. VIII. Learning of host-related odors induced by a brief contact experience with host by-products in *Cotesia marginiventris* (Cresson), a generalist larval parasitoid. *J. Insect Behav.* **2:** 217–225.

van Alphen, J. J. M., and Vet, L. E. M. (1986). An evolutionary approach to host finding and selection. In Waage, J. K., and Greathead, D. J. (eds.), *Insect Parasitoids*, Academic Press, London, pp. 23–61.

Vet, L. E. M. (1983). Host-habitat location through olfactory cues by *Leptopilina clavipes* (Hartig) (Hym.: Eucoilidae), a parasitoid of fungivorous *Drosophila*: The influence of conditioning. *Neth. J. Zool.* **33:** 225–248.

Vet, L. E. M. (1985). Olfactory microhabitat location in some eucoilid and alysiine species (Hymenoptera), larval parasitoids of Diptera. *Neth. J. Zool.* **35:** 720–730.

Vet, L. E. M. (1988). The influence of learning on habitat location and acceptance by parasitoids. In *Parasitoid Insects* (Lyon, September 7–10, 1987), Les Colloques de l'INRA 48, INRA, Paris, pp. 29–34.

Vet, L. E. M., and van Alphen, J. J. M. (1985). A comparative functional approach to the host detection behaviour of parasitic wasps. I. A qualitative study on Eucoilidae and Alysiinae. *Oikos* **44:** 478–486.

Vet, L. E. M., and Groenewold, A. W. (1990). Semiochemicals and learning in parasitoids. *J. Chem. Ecol.* **16**(11) (in press).

Vet, L. E. M., and Janse, C. J. (1984). Fitness of two sibling species of *Asobara* (Braconidae: Alysiinae), larval parasitoids of Drosophilidae in different microhabitats. *Ecol. Entomol.* **9:** 345–354.

Vet, L. E. M., and Schoonman, G. (1988). The influence of previous foraging experience on microhabitat acceptance in *Leptopilina heterotoma*. *J. Insect Behav.* **1:** 387–392.

Vet, L. E. M., and van Opzeeland, K. (1984). The influence of conditioning on olfactory microhabitat and host location in *Asobara tabida* (Nees) and *A. rufescens* (Foerster) (Braconidae: Alysiinae), larval parasitoids of Drosophilidae. *Oecologia* **63:** 171–177.

Vet, L. E. M., van Lenteren, J. C., Heymans, M., and Meelis, E. (1983). An airflow olfactometer for measuring olfactory responses of hymenopterous parasitoids and other small insects. *Physiol. Entomol.* **8:** 97–106.

Vet, L. E. M., Janse, C., van Achterberg, C., and van Alphen, J. J. M. (1984). Microhabitat location and niche segregation in two sibling species of Drosophilid parasitoids: *Asobara tabida* (Nees) and *A. rufescens* (Foerster) (Braconidae: Alysiinae). *Oecologia* 61: 182–188.

Vinson, S. B. (1976). Host selection by insect parasitoids. *Annu. Rev. Entomol.* **21:** 109–134.

Vinson, S. B. (1981). Habitat location. In Nordlund, D. A., Jones, R. L., and Lewis, W. J. (eds.), *Semiochemicals: Their Role in Pest Control*, Wiley, New York, pp. 51–77.

Vinson, S. B. (1984). How parasitoids locate their hosts: A case of insect espionage. In Lewis, T. (ed.), *Insect Communication*, R. Entomol. Soc., London, pp. 325–348.

Vinson, S. B., Barfield, C. S., and Henson, R. D. (1977). Oviposition behaviour of Bracon mellitor, a parasitoid of the boll weevil (*Anthonomus grandis*). II. Associate learning. *Physiol. Entomol.* **2:** 157–164.

Visser, J. H. (1988). Host-plant finding by insects: Orientation, sensory input and search patterns. *J. Insect Physiol.* **34:** 259–268.

Waage, J. K. (1979). Foraging for patchily-distributed hosts by the parasitoid, *Nemeritis canescens. J. Anim. Ecol.* **48:** 353–371.

Wardle, A. R., and Borden, J. H. (1986). Detrimental effect of prior conditioning on host habitat location by *Exeristes roborator. Naturwissenschaften* **73:** 559–560.