Insect-Plant Interactions

Volume II

Editor

Elizabeth A. Bernays, Ph.D.
Professor and Head
Department of Entomology
University of Arizona
Tucson, Arizona

1990

CRC Press
Boca Raton Ann Arbor Boston

2

The Role of Experience in Host Plant Choice by Phytophagous Insects

Árpád Szentesi and Tibor Jermy
Plant Protection Institute
Hungarian Academy of Sciences
Budapest, Hungary

TABLE OF CONTENTS

I. INTRODUCTION

Insect behavior was generally thought to be determined largely by closed genetic programs, leaving little room for learning in behavioral development. This picture has changed over the last decades, especially since the highly developed learning ability of social Hymenoptera has been demonstrated. The number of publications dealing with learning in phytophagous species is also increasing rapidly. As a consequence, there is now a growing danger of overemphasizing the role of learning in insects, because most authors stress abilities without pondering the limits and imperfections of processes involved, and this may easily lead to false conclusions. In addition, in some insect species learning could not be demonstrated.[53] A further problem is that the experiments, especially with phytophagous insects, are carried out mostly in the laboratory and it is difficult to estimate how the learning ability demonstrated under such conditions influences the survival and fitness of insects in nature.

For students of insect-plant relationships it is of considerable importance to know how plastic the phytophagous insects' nervous system is in "solving" tasks in natural circumstances. If the insects' food-related behavior can be optimal[120,121] (see criticism on optimal foraging[163]), it is learning that might contribute to optimal "decisions" (see more in Section VIII).

With these constraints in mind, we try to give an objective survey on the state-of-the-art of investigations into the experience-induced behavioral changes in phytophagous insects as related to food selection and host finding. The majority of mostly theoretical papers[93,141,142,171,220,221] are not considered although these are of exceptional value in defining the criteria and circumstances for learning studies, or approximating the ultimate mechanisms of learning by the use of mutant strains[61,88] or various sensory modalities.[18,71,197] The studies of accompanying events, for instance central excitatory state (CES)[222] and experience-dependent behavioral elements,[65] are equally important and briefly dealt with.

II. TYPES OF LEARNING

In the following, a list of learning phenomena similar to the one presented in a recent review[58] and thought to be involved in the host selection behavior of phytophagous insects is prepared with definitions based on works of several authors.[83,96,102,140,141,160] Learning will be divided into nonassociative (habituation, sensitization, and pseudoconditioning) and associative (classical and instrumental conditioning) types (see definitions under separate headings). Imprinting is discussed separately as it is usually considered a special type of learning,[229] although not all authors agree on this.[211]

The generally accepted broad definition of learning that will be used also by the authors is modification of behavior through experience. With learning, a central nervous system process is generally implied, in contrast to peripheral events, such as (sensitivity) changes in receptor function which may also result in behavioral changes (see Section III).

Learning types in insects can range from simple habituation to complex associative processes. The proper conditions set for the definition of different types of associative learning are quite specific (see below), but involve a clear demonstration of association between the unconditioned stimulus (US) which stimulates the behavioral response prior to learning, and the conditioned stimulus (CS) which becomes a signal for the response as result of learning.

The term "conditioning" is generally reserved for associativ[illegible]lassical and instrumental) learning. Therefore, it is misleading to use it in its "loose sense"[161] and to equate induced preference with conditioning as "conditioning of host-plant preference"[154] because induced preference does not meet all the criteria set for associative learning.[57]

In the literature there are other aspects of confusion in the use of the terminology of learning, and especially in the way in which changes in food preferences are discussed. For example, Blaney and Simmonds[21] refer to short-term changes in food selection behavior as learning and long-term changes by contrast as "induction" although they do not define the time scale involved. However, we believe that long-lasting experiences in phytophagous insects can involve both associative and nonassociative learning[138] and that the well known phenomenon of induced preference for the rearing food[115] could well involve learning (see below).

A. HABITUATION

Habituation is the waning of response to a repeatedly presented stimulus over time.[83,96,140,207] Kandel and Spencer[123] (cited by Eisestein[63]) listed criteria that define habituation. A response decrement characteristic of the habituation process may occur for a number of reasons and several different mechanisms may underlie it. It is usually thought of as the most primitive, simplest type of learning.

There is also some controversy on certain aspects of habituation. For instance, its retention depends on the rate of stimulation. Thompson and Spencer[207] predicted a faster response decrement to more frequent stimulation, while Thon[208] found the opposite with *Calliphora vomitoria*. Weak and frequently presented stimuli are more generally likely to elicit habituation than strong ones. Though certain stimuli (e.g., a predator's silhouette for a young bird) will never produce a habituation response, the importance of different types of stimuli is generally small.

Habituation can be elicited by both stimulatory and inhibitory stimuli. Dethier[50] (cited by Duerr and Quinn[62]) observed a response decrement upon presentation of the phagostimulant sucrose to *Phormia*; the change was mediated centrally. Szentesi and Bernays[203] demonstrated that habituation of *Schistocerca gregaria* to a deterrent was also a central nervous phenomenon. (See Section V.A for further examples of habituation.) All sensory modalities can be involved in eliciting a habituation response, but the habituation is specific to the particular stimuli participating in its induction, and as a consequence underlying mechanisms may also differ.[125]

Finally, Thon and Pauzie[209] (p. 119) concluded from a study conducted on cardiac and motor response habituation (i.e., on two "response systems") in *C. vomitoria* the "habituation processes develop independently in different response systems, even if they have the same sensory input."

B. SENSITIZATION AND PSEUDOCONDITIONING

Sensitization may be defined as a state of excitation or increased responsiveness of the organism to biologically significant stimuli. However, applying the more precise learning paradigm terminology[141] (p. 481), "we speak of sensitization if a change in response occurs after repeated presentation of a conditioned stimulus (CS) that has not been paired with an unconditioned stimulus (US)." By pairing US and CS we expect an enhanced response to CS, although increased responses can also appear from presenting the US alone.

Authors generally agree that sensitization is a nonassociative type of learning[83,140,141] although sensitization can be considered "as a necessary precursor of associative learning or conditioning . . . "[140] (p. 339). The dual-process theory[83] presumes that the two contrasting processes (habituation and sensitization) have evolved and occur independently, [illegible] interact. As it has been pointed out " . . . the strength of the behavioral response elicited by a repeated stimulus is the net outcome of the two independent processes of habituation and sensitization" (pp. 441-442).[83] This can be illustrated by the following. Städler and Hanson[199] showed that wheat germ extract was deterrent for larvae of *Manduca sexta* reared on host plant leaves, but the response to the deterrent was significantly reduced in larvae reared on wheat germ diet. On the other hand, diet-reared larvae preferred diet to host plant leaves. It may be that ingestion of a certain food leads, through sensitization, to a habituation to food-specific deterrents.

In connection with sensitization the phenomenon of the central excitatory state (CES) has to be mentioned. It was first described by Dethier et al.[59] who found that immediately after the presentation of a drop of sucrose solution to the labellar hair of a water-satiated *Phormia regina*, the fly would extend its proboscis immediately afterwards when water only is offered. This increased reactivity was attributed by the authors to an excitatory state of the central nervous system (CNS). The duration of the CES varies significantly: e.g., 15 s in *Leptinotarsa decemlineata*;[110] up to 120 s in *P. regina*;[59,219] (cited in Reference 222) at least 10 min in *Drosophila*.[222] We agree with Duerr and Quinn's opinion[62] who came to the conclusion, when measuring sensitization after sucrose stimulation in *Drosophila*, that this phenomenon is basically identical with the CES described by Dethier et al.[59] We also propose that sensitization in this broader sense is relevant to the explanation of induced feeding preference and early imaginal (oviposition) experiences in phytophagous insects (see Sections V.B and VII).

Upon repeated presentation only of an unconditioned stimulus (US) without pairing it with a conditioned one (CS), the increased response to the CS shown by the animal is termed *pseudoconditioning*.[141] For our further discussion the involvement of US has a special importance, as it refers to food or other vitally important environmental features. There is usually a CS (e.g., shape of food) present, although much separated in time from the reinforcing US (e.g., chemical features). It is the time separation feature which is used to separate it from associative learning. Thus pseudoconditioning is used as a proper control for associative learning.[150,171] Krasne[125] equates sensitization with pseudoconditioning, emphasizing the role of the US only, while McGuire[141] and others separate the two phenomena, as we do, by altered responses to either CS or US.

C. IMPRINTING

It has frequently been observed that animals possess one or more especially sensitive periods in ontogenesis to environmental stimuli, such as those representing parent, mate, habitat, or food. As a result they tend to persistently respond to stimuli corresponding to the first experiences. The learning process through which the perceptual change is acquired was termed imprinting.[102,140]

Imprinting is a quick learning process, resulting in long-term memory.[229] Some students of animal behavior[91,211] do not consider it as a separate type of learning, while others (e.g., Wallace[229]) argue that it is a special learning type that can be characterized by its fast formation. It is similar to instrumental conditioning, except that usually only one experience is sufficient and no further reinforcement is required. The persistence of imprinted experience may be life long.

Its concept has developed considerably since the original description.[134] Immelmann[102] discussed in detail the cases of imprinting known so far and came to the conclusion that there are only two important criteria: (1) the existence of a sensitive period, and (2) the subsequent stability (rigidity) of response to experience gained during that period. Imprinting-like behavior has mostly been demonstrated in vertebrates, and with the exception of parasitic insects (e.g., *Nemeritis canescens*[212] and *Asobara* species[223]), the number of instances with insects are few. Apart from involvement in various social contexts, "ecological" imprinting[102] involves food preference, habitat or host selection.

The notion of ecological imprinting provides the framework within which we interpret induction of food preference (see Section V.B).

D. ASSOCIATIVE LEARNING

Associative learning is by far the most complex type of learning, embracing at least two main types: classical and instrumental conditioning. A behavioral change is generally termed conditioning when a strict timely coincidence or pairing of a conditioned stimulus, the CS (which is quite ineffective in this context in itself), and an unconditioned stimulus, the US, occurs, and after only one or several experiences the CS serves to elicit a response previously elicited by the US, but not the CS (classical conditioning). While in classical conditioning a close temporal relationship of stimulus and reinforcer is provided, in instrumental (operant) conditioning a connection of response and reinforcer is required,[140,229] which may also be the essential process in trial-and-error learning.[211] Careful experimentation must exclude pseudoconditioning, CES or sensitization, and habituation.

One of the early reports on conditioning with arthropods (locusts) is that of Horridge.[97] Subsequently Nelson[150] showed convincingly that the blowfly, *Phormia regina* is able to acquire a conditional response. Fukushi[66] used houseflies (*Musca domestica*) to demonstrate olfactory conditioning. The increase of CS-US interval, i.e., "weakening" of the contingency of the US upon the CS decreased the probability of a conditioned response. Fukushi[67] conditioned houseflies also to perform a characteristic food searching behavior, "dance"[151] for sucrose droplets containing any of the test substances as CS. The information about the odor of the food source was stored for at least 3 h without loss of performance. A fast discrimination learning was demonstrated with intact *Periplaneta americana*.[8] Operant conditioning has also been demonstrated in a number of cases with insects.[28]

The above and similar reports convincingly demonstrate that many insect species are capable of performing learning tasks and have the capacity to store important information about the environment, at least temporarily.

It is perhaps the importance of testing a given insect species in circumstances resembling its natural environment that explains some more successful associative learning studies. Some early work on learning, applying naturalistic conditions, demonstrates the importance of relevant conditions (see Fukushi[67] p. 248, for references). The carabid beetle, *Pterostichus melanarius*, was unable to learn a maze, but successful learning was demonstrated in the open field, using an apparatus in which the insects could contact the wall.[165] Water-deprived beetles showed a marked decrease in time necessary to locate a centrally placed water source after trials on 4 consecutive days, but the information was not retained over 24 h.

Focusing here on phytophagous insects, we consider associative learning mainly in food-aversion learning as well as food and oviposition site finding (see Sections V and VI).

III. NEURAL MECHANISMS UNDERLYING EXPERIENCE-INDUCED CHANGES OF BEHAVIOR

The decision whether to eat a plant or not depends on the sensory pattern provided primarily by the chemoreceptors as well as on the processing and retention of the incoming information by the CNS.

Several experimental studies have shown that feeding experience may change receptor characteristics. Schoonhoven[184] exposed *Manduca sexta* larvae for 2.5 days to an artificial diet containing the feeding inhibitor salicin that stimulated the deterrent receptor. After exposure, the sensitivity of that receptor was considerably lower than in unexperienced larvae. As the effect developed gradually, sensory adaptation of receptors could be excluded. The same author later[185] adopted the view that long-term sensitivity changes occurred in the chemosensory system. The characteristics of the receptor sites remained constant but the spike generating process was changed. The role of the CNS in the process of changes in response to deterrents was not raised.

When allelochemicals such as azadirachtin, nicotine, or sinigrin were added to the artificial diet on which larvae of *Spodoptera* spp. were reared, the sensitivity of the chemoreceptors to these compounds was strongly reduced with experience.[20,194] Schoonhoven[183] found that in *M. sexta* larvae that were fed on an artificial diet, the maxillary sensilla responded differently to saps of various plants compared with those of plant-fed larvae. When caterpillars were grown on two different host plant species, their responses to the saps of these plants also differed.[198] The responsiveness of the deterrent receptor to strychnine in *Pieris rapae* larvae was somewhat lowered relative to control larvae reared on untreated leaves[143] (cited by Blaney et al.[19]) when the larvae were reared on cabbage leaves sprayed with this chemical. The possible mechanisms regulating receptor responsiveness have been discussed in detail[19] but very few experimental data are available for phytophagous insects.

The central mechanisms regulating receptor sensitivity may be neural and/or hormonal, and it is possible that chemicals form the hemolymph act on the development and function of receptors (Bernays, personal communication). It is a general belief that there are no efferent pathways from higher nervous centers actually modifying receptor responses in insects.[19] However, axons of unknown origin have been found close to the receptor neurons in the A1 sensilla of the clypeo-labrum in *Locusta migratoria*.[36] As for the possibility of hormonal regulation, it was found that in *L. migratoria*, midgut distension stimulates release of a hormone from the corpora cardiaca that activates the closing mechanism of the palp-tip sensilla, and by this change their responsiveness.[13,14] Several authors have demonstrated the endocrine control of receptor sensitivity in adults of Diptera (see Blaney et al.[19] for references). It has been found that specific chemical stimuli are able to change the responsiveness of a single receptor type, and this argues against hormonal control. Therefore, it is most probable that the receptor cells are actively involved in controlling their own sensitivity,[19] although the mechanism by which this is achieved is not understood.

No changes in peripheral receptors were found by Ma[135] in the larvae of *Pieris brassicae* however, when they were reared on an artificial diet instead of on the host plant. Therefore, he proposed that in this case changes in preference behavior may be attributed entirely to changes in the CNS.

Memory is here defined as the timely persistence of experience, not referring to the neuroanatomical locus where it is formed. Therefore, it also applies to habituation, though its development and maintenance, partly at least, take place at early synaptic levels.[29] In the literature the persistence of information is usually classified as short- and long-term memory.[3] This applies also to arthropods, where the examples of nonassociative and associative learning infer various "kinds" and duration of memory, the proximate processes of which are almost unknown. Longer lasting memory may often cover associative learning while shorter term memory may at least sometimes correspond with certain kinds of nonassociative learning (e.g., pseudoconditioning).

From behavioral studies it is well established that certain lifestyles, especially eusociality, is accompanied by the ability to retain information gained from experience, and the memory of previous experience has been best demonstrated with Hymenoptera.[7] Experience may be retained in many insect species in spite of the dramatic changes taking place during metamorphosis.[4,76] Short-term memory contributed to more efficient foraging in *Colias* and *Pieris* butterflies.[132,200] Visual spatial and landmark memory are supposed to operate with bees,[5,77] and in the ant *Cataglyphis*.[234] A "novelty-effect" was described with *Musca domestica* induced by odor stimuli that lasted for ca. 30 min, and it was assumed that this resulted from memory.[240] Similarly, the information gained by females of the moth *Acrolepiopsis assectella* about host-plant allelochemicals was retained for ca. 1 day.[206]

A semblance of memory can be given by the "chemical legacy" effects.[38] This hypothesis states that the effect of larval chemosensory experience on adult responsiveness may depend on traces of chemical cues remaining inside or outside the insect's body after molting and influences adult behavior as a result of experience at eclosion (see also Sections VII and VIII).

With regard to the neural mechanisms underlying the four types of learning discussed in Section II, the following can be said:

- Habituation is believed to result from depression of transmitter release at synaptic junctions,[29,125] or from collateral inhibition.[177] Duerr and Quinn[62] directly demonstrated the central mediation of habituation with *Drosophila*. Sucrose stimulation on the right prothoracic tarsus resulted in a decreased responsiveness by the contralateral leg to the same subsequent stimulation.
- The mechanism(s) underlying sensitization are not known,[125] although it is supposed that it occurs in the CNS regions that set the level of responsiveness of the animal, and not along the stimulus-response pathways.[83]
- Food imprinting may arise partly through changes in chemoreceptor sensitivity resulting from feeding experience. Though direct experimental evidence is lacking, the role of the CNS cannot be excluded either.[199]
- As for associative learning, both elementary physiological processes and cellular level correlates of associative learning are discussed in recent papers.[28,125] In case of invertebrates, the study of *Drosophila* mutants has proved to be especially useful in understanding such mechanisms (e.g., References 61, 88, and 171).

IV. CATEGORIES OF PLANTS AS RELATED TO HOST SELECTION

In the literature on host plant selection by phytophagous insects the plant species are classified mostly as host plants and non-host plants, respectively. The former are represented by plants that are readily acceptable by and are suitable food for a certain insect species, while the latter are not accepted. However, the border between these two categories is often indistinct. For example, in case of the solanaceous feeder *Leptinotarsa decemlineata*, the plant species tested can be arranged in a "triangle of food preferences" based on the intensity of acceptable and unacceptable attributes (Figure 1).[109] The plant species located on the upper part, left of the dotted line, are the primary and secondary solanaceous host plants that are also attacked in nature, while further down on the left side are nonsolanaceous species that are more or less readily consumed (also in nature) by water- and food-deprived beetles. Plant species to the right of the dotted line are rejected even in forced-feeding situations. Based on this kind of distinction de Boer and Hanson[47] classified the plant species with respect to their acceptability by the oligophagous *Manduca sexta* as (1) host plants, (2) acceptable non-host plants that are not fed upon in nature but can act as food plants in the laboratory, and (3) unacceptable non[illegible]st plants, emphasizing that the hierarchy shows a graded continuum of acceptability extending across host and non-host species. In the following discussions these three categories are used.

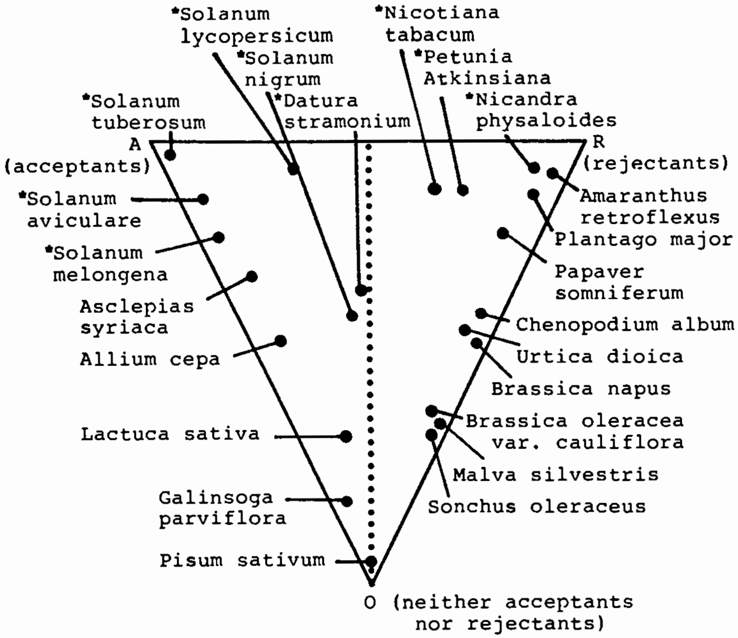

FIGURE 1. The "triangle of food preferences" as determined by leaf disc tests and sandwich tests for *Leptinotarsa decemlineata*. The effect of acceptants and rejectants decreases with the distance from A and R, respectively. Asterisks indicate solanaceous species. (From Jermy, T., *Acta Zool. Acad. Sci. Hung.*, 7, 119, 1961. With permission.)

It can be assumed that this categorization is valid for most oligophagous and polyphagous insects. To which category a certain plant species belongs in relation to an insect species presumably varies within limits depending on varietal differences and growing conditions that determine plant quality.[112] On the other hand, host-plant hierarchies may also change with experience gained by the insect[47,135] and may differ in relation to different populations of the same insect species.[100]

V. EXPERIENCE-INDUCED CHANGES IN FEEDING BEHAVIOR

A. HABITUATION TO FOOD-RELATED STIMULI

Besides theoretical aspects, studies on habituation have been initiated by considerations of the practical use of feeding inhibitory substances, since it has been observed that by the repeated contact of feeding insects with a deterrent-containing diet will increase its acceptance over time.[75,184,201] Schoonhoven and Jermy,[186] on the basis of field experiments conducted by Murbach and Corbaz[149] and Murbach[148] on the efficiency of Bordeaux mixture [a suspension of $CaSO_4$. $Cu(OH)_2$. $3Ca(OH)_2$], against *Leptinotarsa decemlineata*, and of their own behavioral observations on the same species and on *Pieris brassicae*, came to the conclusion that habituation at least to Cu-ions is not probable. On the other hand, Chapman[31] expressed the opinion that habituation to deterrent substances was a possibility. Bernays[12] did report da[illegible]f reduced effectiveness of a neem extract sprayed against *Zonocerus variegatus* when tested after 12 days of treatment, that was attributed to habituation and not to inactivation of active component(s). Subsequently, an increased consumption of deterrent-containing food over time was demonstrated in laboratory with the polyphagous *Mamestra brassicae* and *Schistocerca gregaria*, and the oligophagous *Pieris brassicae* and *Locusta migratoria*.[114,116,203]

In an examination of habituation to a feeding deterrent (nicotine hydrogen tartrate, NHT) with last instar nymphs of *S. gregaria*,[203] small pieces of nylon tubing were attached to both maxillary palpi of the nymphs. For the experimental group, the tubing was filled with NHT solution for given periods of time daily. The control group received distilled water in the tubes. On the test day, no chemical was applied to the capillaries, but feeding response was measured by the quantity of plant material consumed when treated with the same chemical. The insects that had been repeatedly exposed to the chemical consumed more of the treated leaves compared with the control group, despite the fact that direct perception of the chemical by the sensilla on the maxillary palpi was prevented by the nylon tubing still in place. The experiment proved that by the time of final test habituation had occurred and was mediated centrally.

The study with *S. gregaria*[203] demonstrated that weak stimuli can be more successful in eliciting habituation than stronger ones.[96] Habituation to NHT was shown by 1% concentration of the chemical, but not by 5 or 20%.

Jermy et al.[114] observed differences with species differing slightly in their patterns of habituation to different chemicals. For example, the pattern of development of the responses by *M. brassicae* and *P. brassicae* to strychnine was different, and the same is true of *P. brassicae* tested on strychnine or quinine. Furthermore, the method of presentation of the stimulus affected the outcome considerably. If NHT was presented to either *S. gregaria* or *L. migratoria* on living plant tissue, habituation to the chemical occurred. However, if the same substance was offered on a glass fiber disk, the insects developed an aversion (see Section V.C for further discussion).

From the few cases known so far it seems that polyphagous species habituate to single chemicals in the laboratory more readily than oligophagous species.[114]

B. FOOD IMPRINTING (INDUCTION OF FOOD PREFERENCE, IFP)

Entomologists have long known that lepidopterous larvae, after having fed on one host-plant species, would only reluctantly accept other host species. Darwin[44] (P. 293) mentions the observation made by Michely:[145] "The caterpillars of the *Bombyx hesperus* feed in a state of nature on the leaves of the *Café diable*, but, after having been reared on the *Ailanthus*, they would not touch the *Café diable*, and actually died of hunger."

The term IFP was given to this phenomenon by Jermy et al.[115] who thoroughly investigated it. Dethier[57] emphasized that this neutral term should be preserved because the nature of the phenomenon is largely unknown. The latter opinion has been shared by many others until recently,[112] although the possible relationship of IFP with learning has been noted. Bernays and Wrubel[17] wrote in connection with food selection learning (see more details in Section V.E): "This process, known as induction, could involve elements of learning" (p. 359).

We assume that IFP is a type of learning and it meets two main criteria listed for imprinting:[102] the existence of a sensitive period and the subsequent stability (rigidity, "irreversibility") of the resulting behavior. As for the first criterion: in some lepidopterous species early food experience with certain plant species definitively determines food preference for the larvae[65,135,241] indicating that the young instars are very sensitive in this respect. Although induction proved to be possible also in later instars,[115] so that there is not such a clearly definable sensitive period, in nature it may be of decisive importance that the first instar lepidopterous larvae become "imprinted" on the plant on which they emerge from the eggs.[236]

The criterion of stability is better met; for example, food experience of early instar *Pieris brassicae* larvae may last till the end of larval development.[135] It can be formed after brief (e.g., 4 h long[135]) experience with the food, and can be so rigid that the insect may rather starve to death than consume another host plant.[88,135,191] The degree of rigidity of induction is a relative measure. This is demonstrated by the induction index[47] (see Section V.B.2). In several cases induced food preference was found to be changeable,[30,135] but similar lability has also been observed in cases of typical imprinting,[102] as well as individual variability of imprintability.[102]

Based on the above we argue that IFP basically meets the criteria of imprinting on food, and should, therefore, be referred to as "food imprinting". Moreover, the term "food imprinting" more explicitly refers to a learning process. (It would be tempting to use the term "host-plant imprinting"; however, lepidopterous larvae can be imprinted also on artificial diets.[199])

1. Incidence of Food Imprinting

Several authors have dealt with this phenomenon in various groups of insects, especially over the last two decades. As can be seen from Table 1, food imprinting may occur in all the main groups of phytophagous insects.

Very few data have been published on the absence of food imprinting. This may partly be due to the fact that negative results are less often published than positive ones. Table 2 shows the insect species with which experience-induced changes of feeding behavior have been looked for and not found.

A comparison of Tables 1 and 2 indicates that with the same insect species (*Acyrtosiphon pisum, Phratora vitellinae, Leptinotarsa decemlineata, Hyphantria cunea, Pieris rapae*) some authors did and some did not find food imprinting. This may be due to (1) different experimental procedures, (2) different ontogenetic stages of the insects, (3) different plants used in the experiments, since it has been found repeatedly that host plants may differ considerably in the degree of food imprinting they are able to induce (see Section V.B.2), and (4) intraspecific differences among populations, e.g., two geographically distant populations of *Ph. vitellinae* differed significantly in the extent to which food imprinting of the same plant species occurred.[178]

2. Degree of Food Imprinting

The degree of food imprinting may be expressed as an "induction index" calculated as follows[47] (p. 179): "The difference in feeding preferences for two plant species is expressed in a choice index (range, −100 to +100) which measures the mean consumption of plant A minus that of plant B. The degree to which preferences are induced is expressed as an induction index (range, 0 to 200) which is the absolute difference between the choice indices for plant pair A,B obtained for two groups of larvae reared on either plant A or plant B."

Surveying the data on lepidopterous larvae there was an inverse correlation between the degree of food imprinting and taxonomic relatedness of plant species paired in the above sense.[47] This was supported by the data on *Pieris brassicae,*[135] *Papilio machaon,*[236] *Callosamia promethea, Polygonia interrogationis, Antheraea polyphemus,*[66] *Lymantria dispar,*[9,233] *Manduca sexta, Limenitis astyanax, L. hybrid rubidus, L. archippus,* and *Heliothis zea.*[47] Presumably this inverse correlation is related to similarities in available gustatory stimuli from closely related plants. In this connection it has to be emphasized, however, that taxonomic relatedness does not always reflect similarity in the plants' chemical "Gestalt" perceived by the insects. The discrepancy between taxonomy and chemical "Gestalt" may explain that, e.g., only wea[illegible]r no food imprinting was found with *Lymantria dispar* when plant pairs belonging t[illegible]he same family (Fa-

Table 1
LIST OF INSECT SPECIES IN WHICH EXPERIENCE WAS FOUND TO CHANGE FEEDING PREFERENCES

Species	Stage tested	Ref.
Orthopetera		
Schistocerca gregaria	L	225
Phasmatodea		
Carausius morosus	L, A	30
Bacillus rossius	L, A	166
Heteroptera		
Dysdercus koenigi	L	180
Homoptera		
Acyrthosiphon pisum	A	101
Schizaphis graminum	A	188
Coleoptera		
Epilachna pustulosa	A	104
Subcoccinella 24-punctata	L, A	2
Haltica lythri	L, A	162
Galerucella lineola	L, A	124
Phratora vitellinae (Swiss population)	A	178
Leptinotarsa decemlineata	A	238
Lepidoptera		
Noctuidae		
Heliothis armigera	L	1
H. zea	L	115, 239
Spodoptera eridania	L	191
Lymantriidae		
Euproctis chrysorrhoea	L	73, 128
Lymantria dispar	L	9, 73, 233
Arctiidae		
Hyphantria cunea	L	81
Sphingidae		
Manduca sexta	L	47, 65, 87, 115, 182, 241
Saturniidae		
Antheraea pernyi	L	73, 196
A. polyphemus	L	86
Callosamia promethea	L	86
Hyalophora cecropia	L	79
Limenitis archippus	L	86
L. astyanax	L	86
L. hybrid rubidus	L	86
Pieridae		
Pieris brassicae	L	118, 135
P. rapae	L	99
Papilionidae		
Papilio aegeus	L	202
P. glauca	L	47
P. machaon	L	236
Nymphalidae		
Chlosyne lacinia	L	214
Polygonia interrogationis	L	86
Pyraustidae		
Lo[illegible]ge sticticalis	L	43

Partial data from Jermy, T., *Perspectives in Chemoreception*, Chapman, R. F., Bernays, E. A., and Stoffolano, J. G., Jr., Eds., Springer-Verlag, New York, 1987, chap. 9.

Table 2
LIST OF INSECT SPECIES WITH WHICH EXPERIENCE WAS FOUND NOT TO CHANGE FEEDING PREFERENCES

Species	Stage tested	Ref.
Coleoptera		
Leptinotarsa decemlineata	A	25
Tribolium castaneum	A	11
Phratora vitellinae (French population)	A	178
Homoptera		
Acyrthosiphon pisum	A	147
Lepidoptera		
Noctuidae		
Mamestra brassicae	L	112
Arctiidae		
Hyphantria cunea	L	112
Pieridae		
Pieris rapae	L	33
Pieris napi macdunnoughii	L	33

gaceae) were tested,[233] but a significant effect could be achieved with *Papilio machaon* when plant pairs chosen also from one family (Umbelliferae) were used.[236]

Since oligophagous insects *ab ovo* can be tested only with closely related plant species, it seems obvious that polyphagous species should be more prone to food imprinting than oligophagous ones. This has been proposed mainly as a result of electrophysiological investigations.[194] However, no correlation could be shown between the degree of polyphagy and the degree of food imprinting when the relevant literature was surveyed.[47] The variability of food imprinting depends more probably on the taxonomic and/or phenetic similarity of plants tested than on the degree of polyphagy.[233]

The degree of food imprinting also shows significant individual variation within insect populations.[30,115,135,162] At present nothing is known about the possible physiological and/or genetic basis of this variability.

3. Persistence of Food Imprinting

Although only a few insects have been studied in this respect, it seems that persistence does vary greatly both with insect and plant species. Jermy et al.[115] have shown with *Heliothis zea* larvae that imprinting on a plant species may persist through two molts and a whole instar between them, when that instar was fed an artificial diet not containing host-plant constituents. In *Carausius morosus* imprinting could be reversed, although this flexibility strongly decreased with ontogeny.[30]

In some cases striking rigidity of food imprinting has been observed. Ma[135] demonstrated that when larvae of *Pieris brassicae* were reared on *Brassica oleracea* and the young fifth instar larvae were transferred to *Tropaeolum majus*, all larvae died of starvation although the latter plant supported normal larval development from the first instar on. A similar observation was made with different plants using larvae of *Callosamia promethea*[86] and *Spodoptera eridania*.[191] This phenomenon was called the "starving-to-death-at-Lucullian-banquets" phenomenon.[112]

Grabstein and Scriber[78] drew attention to the fact that strong and permanent (rigid) food imprinting may strongly hinder discrimination between behavioral (preingestive) and physiological (post-ingestive) effects of different foods on insects. Imprinting has to be taken into consideration also when phytophagous insect species, introduced for biological control of weeds, have to be checked for their possible host plant range in the region of introduction.

4. Phytochemicals Involved in Food Imprinting

It is not generally clear which phytochemicals are involved in food imprinting. The ability of an insect to discriminate among plant species, however, does not guarantee that imprinting will occur,[47] as other factors may limit induction.

Manduca sexta larvae may become imprinted on artificial diets and nutrients, especially lipid components, were found to be responsible for both plant discrimination and food imprinting, although aqueous fractions were also involved.[199] Imprinting for corn oil or linoleic acid alone was also demonstrated. It was concluded[199] that the artificial diet used for rearing the larvae of *M. sexta* was not neutral relative to causing changes in feeding behavior, as had been implicitly suggested by earlier studies.[115,183,241]

Recent investigations[48] have indicated that solanaceous alkaloids are most probably not part of the "chemosensory profile"[47] ("biochemical profile"[111]) perceived by *M. sexta* larvae and thus do not provide chemical information for discrimination and/or food imprinting.

M. sexta larvae reared on two diets containing liquidized leaves of one of two host-plant species, became imprinted on the diet, i.e., they preferred the one on which they were reared, but they did not discriminate between the two plant species used in preparing the diets. Similarly, larvae reared on one of the two plant species did not discriminate between the two diets. This indicates that the larvae were imprinted by a composite taste quality of the leaf diet which was different from that of the leaves, and vice versa.[199]

Behavioral tests carried out with caterpillars that were fed on deterrent-containing diets indicated reduced sensitivity to the compounds used. For example, linolenic acid was deterrent for *M. sexta* larvae in behavioral choice tests but when the larvae were reared on a diet containing this compound, it became less deterrent. Wheat germ diet extract was much less deterrent to larvae reared on wheat germ diet than to plant-reared ones.[199] This implies that food imprinting may result from decreased sensitivity to deterrents. However, increased responses to stimulating extracts with *M. sexta* larvae that were accordingly food-imprinted have also been shown,[199] although the possibility that this was due to decreased responsiveness to deterrent components of the extracts was not excluded.

With regard to the role of volatile substances in food imprinting, it was shown[181,182] that in *M. sexta* larvae close range orientational response to a certain food increased as a result of previous experience. Since *Malacosoma americanum* larvae were found[54] to rely heavily on specific volatile substances for their initial discrimination of plants, and *Leptinotarsa decemlineata* adults were attracted to their host plants by a specific blend of general green leaf volatiles,[136,224] it is possible that olfactory experience of specific plant volatiles may be involved in food imprinting more generally than thought so far.

5. Food Imprinting as Related to Host Range

It was suggested[241] that first-instar larvae of the solanaceous feeder, *Manduca sexta*, were polyphagous because they accepted also nonsolanaceous plants when force-fed. Furthermore, [illegible]*bascum thapsus* (Scrophulariaceae) supported larval development to the fourth instar and *Vigna sinensis* (Fabaceae) was suitable for complete larval development. the conclusion was that oligophagy was the consequence of food imprinting in this species.[65,241] Also Ma[135] has shown that the crucifer-feeding *Pieris brassicae* could be reared normally on *Tropaeolum majus* (Tropaeolaceae) from the first instar on, while *Brassica*-fed larvae did not accept *Tropaeolum*. Similarly, it was found that the first instar larvae of *Papilio machaon* had a genetically determined "spectrum of potential host plants" that was wider than that of the older instars.[236]

On the other hand, de Boer and Hanson[47] found with *M. sexta* that the relative preference for host over acceptable non-host plant species was maintained at the same level by rearing on the former plant species and was reduced by rearing on the latter. Therefore, they concluded that oligophagy in this species is inherited and not the result of experience.

The common feature of all such experiments was that the first instar larvae rejected many non-host plant species, i.e., "unacceptable non-host plants" (see Section IV). It is merely a question of semantics whether the somewhat broader potential food plant spectrum of the newly hatched larvae is regarded as a sign of polyphagy or as of less restricted oligophagy. Nevertheless, these findings clearly demonstrate the slightly greater potential of newly hatched larvae with respect to host-plant range as compared with older larvae. It also suggests and important role of food imprinting in forming the actual host plant spectrum of natural insect populations which may be narrower than the inherited potential spectrum. These results also suggest that care must be taken in experimentally determining the potential host plant ranges even in case of phytophagous insect species known as narrow food specialists.

C. FOOD-AVERSION LEARNING

It is well known that vertebrate generalist feeders (e.g., rats) sample a novel food by taking a small quantity when they first encounter it. After taking a mere mouthful they wait for visceral consequences, and if symptoms of sickness develop, they subsequently, following recovery, avoid that food. The process by which post-ingestional effects are associated with the taste or smell of the sampled food, to induce an altered behavior, is termed food-avoidance or food-aversion learning. Food aversion learning differs from many associative learning processes because of the long interval between the presentation of the CS (in this case the sensory cues of the food plant), and the US (post-ingestive malaise). (See general descriptions in References 10 and 140.)

While the phenomenon is well established with some vertebrates, there are only relatively few examples known in invertebrate animals. However, a similar phenomenon does occur and is best known with molluscs.[49,69,235]

Dethier and Yost[60] tested an oligophagous insect, *Manduca sexta*, for food-aversion learning. They conducted two types of experiments: one using *Atropa belladonna* or *Nerium oleander* leaves sprayed with insecticides, and the other using only *Petunia* sp. without treatment but known to have toxic effects on the insect. On both types of leaves the larvae began feeding and in varying time intervals they became "ill". Only larvae that had recovered from illness were tested again on the same but unsprayed foliage. Surprisingly, larvae that had recovered from the illness did not show a reduction in relative preference for the same plants subsequently.

However, two polyphagous species (*Diacrisia virginica* and *Estigmene congrua*) did show food-aversion learning.[55] Larvae fed *Petunia* for 24 h subsequently showed symptoms of illness. After recovery, the consumption of *Petunia* was compared with two other plant species (*Gaultheria* and *Unifolium*) in preference tests; *Petunia* was significantly less preferred by these insects compared with naive larvae. Bernays and Lee[16] suggest that the altered behavior of the caterpillars in this case may have "resulted from processes other than aversion learning. The alternative food may have become more acceptable...." Nevertheless, the above results are strongly suggestive of the occurrence of food-aversion learning. It is difficult to say how much and how serious symptoms need to be before rejection occurs at the next encounter. It may be that no conspicuous consequence of consumption on a toxic plant can be detected. In any case, *physiological* feedback is normally considered a prerequisite of food-aversion learning, but when no symptoms are measurable, this concept becomes entirely theoretical. Another approach would be to consider it as an associative process directed toward the avoidance of "negative" influences of which timely discovery can happen at sensory levels prior to swallowing or ingestion. For example, two reports with oligophagous species demonstrate another way in which rejection of food can be enhanced by experience[22,23] involving oligophagous species. In the first, *Locusta migratoria* on unpalatable plant species, like *Senecio* and *Brassica*, initially palpated and bit before rejecting the plants, and on a subsequent occasion rejection occurred following palpation without biting. That is, insects apparently learned to associate unpleasant taste stimuli at biting with other characters (e.g., olfactorily acting substances, or materials dissolved in a waxy layer or adhering to the surface of the plant), stored the information and next time on encountering the same species, palpation proved to be enough to cause rejection. Similar results and more detailed analyses of the rejection behavior are given on *Locusta*[23] and *Spodoptera exempta*.[21] The dynamics of rejection showed that on subsequent occasions the frequency of biting decreased and rejection at palpation became dominating.

These findings may possibly be explained by sensitization only, as strong and possibly noxious stimuli might produce a high level CES which would be strengthened by each further biting trial. Sensitization was not controlled for in these experiments, and by definition[141] it can occur when a CS (here specific substances of the plant leading to rejection) *is not paired* with an US (the noxious character of the plant species), though less rigorous definitions also can be found.[83] Perhaps also the notion of aversion learning should be widened or differentiated according to the degree of food specialization shown by the organism under consideration.

It is probable that poly- and oligophagous herbivorous insects possess the same level of chemosensory sophistication, but the processing of information in the CNS is different.[56] As a consequence, polyphagous insects may be less able to differentiate among plant species so substantial consumption of a plant having toxic constituents is more likely. Depending on the quantity and/or noxiousness of such substances, polyphagous insect herbivores may either detoxify or show food-aversion learning at next encounter. An oligophagous species being perhaps less able to tolerate alien plant substances internally will show rejection at the sensory level on the basis of information gained from tiny bites and learn from them. So we should perhaps term both types of reaction as food-aversion learning; this is contrary to the view that "...polyphagous species should be expected to show food-avoidance learning but oligophagous species would not"[70] (p. 202). It may be that one should look for more subtle effects with oligophages.

Several examples of food-aversion learning, and especially those on the polyphagous *S. gregaria*, do not enable us to make sharp distinctions on the basis of food specialization. When *S. gregaria* was fed with NHT-treated *Sorghum*, *habituation* was found, while to the same chemical the nymphs developed an *aversion*-type response if it was presented on glass fiber disk + sucrose. No sign of sickness was reported, however.[114] It is possible that not only the "typical" physiological response (illness) was unnoticeable or missing, but the outcome (habituation or food-aversion-type learning) depended on the stimulus situation provided (but see also Section V.D).

Bernays and Lee[16] studied the food-aversion learning of *Schistocerca americana*, a polyphagous feeder, on acceptable plants: *Brassica oleracea* and *Spinacea oleracea*, artificially associating a meal with subsequent injection of NHT solution into the body. Continuous observations were made using the following parameters: initiation of each meal, length of each meal, interfeed time. Immediately after a meal, either on *Brassica* or *Spinacea*, a dose of 2% aqueous NHT solution was injected into the abdomen of each insect which was then returned to its place where the next meal could be on either one of the two plant species. The results showed that on *Spinacea*, which was generally the less acceptable of the two plants, NHT injection was associated with the plant and caused a significant decrease in the next meal-size. The size of this meal was also significantly less than the meals on different controls. However, this was not the case if the next meal was on *Brassica* or if injection was followed by a meal on it. The experiment, then, demonstrated food-aversion learning, induced by coupling an artificial negative feedback with feeding on a particular plant. Generally, a single meal has been found to be adequate to establish food-aversion (e.g., References 49 and 243).

Another point of theoretical interest is the range of plant species on which food-aversion learning can be seen with phytophagous insects. Bernays and Lee[16] did not find aversion learning with *Schistocerca americana* on a fairly acceptable host, broccoli "A" (*Brassica*). At least for rats, it is known that on less preferred food, aversion may be acquired more easily[84] (cited by Bernays and Lee[16]), but the possibility of inducing food-aversion learning on the most preferred foods cannot be excluded. The use of toxic compounds on highly acceptable plant species to deter further feeding is, in principle, similar to the experimental circumstances provided for aversion learning. It would be interesting to discover in what percentage of cases decreases in consumption reportedly due to antifeedant activity actually involve food-aversion learning.

Experiments with rats[153] indicated another possibility—that of second order conditioning of odor with post-ingestive malaise. The odor alone was not a sufficient cue to associate with a poisonous food; the odor, in turn, had to be associated with taste before it resulted in refusal of the food. Second order conditioning has not yet been demonstrated with phytophagous insects.

D. DIETARY SELF-SELECTION

It has been found that some vertebrates will eat several kinds of food in proportions yielding an optimal nutrient balance (see Waldbauer and Feiedman [226] for references). Such dietary self-selection has been demonstrated also in the polyphagous species *Tribolium confusum*[226] and *Heliothis zea*.[35,227] It can be assumed that self-selection occurs in other phytophagous insects.[226]

The most probable behavioral mechanisms underlying self-selection is proposed by the "malaise hypothesis". Cohen et al.[34] supposed that feeding on a food lacking or deficient in some nutrients causes metabolic disturbance (malaise) that, through a feedback mechanism, results in exploratory behavior until the insect comes to another kind of food that contains the missing nutrient. Feeding on the latter the insect associates the sensory stimuli from that food with the alleviation of the malaise. In this way the insect will switch back and forth between nutritionally incomplete but complementary diets.

It can be added that the first step of the self-selection behavior, i.e., the abandoning of the deficient diet that causes malaise, may involve a learning process. Namely, the chemical stimuli of that diet are associated with the malaise, therefore, the diet becomes sensorially unacceptable and will be avoided. This process is analogous to food-aversion learning, although the aversive behavior may be much less persistent and is easily deleted by feeding on another diet. The second step, i.e., the feeding on a complementary diet, is analogous to food imprinting. Thus, self-selection requires delayed learning mechanisms that have been found in several animals.[176,192]

E. LEARNING IN FOOD FINDING

There are no data on how widespread learning is in the food finding processes of phytophagous insects. Contrary to the abundant examples of oviposition site finding and acceptance behavior in these insects (see Section VI.A), there are, to our knowledge, only a few studies demonstrating learning in food finding.[17,132,181,182]

Bernays and Wrubel[17] attempted to associate visual cues (color and light intensity) with food in nymphs of the grasshopper *Melanoplus sanguinipes*. As a general experimental design, they used a cage in which two 3-sided cardboard boxes painted green or yellow were placed. Experimental insects within the cage stayed on a warm wire roost between feeding bouts and there were three stages of the experiment: (1) pretraining, where they could visit the empty colored boxes without food, (2) training, where they could find food either in the green or the yellow box and were allowed to feed freely for ca. 18 h, and (3) post-training, when both boxes were replaced by new empty boxes. The nymphs were tested both for positional and color learning.

The experiment proved that *M. sanguinipes* nymphs could associate visual stimuli with food rewards. While in the case of the yellow box loaded with food the median length of stay post-training did not increase over the length of stay in the pretraining period, the value for green significantly increased. The association was developed without a positional effect by the boxes. With untrained insects there was a bias toward yellow, but a significant enhancement of the preference for it, when the yellow box contained food, was not demonstrated perhaps because it was already so high. The learning process was quick, as a single trial was enough to locate food faster subsequently.

Saxena and Schoonhoven[181,182] drew attention to the fact that food-imprinting in lepidopterous larvae changes not only feeding behavior but also olfactory orientation that may be of importance in food finding. As a result, changes in host plant preferences due to experience are more obvious in choice tests where olfactory discrimination of plants tested is also involved as compared to no-choice tests where this possibility is excluded.

In laboratory experiments, Lewis[132] demonstrated that in *Pieris rapae* butterflies the time required to find nectar in flowers decreased during subsequent encounters, i.e., they actually learned to discover nectar more efficiently. For switching to a new source then back again to the previous one, first they had to learn then successively relearn the way of "handling" a flower in order to improve performance. (Also see remark in Section VIII.)

VI. EXPERIENCE-INDUCED CHANGES IN OVIPOSITION BEHAVIOR

In this section emphasis is placed on experimental evidence of experience-induced changes in oviposition. However, development of a searching image is also discussed (1) as it might be involved in oviposition behavior, and (2) since there are some shared elements in the learning mechanism. Experience-induced changes of oviposition preferences have been demonstrated only in a few phytophagous insect species so far (see Table 3).

Studies on learned oviposition preference (induced oviposition preference, IOP) fall into the category either of sensitization or of associative learning (both classical and instrumental conditioning, as well as trial-and-error learning). In most cases the adult

Table 3
LIST OF INSECT SPECIES IN WHICH EXPERIENCE WAS FOUND TO CHANGE OVIPOSITON PREFERENCE

Species	Ref.
Caleoptera	
Callosobruchus maculatus	137, 232
Lepidoptera	
Pieridae	
Pieris rapae	216, 217, 218
Papilionidae	
Papilio machaon	237
Battus philenor	74, 154, 155, 156, 172
Heliconius sp.	74
Diptera	
Tephritidae	
Rhagoletis pomonella	167
Ceratitis capitata	37

must "evaluate" and associate visual (spatial, light intensity and reflectance, shape), tactile, and chemical (contact chemical, olfactory) information. As learning would be expected in all these it may seem more appropriate to replace the term IOP by "learned oviposition preference".

In addressing the term "induction" as commonly used in the literature on oviposition, Dethier[57] noticed that "conditioning" (that is to say associative learning) generally had to be excluded as a possible mechanism because of the lack of rigorous criteria set for learning studies. However, we believe that although in earlier studies of induction of oviposition preference the conditions were not designed to meet the criteria for associative learning, nevertheless, elements can be recognized. The more recent studies of associative learning in *oviposition* behavior fall into this group.

Traynier[215] demonstrated a long-term change in the oviposition behavior of the cabbage butterfly, *Pieris rapae*, induced by contact with plants. Gravid females were placed in cages and were allowed contact either with cabbage or lettuce disks for 30 min, then deprived of any leaf disks for 24 and 72 h, and finally retested on cabbage or lettuce. "Cabbage-experienced" butterflies landed on cabbage and laid eggs, whereas on lettuce they frequently moved from disk to disk but rarely laid eggs. The females "experienced" on cabbage landed more frequently on lettuce than those becoming "experienced" on lettuce, but few eggs were laid. Those that had experienced lettuce on each occasion showed a low level of responsiveness in both tests, because the tendency to land decreased after the first two minutes. It could be that the females gained oviposition site "imprinting" or induction and had learned to respond to green disks but it is also possible, as suggested by Traynier,[216] to explain it by sensitization. Likewise, a state of sensitization may account for the results obtained with ovipositing leek moths (*Acrolepiopsis assectella*). The information obtained about specific host substances caused a response corresponding roughly to the duration of exposure and was retained over time.[206]

Traynier[216,217,218] has repeatedly and successfully demonstrated associative learning in ovipositing *Pieris rapae*. Sinigrin stimulates oviposition in this species. "Training" was given by exposing the gravid females for 30 min to green paper disks treated with 10 ppm aqueous sinigrin solution. The oviposition response of females was tested after 1.5 and 21.5 h, on water-only disks. There was a substantial difference between the number of eggs laid by "sinigrin-experienced" and by those butterf[illegible] not having contact with sinigrin. It appears that the butterflies developed an association between green color and chemical suitability of disks as oviposition sites.[216] Since the butterflies showed an intrinsic preference for a green color, the experiment was balanced for such a bias, but it did not control for sensitization and pseudoconditioning.

A subsequent paper[217] on oviposition site learning put more emphasis on visual components. *Pieris rapae* females oviposit readily on paper disks treated with an aqueous sinigrin solution. However, certain colors (violet, red) or black are inherently not preferred, and on these even sinigrin could not release an egglaying response and oviposition occurred only on water-treated disks of acceptable colors. Associative learning in egglaying site selection has been proved to be possible and important also in other phytophagous insect species, such as *Rhagoletis pomonella*,[167-169] *Ceratitis capitata*,[37] and *Battus philenor*.[154-157]

Prokopy et al.[167] trained naive apple maggot flies (four successive oviposition bouts separated by 2-min intervals) on apple. After the last training period the flies were offered a fruit of *Crataegus mollis* which they rejected; conversely, flies trained on *C. mollis* did not accept apple. The experiment showed that flies could learn to accept or reject an oviposition substrate, and that the possible mechanism was associative learning. The fruit flies must have associated several (?) attributes of one fruit with its suitability as oviposition site.

Subsequently, however, this study has received considerable criticism from students of learning and behavioral geneticists. Holliday and Hirsch[93] rejected the learning interpretation for the experiment,[141] objecting to the experimental design. In a reply by McGuire,[142] it was stated (p. 469) that "the study of Prokopy et al. (1982) was not designed to be a learning study and therefore lacks some learning controls. Nevertheless, he regarded their study as an example of instrumental conditioning. In a similar study,[168] naive flies without training showed a great deal of variation in response to an oviposition substrate other than that which served as larval food. In contrast, in field assays, among females that had just finished ovipositing into apple or *Crataegus*, most preferred to continue ovipositing in the same type of fruit. The results could be explained as genetically determined food preference and/or sensitization. However, in the field test, and in a separate case when females were trained to a given fruit type in the laboratory, the females consistently rejected a subsequently offered different test fruit. This behavior can best be explained by associative learning. In the next study[169] the "true nature" of the learned performance was addressed. The question was posed, whether: (a) experienced females acquired a greater propensity to accept the fruit-type on which they were trained as compared to naive females, or (b) experienced females had a greater inclination to reject a novel fruit type. The results suggested that the second alternative was more probable. With a similar experimental set-up learning was demonstrated in *Ceratitis capitata*.[37] An interesting addition is that this species is a highly polyphagous one. In general accordance with the selective advantages of learning to an oligophagous species[169] we expect that polyphagous feeders have an even higher propensity to perform different types of learning. Variability has been found in the level of conditioning with a given fruit type in a wild population, which may reflect the difference in the "quantity" of conditioning stimuli provided by the substrate.[37] We think that the length of exposure, that is, the "quantity of experience" obtained previously on that or a similar type of fruit may also be important.

What characters of the host are associated with the development of the response? Papaj and Prokopy[158,159] studied this and concluded that with *Rhagoletis pomonella* it was fruit size and the surface chemistry which counted. Papaj,[154,155] pursuing Traynier's line, successfully demonstrated with *Battus philenor* association of visual cues with relevant characteristics of the host plant. The butterfly is able to discriminate between the two host *Aristolochia* species visually by leaf shape.[172,174] (See "Searching image" below for details.) The butterflies demonstrated instrumental conditioning in this case. Pseudoconditioning and sensitization were excluded as possible mechanisms. It has been supposed that leaf buds may improve host-seeking behavior in the same way as leaf shape did.[155]

With regard to *Coleoptera*, very few examples[137,232] of learned oviposition preference have been found, all with a bruchid species, *Callosobruchus maculatus*. The plant species tested, however, differed: *Cajanus cajan* and *Phaseolus radiatus* in the earlier study, and *Vigna unguiculata* and *Cicer arietinum* in the later one. A learning process is possible in these studies, since in addition to the effect of inherently preferred host seeds, other specific stimuli such as the seed's surface curvature,[6] chemical constituents of the seed coat, oviposition marking substances, and seed size can all serve as associating reinforcers and therefore influence the response.[146,152]

Searching image. This term was coined following Tinbergen's[213] and Royama's[179] classical works on bird food seeking and food selection behavior. They observed that, in spite of the availability of an alternative food, the birds "insisted" on foraging only a certain type, and ignored others. As an explanation, it was supposed that the foraging animal, being inexperienced with all available food types in a given environment, would discover a cryptic food item and then would look for similar ones, while others went unnoticed, at least until another was suddenly recognized again.

It is assumed that searching image is accompanied by a perceptual change in the predator that enhances its ability to discover cryptic prey. Searching image presupposes discriminating ability and selective attention.[140] It results in a preference[103] for a given food by learning. During foraging, switch-over to another type of cryptic food may occur and new experience (with reinforcement) leads to the formation of another searching image. It is argued[126] that the proper expression for the mechanism was learning to see, because the process was actually breaking the camouflage of a cryptic prey which became suddenly visible, and recognizable for the forager. From the moment of recognizing something edible the process is a quick, one-trial associative learning process reinforced by rewards from the now suddenly visible and similar-looking food items.

Although there are relatively few experimental examples of searching image, a recent paper[84] questions even the by now "classical" results,[41,45,46] stating that they proved only a change in "search rate" and were better explained by this than by the formation of a searching image. (Search rate furnishes the predator with an ability to *vary* the time required for scanning a given part of the environment while foraging.) Furthermore, Krebs[126] collected and listed all those situations where a predator learns those behaviors, sites, etc. that led to more efficient foraging, and found no support for development of a searching image.

Courtney[39] predicts by means of a model that a female insect's searching for the most preferred host by employing a searching image may result in a higher overall host discovery rate as compared to "searching for all host-plant species" (p. 317). (See also Section VIII).

However, in phytophagous insects there are no unambiguously demonstrated instances of searching image formation. It is not surprising that all supposed cases concern species with well developed visual acuity, although nothing would exclude the formation of an olfactory searching image. Formation of a searching image in ovipositing females occurs mostly in connection with certain plant parts, and a similar behavior can be expected in flower visiting. Though the phenomenon shows a superficial resemblance to imprinting, they are probably different, as the latter lasts for a relatively long time, even a lifetime, while foraging requires frequent switching in searching image throughout a season. *Heliconius* species are known to differentiate betwe[illegible]eaf shapes, as well as small details of leaves (egg mimics) while seeking for an egg-laying site.[74] Albeit no searching image formation was shown with *Heliconius*, we assume it is likely to be occurring, especially since Gilbert explicitly states that an associative learning process takes place not only for leaf shape but also for spatial position of particular *Passiflora* vines. Wiklund[237] describing *Papilio machaon* females after laying an egg "on the same plant species a number of times...evidently acquire a 'searching image' of this plant, as it is not uncommon to see swallowtails making initial oviposition approaches towards non-host plants which bear a general superficial resemblance to the dominant host plant of the locality" (p. 194). Rausher[172] discovered by observation in nature that searching image formation took place in *Battus philenor* female butterflies when they were looking for oviposition sites. The two host-plant species, *Aristolochia serpentaria* and *A. reticulata* differ in leaf shape and once a female discovered a host plant, it tended to look for similar ones.

Lawrence and Allen[129] argued that a searching image interpretation is not appropriate for the oviposition site searching behavior in *B. philenor,* because Rausher[172] overlooked alternative learning possibilities[45,46,126] which must first be excluded. The particular alternative is the "preference or avoidance of a prey over others that is independent of the predator's ability to see the different types"[129] (p. 313). It is indeed an inherent preference that is shown by *B. philenor* females for both wide and narrow leaf shapes of *Aristolochia* species, the food plant. Unlike a generalist predator, where a wide spectrum of prey species may be available, there are only two alternatives for *B. philenor* butterflies: to search in one or in the other leaf-shape mode. Females adopt mostly one type of search mode at a time, so although searching image might be involved, this interpretation is not necessary, because instrumental learning may also be involved.

Lawrence and Allen[129] also criticize Rausher[172] for not demonstrating *Aristolochia* to be "cryptic", though it probably was. Among similar looking leaf shapes of other plant species *B. philenor* females searched only in one mode and they were not able to differentiate perfectly between hosts and non-hosts solely by visual cues. It was the chemical information that gave the clue for identification. During this process mistakes of identification did occur;[155] that is also an accompaniment of searching image development. Once again, a critical point that is common in all such studies is the lack of demonstration whether the increased ability to discover food items by the forager comes from changing the search rate[84] (e.g., Figure 2, p. 200 in Reference 172).

Another study with *B. philenor*[154] experimentally proved that the alighting response was reinforced by chemoreceptive experience of the host plant and this in turn aided the recognition of further hosts.

Summing up, it may be stated that, though formation of a searching image has not been proven in insects and such studies certainly face exceptional difficulties, it is still possible that such a learning process does occur and plays a role in the foraging of insects. The formation of a searching image may be restricted to visually searching phytophagous insects.

VII. PRE- AND EARLY-IMAGINAL EXPERIENCE

The discussion of pre- and early-imaginal experience under a separate heading is justified only by the special character and historical significance of the phenomenon in insect-plant interactions. As for its placement into a learning category, opinions differ widely.[141]

For more than a century entomologists suggested that larval experience gained on a specific food would increase the adult's preference for that food.[230,231] This phenomenon was called the "Hopkins Host Selection Principle" (HHSP) because Hopkins[95] was among the first to draw attention to it. Several authors claimed to have proven HHSP in phytophagous insects,[40,99,128,181] in *Drosophila*[90,210] and in parasitoids.[195,212]

Experiments to prove the validity of HHSP should meet the following conditions:

1. The possibility of selection of genetically based oviposition preference should be excluded. Therefore, all experiments that have been carried out using adult field populations for oviposition preference tests,[128] or insects that were reared for several generations on a certain plant,[99,161] are not convincing, because differences in behavior might be determined genetically.
2. The contact of emerging adults with the larval food or its remainders must be excluded since the cases of learned oviposition preference (see Section VI) clearly proved the influence of early adult experience on adult preference behavior. In several cases the above precaution was not taken or at least the authors do not report on it.[90,99,161,195,212] This is especially true for experiments with parasitoid insects where contact of the emerging adults with the remainders of the host (pupal exoskeleton, cocoon, meconium) was presumably not prevented.

Unfortunately, no attempts have been made so far to find out, whether larval (nymphal) feeding experience is transferable to adults in hemimetabolous insects, where the last molt is not accompanied by such basic morphological and physiological changes as in holometabolous groups. Based on experimental evidence several authors explicitly denied the validity of the HHSP.[51,98,106,124,137,162,164,169,204,205,242]

Jaenike[106] (p. 324) proposed a "neo-Hopkins host selection principle" suggesting that the "exposure of adult insects to a particular type of host will often, though not always, increase the subsequent acceptability of that host as an oviposition site" (see also Section VI).

The role of early adult experience has already been demonstrated;[210] washing the fully developed larvae or newly formed puparia of *Drosophila*, i.e., freeing them from the remainders of the rearing media, reduced the effect of the larval food on adult behavior, although it did not eliminate it totally. This and similar cases led to Corbet's[38] "chemical legacy" hypothesis. She claimed that even if the puparia were washed, some chemical cues, originating from the larval food, might persist within the puparial exoskeleton (see Corbet[38] for references), and thus might be contacted by the newly emerging adult.

VIII. ADAPTIVE SIGNIFICANCE OF EXPERIENCE-INDUCED BEHAVIORAL CHANGES

Studies on changes due to experience in feeding and oviposition behavior of phytophagous insects naturally also include discussions on the presumed adaptive advantages of the changes. In this connection one often finds Panglossian types of assumptions that regard the observed learning modalities as perfect solutions for performance of tasks faced by insects.

The function of a certain behavior is often regarded as its adaptive value[127] which implies that the behavior originates from and is maintained by natural selection, and is genetically determined.

Jamieson,[108] however, convincingly proved by concrete examples that a purely functional approach to the causality of the origin, diversity and persistence of behavior patterns may lead to unwarranted and unsupported selectionist explanations, because it ignores extragenetic factors evoking and maintaining new behaviors. For example, it has been shown that in some species generalist or specialist types of behavior depend on the environment where the individuals were raised.[80] Thus behavioral evolution may arise also through adaptation of an unaltered genotype to a persistent environmental change[119] (cited by Jamieson[108]). In most cases of behavioral plasticity learning processes are probably involved.[92] Life cycle studies have also led to the conclusion that phenotypic plasticity can be genetically determined and is subject to selection, but the position of an individual within the range of phenotypic variation is not determined.[26,27]

Thus, if a given intraspecific difference in a behavior proves to be of epigenetic origin, there is no point in measuring costs and benefits of that behavior on the population's overall fitness, because in such cases selection does not influence the average genotype.

Experience may modify individual adult lifetime parameters and "fitness". For instance, males of *Drosophila melanogaster* obtain experience from fertilized females that subsequently modifies their courtship behavior.[193] Studies with *Drosophila* and *Phormia* species,[82] and papers cited therein, demonstrate that learning ability is an individual characteristic, and that roughly 30% of a population would respond as "good learners". Selection experiments and work with mutant strains corroborate that a level of genetic determination is involved (see Section II.D). It is unfortunate that, to the best of our knowledge, there are no similar studies on phytohagous insects. Thus nothing is known about the genetic background of either the behavioral changes due to experience, or the ability of the insects to change. In the following, only the presumed adaptive significance of the behavioral changes themselves will be discussed.

Habituation to feeding deterrents. This enables the insect to feed normally on plant species that belong to the potential host plant spectrum but are in some degree deterrent to "naive", unexperienced individuals. This might be of adaptive value where there is not a strong correlation between deterrence and toxicity of plant phytochemicals. Habituation to food-related stimuli is a type of phenotypic plasticity, the range of which is determined genetically. How widespread the ability to habituate to plants with deterrent stimuli might be is not known, although generally no habituation was found in *Mamestra brassicae* larvae to several acceptable but slightly deterrent non-host plants.[116]

Whether or not the great individual variation in the capacity for habituation to deterrents observed in several phytophagous insect species[114,116,203] is genetically determined is not known, so that we cannot yet comment on whether or not it could be subject to selection.

Food-aversion learning. This prevents the ingestion of deleterious quantities of a poisonous food if there is not a genetically based deterrent response to the food. On the other hand, one might argue that making complex decisions about the food whether learned or unlearned is highly developed in polyphages (E. A. Bernays, personal communication). It is, therefore, not surprising that the capacity for aversion learning should be demonstrated mostly in polyphagous animals,[55,72,114] although it may also have adaptive significance for oligophagous species. Significant individual variability has been observed also with this behavior.[116] If such variability is of epigenetic nature, selection would not alter the average genotype of the population.

Food imprinting. As for the selective advantage of the capacity for food imprinting several authors have assumed that it reduces the probability that in a mixed plant stand an insect would frequently change food plants which, in some cases, has been found to reduce the efficiency of food utilization.[78,79,187,189-191,202] However, in other cases feeding on a sequence of different host-plant species enhanced development and fecundity (see also Section V.D) or had no effect at all.[42,73,79,144]

It is conceivable that in mobile insects foods imprinting enhances the fast refinding of the food at the end of intervals between two meals.[79,181] This might be of special importance, e.g some noctuid moth species whose larvae spend the day in the soil and thus have to refind the food plant every evening. Nevertheless, it is difficult to envisage what adaptive advantage may be attributed to cases when larvae become imprinted for (acceptable) non-host plants[47] that do not permit normal development. Furthermore, rigid food imprinting may be clearly a disadvantage in situations when, e.g., a host plant becomes defoliated by lepidopterous larvae before they complete development and no other plants of the same species occur in the vicinity. With our present knowledge, it is hard to conceive that rigid food imprinting, leading to the "starving-to-death-at-Lucullian-banquets" phenomenon,[112] is adaptively advantageous, although host fidelity could have ecological advantages.[15]

Jermy[112] proposed that food imprinting may simply reflect the limited flexibility of the insect's nervous system, i.e., the restricted capability of recognizing different chemical "Gestalts" as food plants. A specific chemical "Gestalt" becomes "imprinted" in the sensory system, i.e., the insect is not able to "abstract" a general "notion" (chemical "Gestalt" image) of "host plant" that would incorporate the chemical "Gestalts" of all suitable host plant species and would exclude all non-host plant species. When a newly hatched larva begins to feed on one plant species belonging to the potential host plant spectrum, which may contain plant species of quite different chemical composition (see Section V.B.5), it becomes tuned to that plant, but also loses the capability of recognizing another possible host-plant species, the chemical "Gestalt" of which more or less strongly differs from the experienced one. The occurrence of such a "chemical tunnel vision" is also supported by the findings that food imprinting is stronger (high induction index) the more distantly two plant species are related botanically, i.e., the more their chemistry differs.[47]

In conclusion, food imprinting may result from the insects' incomplete plant recognition and relearning capabilities. In some cases it may serve simply for fast refinding of the food by mobile insects; in other cases it might be more or less irrelevant with respect to the fitness of the individual, while in some ecological situations it might be disadvantageous. Since food imprinting is an epigenetic phenomenon, even the occasional disadvantageous consequences do not affect the average genotype of the population in ecological time. The genotype determines the function of the nervous system which, in some insect species, leads to food imprinting. Whether or not there has been selection for or against the capacity for imprinting cannot be determined.

Host finding. Learning is considered to be important in the foraging behavior of higher animals.[122] It is assumed that behaviors incur costs and/or benefits, and as such, measures of "profitability" of different behaviors are often undertaken. The scientific area that has grown on such conceptual grounds is optimality theory. Most examples came from the domain of foraging theory, and specifically on prey-predator relationships (see, e.g., Pyke[170] for a review). However, aspects like mate finding and choice (e.g., Reference 24) and others have also been developed. Optimality theory has received considerable criticism (e.g., Reference 133). Recently Pierce and Ollason,[163] collecting convincing arguments against various aspects of the theory, concluded that it may not be possible at all to test whether an animal behaves optimally.

Optimality studies are generally scanty with phytophagous insects. The following examples demonstrate both the scarcity of knowledge in this domain, and the controversies in their explanation.

Following Holling[94] and Charnov,[32] Futuyma[68] has shown by a mathematical model that under certain conditions a specialized type of host-seeking behavior, like the use of searching image in some *Lepidoptera*, may increase fitness and thus may be selected for. Courtney[39] came to the same conclusion. A model has been constructed on optimal oviposition behavior in phytophagous insects suggesting that imprinting is useful.[105] By another model[131] it was demonstrated that if an egg-laying female insect has only limited capacity for distinguishing between suitable and toxic plants, then it may reach highest fitness by ovipositing only on one identifiable palatable plant species.

Prokopy et al.[169] emphasized that the adaptive significance of learning to discriminate among fruit species by *Rhagoletis pomonella* females is unknown. Nevertheless, they suggested that (p. 105): "learning to reject a novel fruit may reduce the likelihood that an experienced female entering a patch of the rare host type would stay in that patch and continue to search" and by this may enhance the probability of finding abundant conspecific host fruits. This is supported by the findings[175] that the female flies left a tree more quickly after encountering an unsuitable fruit.

It was suggested that learning increases the searching efficiency in females of *Colias* spp. because the host plants are rather cryptic in their natural surroundings.[200] Papaj,[156] discussing the results of investigations into the host plant searching behavior in *Battus philenor*, concludes that selection favors rapid learning by naive females and conservativism in switching from one host to another by experienced ones, both enhancing efficiency of host finding. But this searching behavior is not very accurate, because (p. 306) "even after considerable experience...females land on many non-host leaves whose shape is similar to that of the preferred host.[155]

As regards food finding, grasshoppers were found to associate visual cues (colored boxes in the laboratory) with the presence of food.[17] There is also evidence that they may be able to associate non-nutritive volatile chemical cues (mint) with food, so that they move upwind when exposed to it.[130] Both types of learning may enhance food finding, but evidence is lacking on their importance under natural conditions.

It has been shown that experienced bumblebees may remain constant to a flower type even after it deteriorates as a resource because relearning in foraging is costly in time and energy.[89] In this connection, however, one may also argue that conservatism in switching behavior is not necessarily adaptive, but may originate from the inability of the insects to relearn, as in the case of food imprinting (see above). This is more likely in the case of short-lived butterflies. The wealth of publications on learned oviposition, although they deal with only a few species, tend to suggest that egglaying is, in general, fairly accurate. For example, *Battus philenor* females discriminate "between hosts and non-hosts, among host species, and among individuals within a host species. The facultative adaptation of that preference enables the females to select the most suitable individual plants from a complex non-host background, even as suitability changes over phenological time"[155] (p. 306-307). The other side of the picture, namely, the inability or the restricted ability to learn as well as the imperfections in finding and recognizing the host, were seldom studied although the latter are important for the understanding of insect population dynamics.[52] As an excellent example, Dethier[52] has clearly demonstrated that females of the butterfly *Euchaetias egle* fail to find many scattered host plants in a meadow and the number of eggs laid on individual plants is assessed inadequately in relation to the quantity of available food. This often results in defoliation of some plants before the larvae have completed development, while other individual plants remain unattacked. In such cases the larvae may die of starvation or be killed by predators because they are unable to find more distant host plants. In another example, *Leptinotarsa decemlineata* females often lay eggs on non-host plants, probably because the leaf surface structure of the latter is more suitable for depositing the eggs than that of the host plant. As a result, a considerable number of eggs may be situated several decimeters from the host, though the chance of finding the host by the newly hatched larvae rapidly decreases within a few centimeters.[113] These examples indicate that the use and value of learning in relation to oviposition may vary considerably from species to species.

Significant individual variation has been observed in the host searching behavior of butterflies. Assuming that the variation is genetically determined, Rausher[173] developed a model of the modification of egg-laying behavior by selection. However, if the variation is only of epigenetic origin, which cannot be excluded, the model becomes questionable.

The common feature of both food imprinting and learned oviposition preference is that the insects involved show narrower host-plant specialization than the "naive" ones, the latter presumably indicating the inherited host plant spectrum. It seems, therefore, logical to ask: What is the adaptive advantage of narrowing down the host range during ontogenesis? This leads to the never-ending debate on the adaptive advantage or disadvantage of specialist vs. generalist behaviors. Since it would fall outside the scope of this paper even to outline the essence of this debate, we only refer to two recent publications on the evolution of host-plant specialization in phytophagous insects.[15,117] However, if the behavioral narrowing down of host-plant range results simply from "tunnel vision" caused by experience, and is explainable by the limits of neural mechanisms, then the problem of adaptive advantage or disadvantage becomes dubious.

As can be seen from the foregoing, learning ability is extremely variable in phytophagous insects both in inter- and intraspecific contexts. This does not necessarily reflect the advantages and disadvantages of learning ability. It may simply indicate that in some species the evolution of the nervous system reached a level which enabled the selection for complex learning processes.

IX. BEHAVIORAL CHANGES AND SPECIATION

Mayr[139] expressed the view that changes in behavior may represent the initial step in the subdivision of a species, i.e., in speciation. Naturally this occurs only if the behavioral differences also result in at least some reproductive isolation between the populations involved.[102] With this in mind, the following can be said about the probability of reproductive isolation provided by experience-induced changes of feeding and oviposition behavior.

Food imprinting of larvae itself obviously cannot result in reproductive isolation with endopterygote insects, since it is not transferable from the larval to the adult stage. However, a seeming transfer may result from early-imaginal experience (see Section VII). In such cases the perpetuation of a specific host preference through generations is conceivable, and may be enhanced by selective mating that takes place on the host plant. For example, this may happen in *Haltica* species.[162]

The gene flow between populations imprinted to different host species may be impeded if selective mating also occurs. Although no suitable data are available on food imprinting with Hemimetabola, the transfer of imprinting between larva and adult would seem to be most likely with this group.

Food imprinting in herbivorous adults, if it is connected with oviposition on the same plant species, theoretically may result in isolation of populations in the same way as has been discussed above in case of early-imaginal experience. Without genetic changes, however, the emergence of such "behavioral host races" would not persist in nature. Therefore, when a food-imprinted insect population is found in nature, detailed and long-term investigations are needed before it can be revealed whether the specific behavior persists over subsequent generations or is restricted only to the one in which it was first found.

Learned oviposition preference has been found so far only in *Lepidoptera* and *Diptera*. Since there is no feedback of information from the larval to the adult stage, specific preference does not persist through generations; thus, it cannot result in isolation. However, early-adult experience deserves attention also in these insects. For example, since tephritid flies living in fruit trees pupate in the soil under the tree, the newly emerged adults will probably first encounter that tree on which they developed as larvae. By this the learned specific oviposition behavior may become a seemingly "inherited" trait and may temporarily isolate populations. However, such a process is rather improbable in sympatry without simultaneous and accidental genetic changes promoting reproductive isolation. Gene flow by emigration/immigration could significantly reduce the degree of isolation, especially in highly mobile species.

Jaenike,[107] studying the genetics of host selection behavior in egg-laying *Drosophila tripunctata*, concluded that sequential phases of oviposition behavior are regulated by independently segregating loci. Therefore, the probability of resource-based host race formation and subsequent speciation is unlikely in this species.

The "chemical legacy" hypothesis[38] stresses in general that even minute chemical traces of the host that are transferred from one ontogenetic stage to the next could have significant behavioral effects if they are present in the immediate environment of an insect's sensitive developmental stage. Corbet assumes that cases of host specificity that were hitherto interpreted in genetic terms could also be accounted for by this hypothesis. One of its predictions is that host shifts in phytophagous insects might result from "accidental contacts of a sensitive stage with a novel host"[38] (p. 150). Modern methods of chemical analysis are sensitive enough to prove or disprove the above hypothesis. However, considering the results of behavioral experiments and observations carried out so far by many authors, it is very unlikely that accidental contacts would cause shifts to novel host plants outside the inherited host spectrum.

Thus experimental and observational data available so far do not allow us to draw firm conclusions about the possible role of experience-induced behavioral changes of feeding and oviposition in the processes of speciation.

X. CONCLUSIONS

In recent years, increased attention has been focused on experience-induced changes in the host-selection behavior of phytophagous insects. The studies have provided a wealth of information on a series of behavioral phenomena, but their interpretation, especially in the context of modern learning theories, is still controversial. Such studies often lack planned control experiments which sometimes make them uninterpretable or at least ambiguous. This is especially true for cases where fine distinctions have to be made, e.g., to decide whether a given response is only sensitization or whether associative learning played a role. On the other hand, the set of criteria that defines a certain type of learning is difficult to meet experimentally; therefore, the evidence gained often allows only an *a posteriori* and frequently inadequate explanation. Further studies could answer the questions of general importance: How fixed is the host selection behavior in various groups of phytophagous insects (e.g., euryphagous vs. stenophagous species) and what are the limits of behavioral changes, i.e., how far can learning change behavior? Such investigations may provide important contributions to the knowledge of learning capabilities of insects.

Optimality approach views behavior as a series of processes in which cost/benefit measurement can be done. Taking into consideration the arguments and debates surrounding the topic, optimality models should be predictive enough to allow understanding elementary rules in animal decision making. Nevertheless, once learning is incorporated as a possible behavior modifying factor, models may become too complex to handle or understand; the better learning abilities an animal has the more alternative behavioral outcomes are possible. Naturally, not only the learning abilities, but also the limits of learning, of a given animal species should be known.

Another large group of open questions relates to the neural mechanisms underlying behavioral changes. The interesting results of electrophysiological experiments obtained so far indicate that further studies may shed new light on the function of the insect peripheral nervous system and its relation to learning.

The overwhelming majority of experiments and observations have shown that considerable individual and interpopulational variations of behavioral phenomena exist. How much is due to genetic or to epigenetic factors is totally unknown. The behavioral genetic approach should urgently be extended to those phytophagous insect species whose behavior has already been studied in detail.

A further serious insufficiency of the studies carried out so far is the almost total lack of experiments and detailed observations in nature. Clearly, such investigations meet with enormous methodological difficulties. Without such studies, however, it is very dangerous to extrapolate the results of laboratory experiments to natural populations, and trying to estimate the "raison d'être" of any experience-induced behavioral change may provide very vague conclusions. At the present time the genetic or epigenetic nature of the behavioral phenomena is an open question. If only epigenetic causes are involved, the learned behavior is not affected by selection, because it has no effect on the average genotype of the population. Thus, at present most speculations about the evolutionary significance of experience-induced changes in host selection behavior of phytophagous insects are built on loose ground.

ACKNOWLEDGMENTS

The authors are deeply indebted to Professors Elizabeth A. Bernays, Reginald Chapman, Endre Grastyán, Dr. György Kemenes, and to three anonymous reviewers for critical comments, advice, and corrections. Special thanks are due to Mrs. Judit Horváth for practical assistance in many different ways.

REFERENCES

1. **Aboul-Nasr, A., Mansour, M. H., and Salem, N. Y.,** The phenomenon of induction of preference in the cotton bollworm *Heliothis armigera, Z. Pflanzenkr. Pflanzenschutz,* 88, 116, 1981.
2. **Ali, M.,** Studies on the induction of food preference in alfalfa ladybird, *Subcoccinella* 24-*punctata* L., (Coleoptera, Coccinellidae), *Symp. Biol. Hung.,* 16, 23, 1976.
3. **Alloway, T. M.,** Learning and memory in insects, *Annu. Rev. Entomol.,* 17, 43, 1972.
4. **Alloway, T. M.,** Retention of learning through metamorphosis in the grain beetle *(Tenebrio molitor), Am. Zool.,* 12, 471, 1972.
5. **Anderson, A. M.,** A model for landmark learning in the honey bee, *J. Comp. Physiol.,* 114, 335, 1977.
6. **Avidov, Z., Berlinger, M. J., and Applebaum, S. W.,** Physiological aspects of host specificity in the Bruchidae. III. Effect of curvature and surface area on oviposition of *Callosobruchus chinensis* L., *Anim. Behav.,* 13, 178, 1965.
7. **Baerends, G. P.,** Fortpflanzungsverhalten und Orientierung der Grabwespe, *Ammophila campestris* Jur., *Tijdschr. Entomol.,* 84, 68, 1941.
8. **Balderrama, N.,** One trial learning in the American cockroach, *Periplaneta americana, J. Insect Physiol.,* 26, 499, 1980.
9. **Barbosa, P., Greenblatt, J., Withers, W., Cranshaw, W., and Harrington, E. A.,** Host-plant preferences and their induction in larvae of the gypsy moth, *Lymantria dispar, Entomol. Exp. Appl.,* 26, 180, 1979.
10. **Barker, L. M., Best, M. R., and Domjan, M., Eds.,** *Learning Mechanisms in Food Selection,* Baylor University Press, Waco, Texas, 1977.
11. **Bergson, O. and Wool, D.,** Attraction of flour beetles, *Tribolium castaneum* (Herbst) (Coleoptera, Tenebrionidae) to wheat flour: heritable character or "conditioning"?, *J. Appl. Entomol.,* 104, 179, 1987.
12. **Bernays, E. A.,** [illegible]feedants in crop pest management, in *Natural Products for In-*

novative Pest Management, Whitehead, D. L. and Bowers, W. S., Eds., Pergamon Press, Oxford, 1983, 586.

13. **Bernays, E. A., Blaney, W. M., and Chapman, R. F.,** Changes in chemoreceptor sensilla on the maxillary palps of *Locusta migratoria* in relation to feeding, *J. Exp. Biol.,* 57, 745, 1972.
14. **Bernays, E. A. and Chapman, R. F.,** The control of changes in the peripheral sensilla associated with feeding in *Locusta migratoria* (L.), *J. Exp. Biol.,* 57, 755, 1972.
15. **Bernays, E. A. and Graham, M.,** On the evolution of host range in phytophagous arthropods, *Ecology,* 69, 886, 1988.
16. **Bernays, E. A. and Lee, J. C.,** Food aversion learning in the polyphagous grasshopper *Schistocerca americana, Physiol. Entomol.,* 13, 131, 1989.
17. **Bernays, E. A. and Wrubel, R. P.,** Learning by grasshoppers: association of colour/light intensity with food, *Physiol. Entomol.,* 10, 359, 1985.
18. **Beugnon, G.,** Learned orientation in landward swimming in the cricket *Pteronemobius lineolatus, Behav. Process.,* 12, 215, 1986.
19. **Blaney, W. M., Schoonhoven, L. M., and Simmonds, M. S. J.,** Sensitivity variations in insect chemoreceptors; a review, *Experientia,* 42, 13, 1986.
20. **Blaney, W. M. and Simmonds, M. S. J.,** Electrophysiological activity in insects in response to antifeedants, *Trop. Dev. Res. Inst. Misc. Pub. London.,* 219, 1983.
21. **Blaney, W. M. and Simmonds, M. S. J.,** Experience: a modifier of neural and behavioural sensitivity, in *Insects-Plants, Proc. 6th Int. Symp. on Insect-Plant Relationships,* Pau, Labeyrie, V., Fabres, G., and Làchaise, D., Eds., W. Junk, Dodrecht, 1987, 237.
22. **Blaney, W. M. and Winstanley, C.,** Food selection behaviour in *Locusta migratoria,* in *Proc. 5th Int. Symp. Insect-Plant Relationships,* Wageningen, Visser, J. H., and Minks, A. K., Eds., PUDOC, Wageningen, 1982, 365.
23. **Blaney, W. M., Winstanely, C., and Simmonds, M. S. J.,** Food selection by locusts: an analysis of rejection behaviour, *Entomol. Exp. Appl.,* 38, 35, 1985.
24. **Blum, M. S. and Blum, N. A., Eds.,** *Sexual Selection and Reproductive Competition in Insects,* Academic Press, New York, 1979, 463.
25. **Bongers, W.,** External factors in the host plant selection of the Colorado beetle *Leptinotarsa decemlineata* Say, *Meded. Landbouwhogesch. Opzoekingsstn. Staat Gent,* 30, 1516, 1965.
26. **Bonner, J. T.,** *and Cycle. An Essay on the Structure of Biology,* Princeton University Press, Princeton, 1965.
27. **Bradshaw, W. E.,** Pervasive themes in insect life cycle strategies, in *the Evolution of Insect Life Cycles,* Taylor, F. and Karban, R., Eds., Springer Verlag, New York, 1986, 287.
28. **Byrne, J. H.,** Cellular analysis of associative learning, *Physiol. Rev.,* 67, 329, 1987.
29. **Callec, J. -J.,** Synaptic transmission in the central nervous system of insects, in *Insect Neurobiology,* Treherne, J. E., Ed., North-Holland, Amsterdam, 1974, 450.
30. **Cassidy, M. D.,** Development of an induced food plant preference in the Indian stick insect, *Carausius morosus, Entomol. Exp. Appl.,* 24, 287, 1978.
31. **Chapman, R. F.,** The chemical inhibition of feeding by phytophagous insects, a review, *Bull. Entomol. Res.,* 64, 339, 1974.
32. **Charnov, E. L.,** Optimal foraging: attack strategy of a mantid, *Am. Nat.,* 110, 141, 1976.
33. **Chew, F. S.,** Foodplant preferences of *Pieris* caterpillars (Lepidoptera), *Oecologia (Berlin),* 46, 1980.
34. **Cohen, R. W., Heydon, S. L., Waldbauer, G. P., and Friedman, S.,** Nutrient self-selection by the omnivorous cockroach *Supella longipalpa, J. Insect Physiol.,* 33, 77, 1987.
35. **Cohen, R. W., Waldbauer, G. P., Friedman, S., and Schiff, N. M.,** Nutrient self-selection by *Heliothis zea* larvae: a time-lapse film study, *Entomol. Exp. Appl.,* 44, 65, 1987.
36. **Cook, A. G.,** The ultrastructure of the A1 sensilla on the posterior surface of the clypeo-labrum of *Locusta migratoria migratorioides* (R & F), *Z. Zellforsch. Mikrosk. Anat.,* 134, 539, 1972.
37. **Cooley, S. S., Prokopy, R. J., McDonald, P. T., and Wong, T. T. Y.,** Learning in oviposition site selection by *Ceratitis capitata* flies, *Entomol. Exp. Appl.,* 40, 47, 1986.
38. **Corbet, S. A.,** Insect chemosensory responses: a chemical legacy hypothesis, *Ecol. Entomol.,* 10, 143, 1985.
39. **Courtney, S. P.,** Models of host plant location by butterflies: the effect of search images and search efficiency, *Oecologia (Berlin),* 59, 317, 1983.
40. **Craighead, F.,** Hopkins host-selection principle as related to certain cerambycid-beetles, *J. Agric. Res.,* 22, 189, 1921.
41. **Croze, H.,** Searching image in carrion crows, *Z. Tierpsychol.,* 5, 1, 1970.
42. **Dadd, R. H.,** Feeding behaviour and nutrition in grasshoppers and locusts, *Adv. Insect Physiol.,* 1, 47, 1963.
43. **Danilevsky, A. S.,** Rol' pytayushtshikh rastenii v biologii lugovogo motyl'ka, *Entomol.*

Obozr., 26, 91, 1935.

44. **Darwin, C.**, *The Variation of Animals and Plants Under Domestication*, 2nd ed., Methuen, London, 1875, 495.
45. **Dawkins, M.**, Perceptual changes in chicks: another look at the "search image" concept, *Anim. Behav.*, 19, 566, 1971.
46. **Dawkins, M.**, Shifts of "attention" in chicks during feeding, *Anim. Behav.*, 19, 575, 1971.
47. **de Boer, G. and Hanson, F. E.**, Food plant selection and induction of feeding preference among host and non-host plants in larvae of the tobacco hornworm *Manduca sexta, Entomol. Exp. Appl.*, 35, 177, 1984.
48. **de Boer, G. and Hanson, F. E.**, Feeding responses to solanaceous allelochemicals by larvae of the tobacco hornworm, *Manduca sexta, Entomol. Exp. Appl.*, 45, 123, 1987.
49. **Delaney, K. and Gelperin, A.**, Post-ingestive food-aversion learning to amino acid deficient diets by the terrestrial slug *Limax maximus, J. Comp. Physiol.*, 159, 281, 1986.
50. **Dethier, V. G.**, Adaptation to chemical stimulation of the tarsal receptors of the blowfly, *Biol. Bull.*, Woods Hole, Mass., 103, 1952.
51. **Dethier, V. G.**, Evolution of feeding preferences in phytophagous insects, *Evolution*, 8, 33, 1954.
52. **Dethier, V. G.**, Egg-laying habits of Lepidoptera in relation to available food, *Can. Entomol.*, 91, 554, 1959.
53. **Dethier, V. G.**, *The Hungry Fly. A Physiological Study of the Behavior Associated with Feeding*, Harvard University Press, Cambridge, 1976, 489.
54. **Dethier, V. G.**, Responses of some olfactory receptors of the eastern tent caterpillar *(Malacosoma americanum)* to leaves, *J. Chem. Ecol.*, 6, 213, 1980.
55. **Dethier, V. G.**, Food-aversion learning in two polyphagous caterpillars, *Diacrisia virginica* and *Estigmene congrua, Physiol. Entomol.*, 5, 321, 1980.
56. **Dethier, V. G.**, Evolution of receptor sensitivity to secondary plant substances with special reference to deterrents, *Am. Nat.*, 115, 45, 1980.
57. **Dethier, V. G.**, Mechanism of host plant recognition, *Entomol. Exp. Appl.*, 31, 49, 1982.
58. **Dethier, V. G.**, Analyzing proximate causes of behavior, in *Evolutionary Genetics of Invertebrate Behavior*, Huettel, M.D., Ed., Plenum Press, New York, 1987, 319.
59. **Dethier, V. G., Solomon, R. L., and Turner, L. H.**, Sensory input and central excitation and inhibition in the blowfly, *J. Comp. Physiol. Psychol.*, 60, 303, 1965.
60. **Dethier, V. G. and Yost, M. T.**, Oligophagy and absence of food-aversion learning in tobacco hornworms, *Manduca sexta, Physiol. Entomol.*, 4, 125, 1979.
61. **Dudai, Y. and Bicker, G.**, Comparison of visual and olfactory learning in *Drosophila, Naturwissenschaften*, 65, 495, 1978.
62. **Duerr, J. S. and Wuinn, W. G.**, Three *Drosophila* mutations that block associative learning also affect habituation and sensitization, *Proc. Nat. Acad. Sci. U.S.A.*, 79, 3646, 1982.
63. **Eisestein, E. M.**, Learning and memory in isolated insect ganglia, *Adv. Insect Physiol.*, 9, 111, 1972.
64. **Etscorn, F.**, Effects of a preferred vs a nonpreferred CS in the establishment of a taste aversion, *Physiol. Psychol.*, 1, 5, 1973.
65. **Flowers, R. W. and Yamamoto, R. T.**, Feeding on non-host plants by the tobacco hornworm, *Manduca sexta*, (Lepidoptera, Sphingidae), *Fla. Entomol.*, 65, 523, 1982.
66. **Fukushi, T.**, Properties of olfactory conditioning in the housefly, *Musca domestica, J. Insect Physiol.*, 25, 155, 1979.
67. **Fukushi, T.**, The role of learning on the finding of food in the searching behavior of the housefly, *Musca domestica* (Diptera: Muscidae), *Entomol. Gener.*, 8, 241, 1983.
68. **Futuyma, D. J.**, Selective factors in the evolution of host choice by phytophagous insects, in *Herbivorous Insects, Host-Seeking Behavior and Mechanisms*, Ahmad, S., Ed., Academic Press, New York, 1983, chap. 8.
69. **Gelperin, A.**, Rapid food-aversion learning by a terrestrial mollusk, *Science*, 189, 567, 1975.
70. **Gelperin, A.**, Neuroethological studies of associative learning in feeding control systems, in *Neuroethology and Behavioral Physiology*, Huber, F. and Markl, H., Eds., Springer-Verlag, Berlin, 1983, 189.
71. **Gelperin, A.**, Plasticity in control systems for insect feeding behavior, in *Perspectives in Chemoreception and Behavior*, Chapman, R. F., Bernays, E. A., and Stoffolano, J. G., Jr., Eds., Springer-Verlag, New York, 1987, chap. 3.
72. **Gelperin, A. and Forsythe, D.**, Neuroethological studies of learning in mollusks, in *Simpler Networks and Behavior*, Fentress, J. C., Ed., Sinauer Associates, Sunderland, 1975, 239.
73. **Getzova, A. B. and Lozina-Lozinskil, L. K.**, Rol' povedeniya nasekomykh v protsesse prisposobleniya ikh k rastitel'noy pishtshe, *Zool. Zh.*, 34, 1066, 1955.
74. **Gilbert, L. E.**, Ecological consequences of a coevolved mutualism between butterflies and plants, in *Coevolution of Animals and plants*, Gilbert, L. E. and Raven, P. H., Eds., University of Texas Press, Austin, 1975, 246.
75. **Gill, J. S.**, Studies on Insect Feeding Deterrents with Special Reference to the Fruit Extracts of the Neem Tree, *Azadirachta indica* A. Juss, Ph.D thesis, University of Lon-

don, 1972.

76. **Goldsmith, C. M., Hepburn, H. R., and Mitchell, D.**, Retention of an associative learning task after metamorphosis in *Locusta migratoria migratorioides, J. Insect Physiol.*, 24, 737, 1978.
77. **Gould, J. L.**, The locale map of honey bees: do insects have cognitive maps?, *Science*, 232, 861, 1986.
78. **Grabstein, E. M. and Scriber, J. M.**, The relationship between restriction of host plant consumption and postingestive utilization of biomass and nitrogen in *Hyalophora cecropia, Entomol. Exp. Appl.*, 31, 202, 1982.
79. **Grabstein, E. M. and Scriber, J. M.**, Host-plant utilization by *Hyalophora cecropia* as affected by prior feeding experience, *Entomol. Exp. Appl.*, 32, 262, 1982.
80. **Gray, L.**, Genetic and experiential differences affecting foraging behavior, in *Foraging Behavior. Ecological, Ethological and Psychological Approaches*, Kamil, A. C. and Sargent, T. D., Eds., Garland STPM Press, New York, 1981, 455.
81. **Greenblatt, J. A., Calvert, W. H., and Barbosa, P.**, Larval feeding preferences and inducibility in the fall webworm, *Hyphantria cunea, Ann. Entomol. Soc. Am.*, 71, 605, 1978.
82. **Grossfield, J.**, Non-sexual behavior of *Drosophila*, in *The Genetics and Biology of Drosophila*, Vol. 2b, Ashburner, M., and Wright, T. R. F., Eds., Academic Press, 1978, chap. 10.
83. **Groves, P. M. and Thompson, R. F.**, Habituation: a dual-process theory, *Psychol. Rev.*, 77, 419, 1970.
84. **Guilford, T. and Dawkins, M. S.**, Search images not proven: a reappraisal of recent evidence, *Anim. Behav.*, 35, 1838, 1987.
85. **Hall, J. C.**, Learning and rhythms in courting, mutant *Drosophila, Trends Neuro. Sci.*, 9, 414, 1986.
86. **Hanson, F. E.**, Comparative studies on induction of food choice preferences in lepidopterous larvae, *Symp. Biol. Hung.*, 16, 71, 1976.
87. **Hanson, F. E. and Dethier, V. G.**, Role of gustation and olfaction in food plant discrimination in the tobacco hornworm, *Manduca sexta, J. Insect Physiol.*, 19, 1019, 1973.
88. **Hay, D. A.**, Strain differences in maze-learning ability of *Drosophila melanogaster, Nature (London)*, 257, 44, 1975.
89. **Heinrich, B.**, "Majoring" and "minoring" by foraging bumblebees, *Bombus vagans:* an experimental analysis, *Ecology*, 60, 245, 1979.
90. **Hershberger, W. A. and Smith, M. P.**, Conditioning in *Drosophila melanogaster, Anim. Behav.*, 15, 259, 1967.
91. **Hinde, R. A.**, *Animal Behaviour. A Synthesis of Ethology and Comparative Psychology*, McGraw-Hill, London, 1966, 534.
92. **Hinde, R. A. and Tinbergen, N.**, The comparative study of species-specific behavior, in *Behavior and Evolution*, Roe, A., and Simpson, G. S., Eds., Yale University Press, New Haven, 1958, 251.
93. **Holliday, M. and Hirsch, J.**, A coment on the evidence for learning in Diptera, *Behav. Genet.*, 16, 439, 1986.
94. **Holling, C. S.**, Some characteristics of simple types of predation and parasitism, *Can. Entomol.*, 91, 385, 1959.
95. **Hopkins, A. D.**, A discussion of C. G. Hewitt's paper on "Insect Behavior", *J. Econ. Entomol.*, 10, 92, 1917.
96. **Horn, G. and Hinde, R. A., Eds.**, *Short-term Changes in Neural Activity and Behaviour*, Cambridge University Press, Cambridge, 1970, 628.
97. **Horridge, G. A.**, Learning of leg positions by headless insects, *Nature (London)*, 193, 697, 1962.
98. **Hough-Goldstein, J. A.**, Oviposition site selection by seedcorn maggot flies (Diptera: Anthomyiidae) unaffected by prior experience of larval host, *Environ. Entomol.*, 14, 289, 1985.
99. **Hovanitz, W. and Chang, V. C. S.**, Ovipositional preference tests with *Pieris, J. Res. Lipid.*, 2, 185, 1963.
100. **Hsiao, T. H.**, Host plant adaptations among geographic populations of the Colorado potato beetle, *Entomol. Exp. Appl.*, 24, 437, 1978.
101. **Hubert-Dahl, M. L.**, Aenderung des Wirtswahlverhaltens dreier Biotypen von *Acyrthosiphon pisum* Harris nach Anzucht auf verschiedenen Wirtspflanzen, *Beitr. Entomol.*, 25, 77, 1975.
102. **Immelmann, K.**, Ecological significance of imprinting and early learning, *Annu. Rev. Ecol. Syst.*, 6, 15, 1975.
103. **Irwin, F. W.**, An analysis of the concepts of discrimination and preference, *Am. J. Psychol.*, 58, 152, 1958.
104. **Iwao, S.**, Some experiments on the host-plant preference in a phytophagous lady beetle, *Epilachna pustulosa* Kono, with special reference to its individual variation, *Insect Ecol.*, 8, 10, 1959.
105. **Jaenike, J.**, On optimal oviposition behavior in phytophagous insects, *Theor. Popul. Biol.*, 14, 350, 1978.
106. **Jaenike, J.**, Induction of host preference in *Drosophila melanogaster, Oecologia (Berlin)*, 58, 320, 1983.
107. **Jaenike, J.**, Genetic complexity of host-selection behavior in *Drosophila, Proc.Natl. Acad. Sci. U.S.A.*, 83, 2148, 1986.
108. **Jamieson, I. G.**, The functional approach to behavior: is it useful?, *Am. Nat.*, 127, 195,

1986.

109. **Jermy, T.,** On the nature of the oligophagy in *Leptinotarsa decemlineata* Say (Coleoptera, Chrysomelidae), *Acta Zool. Acad. Sci. Hung.,* 7, 119, 1961.
110. **Jermy, T.,** Biological background and outlook of the antifeedant approach to insect control, *Acta Phytopathol. Acad. Sci. Hung.,* 6, 253, 1971.
111. **Jermy, T.,** Multiplicity of insect antifeedants in plants, in *Current Themes in Tropical Science,* Odhiambo, T. R., Ed., Vol. 2, *Natural Products for Innovative Pest Management,* Whitehead, D. L. and Bowers, W. S., Eds., Pergamon Press, Oxford, 1983, chap. 12.
112. **Jermy, T.,** The role of experience in the host selection of phytophagous insects, in *Perspectives in Chemoreception,* Chapman, R. F., Bernays, E. A., and Stoffolano, J. G., Jr., Eds., Springer-Verlag, New York, 1987, chap. 9.
113. **Jermy, T.,** unpublished.
114. **Jermy, T., Bernays, E. A., and Szentesi, A.,** The effect of repeated exposure to feeding deterrents on their acceptability to phytophagous insects, in *Proc. 5th Int. Symp. Insect-Plant Relationships,* Wageningen, Visser, J. H. and Minks, A. K., Eds., PUDOC, Wageningen, 1982, 25.
115. **Jermy, T., Hanson, F. E., and Dethier, V. G.,** Induction of specific food preference in lepidopterous larvae, *Entomol. Exp. Appl.,* 11, 211, 1968.
116. **Jermy, T., Horváth, J., and Szentesi, A.,** The role of habituation in food selection of lepidopterous larvae: the example of *Mamestra brassicae* L. (Lepidoptera, Noctuidae), in *Insects-Plants, Proc. 6th Int. Symp. on Insect-Plant Relationships,* Pau, Labeyrie, V., Fabres, G., and Lachaise, D., Eds., W. Junk, Dordrecht, 1986, 231.
117. **Jermy, T., Lábos, E., snd Molnár, I.,** Stenophagy of phytophagous insects — a result of constraints on the evolution of the nervous system, in *Organizational Constraints on the Dynamics of Evolution,* Maynard-Smith, J. and Vida, G., Eds., Manchester University Press, Manchester, in press.
118. **Johansson, A. S.,** The food plant preference of the larvae of *Pieris brassicae* L., *Nor. Entomol. Tidsskr. B,* 8, 187, 1951.
119. **Johnston, T. and Gottlieb, G.,** manuscript.
120. **Kamil, A. C.,** Optimal foraging theory and the psychology of learning, *Am. Zool.,* 23, 291, 1983.
121. **Kamil, A. C. snd Roitblat, H. L.,** The ecology of foraging behavior: implications for animal learning and memory, *Annu. Rev. Psychol.,* 36, 141, 1985.
122. **Kamil, A. C. and Sargent, T. D., Eds.,** *Foraging Behavior. Ecological, Ethological and Psychological Approaches,* Garland STPM Press, New York, 1981, 534.
123. **Kandel, E. R. and Spencer, W. A.,** Cellular neurophysiological approaches in the study of learning, *Psychol. Rev.,* 48, 65, 1968.
124. **Kozhantshikov, I. V.,** Biologitsheskie osobennosti evropeyskikh vidov roda *Galerucella* i usloviya obrazovaniya biologitsheskikh form u *Galerucella lineola* F., *Trudy Zool. Inst. Akad. Nauk. SSSR,* 24, 271, 1958.
125. **Krasne, F. B.,** Physiological analysis of learning in invertebrates, in *Cortical Integration,* Reinoso-Suarez, F. and Ajmone-Marsan, C., Eds., Raven Press, New York, 1984, 53.
126. **Krebs, J. R.,** Behavioural aspects of predation, in *Perspectives in Ethology,* Bateson, P. P. G. and Klopfer, P. H., Eds., Plenum Press, New York 1973, 73.
127. **Krebs, J. R. and Davis, N. B.,** *An Introduction to Behavioural Ecology,* Blackwell Scientific, Oxford, 1981, 292.
128. **Kuznetzov, V. I.,** Voprosy prisposoblenii tsheshuekrylykh k novym pishtshevym usloviyam, *Trudy Zool. Inst. Akad. Nauk SSSR,* 11, 166, 1952.
129. **Lawrence, E. S. and Allen, J. A.,** On the term 'search image', *Oikos,* 40, 313, 1983.
130. **Lee, J. C., Bernays, E. A., and Wrubel, R. P.,** Does learning play a role in host location and selection by grasshoppers?, in *Insects-Plants, Proc. 6th Int. Symp. on Insect-Plant Relationships,* Pau, Labeyrie, V., Fabres, G., and Lachaise, D., Eds., W. Junk, Dordrecht, 1986, 125.
131. **Levins, R. and MacArthur, R.,** An hypothesis to explain the incidence of monophagy, *Ecology,* 50, 910, 1969.
132. **Lewis, A. C.,** Memory constraints and flower choice in *Pieris rapae, Science,* 232, 863, 1986.
133. **Lewontin, R. C.,** Fitness, survival and optimality, in *Analysis of Ecological Systems,* Horn, D. J., Stairs, G. R., and Mitchell, R. D., Eds., Ohio State University Press, Columbus, 1979, chap. 1.
134. **Lorenz, K.,** Der Kumpan in der Umwelt des Vogels, *J. Ornithol.,* 83, 137, 289, 1935.
135. **Ma, W. C.,** Dynamics of feeding responses in *Pieris brassicae* Linn., as a function of chemosensory input: a behavioural, ultrastructural and electrophysiological study, *Meded. Landbouwhogesch. Wageningen,* 72-11, 1, 1972.
136. **Ma, W. C. and Visser, J. H.,** Single unit analysis of odour quality coding by the olfactory antennal receptor system of the Colorado beetle, *Entomol. Exp. Appl.,* 24, 520, 1978.
137. **Mark, G. A.,** Induced oviposition preference, periodic environments, and demographic cycles in the bruchid beetle *Callosobruchus [illegible]culatus, Entomol. Exp. Appl.,* 32, 155, 1982.

138. **Marlin, N. A. and Miller, R. R.,** Associations to contextual stimuli as a determinant to long-term habituation, *J. Exp. Psychol. Anim. Behav. Process.*, 7, 313, 1981.
139. **Mayr, E.,** Evolution and Verhalten, *Verh. Dtsch. Zool. Ges. Koeln.* 64, 322, 1970.
140. **McFarland, D., Ed.,** *The Oxford Companion to Animal Behaviour*, Oxford University Press, Oxford, 1981, 657.
141. **McGuire, T.,** Learning in three species of Diptera: the blowfly *Phormia regina*, the fruit fly *Drosophila melanogaster*, and the house fly *Musca domestica*, *Behav. Genet.*, 14, 479, 1984.
142. **McGuire, T.,** Further evidence for learning in Diptera: a reply to Holliday and Hirsch, *Behav. Genet.*, 16, 457, 1986.
143. **Meijsser, F. M.,** Internal report, Department of Animal Physiology, Agricultural University, Wageningen, 1983.
144. **Merzheevskaya, O. I.,** O pishtshevoi spetzializatzii sovok - ogorodnoy (*Polia oleracea* L., *P. dissimilis* Knoch), *Zool. Zh.*, 40, 707, 1961.
145. **Michely, M.,** Extrait d'une lettre parvenue par Sacc., *Bull. Soc. Imper. Zool. d'Acclimat.*, 8, 563, 1861.
146. **Mitchell, R.,** The evolution of oviposition tactics in the bean weevil, *Callosobruchus maculatus* (F.), *Ecology*, 56, 696, 1975.
147. **Müller, F. P.,** Genetic and evolutionary aspects of host choice in phytophagous insects, especially aphids, *Biol. Zbl.*, 104, 225, 1985.
148. **Murbach, R.,** Effect on plein champ de fongicides à base de fentin-acétate, de manèbe et d'oxychlorure de cuivre sur la densité de population du doryphore de la pomme de terre (*Leptinotarsa decemlineata* Say.), *Rech. Agron. Suisse*, 6, 345, 1967.
149. **Murbach, R. and Corbaz, R.,** Influence de trois types de fungicides utilisés en Suisse contre le mildiou de la pomme de terre [*Phytophthora infestans* (Mont.) de Bary] sur la densité de population du doryphore (*Leptinotarsa decemlineata* Say), *Phytopathol. Z.*, 47, 182, 1963.
150. **Nelson, M. C.,** Classical conditioning in the blowfly, *(Phormia regina)*: associative and excitatory factors, *J. Comp. Physiol. Psychol.*, 77, 353, 1971.
151. **Nelson, M. C.,** The blowfly's dance: role in the regulation of food intake, *J. Insect Physiol.*, 23, 603, 1977.
152. **Oshima, K., Honda, H., and Yamamoto, I.,** Isolation of an oviposition marker from the azuki bean weevil, *Callosobruchus chinensis* (L.), *Agric. Biol. Chem.*, 37, 2679, 1973.
153. **Palmerino, C. C., Rusiniak, K. W., and Garcia, J.,** F[illegible]vor-illness aversions: the peculiar roles [illegible]dor and taste in memory for poison, *Science*, 208, 753, 1980.
154. **Papaj, D. R.,** Conditioning of leaf-shape discrimination by chemical cues in the butterfly, *Battus philenor*, *Anim. Behav.*, 34, 1281, 1986.
155. **Papaj, D. R.,** Leaf buds, a factor in host selection by *Battus philenor* butterflies, *Ecol. Entomol.*, 11, 301, 1986.
156. **Papaj, D. R.,** Shifts in foraging behavior by a *Battus philenor* population: field evidence for switching by individual butterflies, *Behav. Ecol. Sociobiol.*, 19, 31, 1986.
157. **Papaj, D. R.,** Interpopulation differences in host preference and the evolution of learning in the butterfly, *Battus philenor*, *Evolution*, 40, 518, 1986.
158. **Papaj, D. R. and Prokopy, R. J.,** Phytochemical basis of learning in *Rhagoletis pomonella* and other herbivorous insects, *J. Chem. Ecol.*, 12, 1125, 1986.
159. **Papaj, D. R. and Prokopy, R. J.,** Learning of host acceptance in the apple maggot fly, *Rhagoletis pomonella:* the role of fruit size, in *Insects-Plants, Proc. 6th Int. Symp. on Insect-Plant Relationships*, Pau, Labeyrie, V., Fabres, G., and Lachaise, D., Eds., W. Junk, Dordrecht, 1987, 408.
160. **Papaj, D. R. and Rausher, M. D.,** Individual variation in host location by phytophagous insects, in *Herbivorous Insects: Host-Seeking Behavior and Mechanisms*, Ahmad, S., Ed., Academic Press, New York, 1983, 77.
161. **Phillips, P. A. and Barnes, M. M.,** Host race formation among sympatric apple, walnut, and plum populations of the codling moth, *Laspeyresia pomonella*, *Ann. Entomol. Soc. Am.*, 68, 1053, 1975.
162. **Phillips, W. M.,** Modification of feeding "preference" in the flea-beetle, *Haltica lythri* (Coleoptera, Chrysomelidae), *Entomol. Exp. Appl.*, 21, 71, 1977.
163. **Pierce, G. J. and Ollason, J. G.,** Eight reasons why optimal foraging theory is a complete waste of time, *Oikos*, 49, 111, 1987.
164. **Pimbert, M. P.,** Reproduction and oviposition preferences of *Zabrotes subfasciatus* stocks reared from two host plant species, *Entomol. Exp. Appl.*, 38, 273, 1985.
165. **Plotkin, H. C.,** Learning in a carabid beetle *(Pterostichus melanarius)*, *Anim. Behav.*, 27, 567, 1979.
166. **Polyakova, D. I.,** Obutshenie pri vybore kormovogo rasteniya u palotshnika *Bacillus rossius* (Phasmatoidea, Phyllinae), *Zool. Zh.*, 65, 1088, 1986.
167. **Prokopy, R. J., Averill, A. L., Cooley, S. S., and Roitberg, C. A.,** Associative learning in egglaying site selection by apple maggot flies, *Science*, 218, 76, 1982.
168. **Prokopy, R. J., Averill, A. L., Cooley, S. S., Roitberg, C. A., and Kallet, C.,** Variation in host acceptance pattern in apple maggot flies, in *Proc. 5th Int. Symp. Insect-Plant Relationships*, Wageningen, Visser,

J. H. and Minks, A. K., Eds., PUDOC, Wageningen, 1982, 123.

169. **Prokopy, R. J., Papaj, D. R., Cooley, S. S., and Kallet, C.,** On the nature of learning in oviposition site acceptance by apple maggot flies, *Anim. Behav.*, 34, 98, 1986.
170. **Pyke, H.,** Optimal foraging theory: a critical review, *Annu. Rev. Ecol. Syst.*, 15, 523, 1984.
171. **Quinn, W. G., Harris, W. A., and Benzer, S.,** Conditioned behavior in *Drosophila melanogaster, Proc. Nat. Acad. Sci., U.S.A.*, 71, 708, 1974.
172. **Rausher, M. D.,** Search image for leaf shape in a butterfly, *Science,* 200, 1071, 1978.
173. **Rausher, M. D.,** Variability for host preference in insect populations: mechanistic and evolutionary models, *J. Insect Physiol.*, 31, 873, 1985.
174. **Rausher, M. D. and Papaj, D. R.,** Foraging by *Battus philenor* butterflies: evidence for individual differences in searching behaviour, *Anim. Behav.*, 31, 341, 1983.
175. **Roitberg, B. D., van Lenteren, J. C., van Alphen, J. J. M., Galis, F., and Prokopy, R. J.,** Foraging behaviour of *Rhagoletis pomonella,* a parasite of hawthorn *(Crataegus viridis),* in nature, *J. Anim. Ecol.*, 51, 307, 1982.
176. **Rozin, P.,** The selection of foods by rats, humans, and other animals, *Advan. Study Behav.*, 6, 21, 1976.
177. **Rowell, C. H. F.,** Incremental and decremental processes in the insect central nervous system, in *Short-term Changes in Neural Activity and Behaviour,* Horn, G. and Hinde, R. A., Eds., Cambridge University Press, Cambridge, 1970, 237.
178. **Rowell-Rahier, M.,** The food plant preferences of *Phratora vitellinae* (Coleoptera, Chrysomelidae). B. A laboratory comparison of geographically isolated populations and experiments on conditioning, *Oecologia (Berlin)*, 64, 375, 1984.
179. **Royama, T.,** Factors governing the hunting behaviour and selection of food by the great tit (*Parus major* L.), *J. Anim. Ecol.*, 39, 619, 1970.
180. **Saxena, K. N.,** Some factors governing olfactory and gustatory responses of insects, in *Olfaction and Taste II*, Hayashi, T., Ed., Pergamon Press, Oxford, 1967, 799.
181. **Saxena, K. N. and Schoonhoven, L. M.,** Induction of orientational and feeding preferences in *Manduca sexta* larvae for an artificial diet containing citral, *Entomol. Exp. Appl.*, 23, 72, 1978.
182. **Saxena, K. N. and Schoonhoven, L. M.,** Induction of orientational and feeding preferences in *Manduca sexta* larvae for different food sources, *Entomol. Exp. Appl.*, 32, 173, 1982.
183. **Schoonhoven, L. M.,** Loss of host plant specificity by *Manduca sexta* after rearing on an artificial diet, *Entomol. Exp. Appl.*, 10, 270, 1967.
184. **Schoonhoven, L. M.,** Sensitivity changes in some insect chemoreceptors and their effect on food selection behaviour, *Proc. K. Ned. Akad. Wet., Ser. C.*, 72, 491, 1969.
185. **Schoonhoven, L. M.,** Long-term sensitivity changes in some insect taste receptors, *Drug. Res.*, 28, 1978, (reprint).
186. **Schoonhoven, L. M. and Jermy, T.,** A behavioural and electrophysiological analysis of insect feeding deterrents, in *Crop Protection Agents — Their Biological Evaluation,* McFarlane, N.R., Ed., Academic Press, New York, 1977, 133.
187. **Schoonhoven, L. M. and Meerman, J.,** Metabolic cost of changes in diet and neutralization of allelochemics, *Entomol. Exp. Appl.*, 24, 689, 1978.
188. **Schweissing, F. C. and Wilde, G.,** Predisposition and nonpreference of the greenbug for certain host plants, *Environ. Entomol.*, 8, 1070, 1979.
189. **Scriber, J. M.,** The effects of sequentially switching foodplants upon biomass and nitrogen utiization by polyphagous and stenophagous *Papilio* larvae, *Entomol. Exp. Appl.*, 25, 203, 1979.
190. **Scriber, J. M.,** Sequential diets, metabolic cost, and growth of *Spodoptera eridania* feeding upon dill, lima bean and cabbage, *Oecologia (Berlin)*, 51, 175, 1981.
191. **Scriber, J. M.,** The behaviour and nutritional physiology of southern armyworm larvae as a function of plant species consumed in earlier instars, *Entomol. Exp. Appl.*, 31, 359, 1982.
192. **Shettleworth, S. J.,** Learning and behavioral ecology, in *Behavioral Ecology, an Evolutionary Approach,* Krebs, J. B. and Davies, N. B., Eds., Sinauer Assoc., Sunderland, MA, 1984, 170.
193. **Siegel, R. W. and Hall, J. C.,** Conditioned responses in courtship behavior of normal and mutant *Drosophila, Proc. Natl. Acad. Sci., U.S.A.*, 76, 3430, 1979.
194. **Simmonds, M. S. J. and Blaney, W.M.,** Some neurophysiological effects of azadirachtin on lepidopterous larvae and their feeding responses, in *Natural Pesticides from the Neem Tree, (Azadirachta indica A. Juss) and Other Tropical Plants,* Proc. 2nd Int. Neem Conf., Rauischholzhausen, Schmutterer, H., and Ascher, K. R. S., Eds., Deutsche GTZ GmbH, Eschborn, 1983, 587.
195. **Smith, M. A. and Cornell, H. V.,** Hopkins host-selection in *Nasonia vitripennis* and its implications for sympatric speciation, *Anim. Behav.*, 27, 365, [illegible].
196. **Solodovnikov, V[illegible],** Ismeneniya povede-

niya gusenitz kitayskogo dubovogo shelkopryada *(Antheraea pernyi)* na kormovom gradiente, *Dokl. Akad. Nauk SSSR*, 60, 321, 1948.

197. **Spatz, H.-Ch.**, Visuelles Lernen bei *Drosophila*. Wege zu einer Molekularbiologie des Lernens?, *Funkt. Biol. Med.*, 5, 276, 1985.
198. **Städler, E. and Hanson F. E.**, Influence of induction of host preference on chemoreception of *Manduca sexta:* behavioral and electrophysiological studies, *Symp. Biol. Hung.*, 16, 267, 1976.
199. **Städler, E. and Hanson, F. E.**, Food discrimination and induction of preference for artificial diets in the tobacco hornworm, *Manduca sexta, Physiol. Entomol.*, 3, 121, 1978.
200. **Stanton, M. L.**, Short-term learning and the searching accuracy of egg-laying butterflies, *Anim. Behav.*, 32, 33, 1984.
201. **Strebel, O.**, Biologische Studien an einheimischen Collembolen. II. Ernährung und Geschmackssinn bei *Hypogastrura purpurascens* (Lubb.), *Z. Wiss. Insektenbiol.*, 23, 135, 1928.
202. **Stride, G. O. and Straatman, R.**, The host plant relationship of an Australian swallowtail *Papilio aegeus*, and its significance in the evolution of host plant selection, *Proc. Linn. Soc. NSW*, 87, 69, 1962.
203. **Szentesi, A. and Bernays, E. A.**, A study of behavioural habituation to a feeding deterrent in nymphs of *Schistocerca gregaria, Physiol. Entomol.*, 9, 329, 1984.
204. **Tabashnik, B. E., Wheelock, H., Rainbolt, J. D., and Watt, W. B.**, Individual variation in oviposition preference in the butterfly *Colias eurytheme, Oecologia (Berlin)*, 50, 225, 1981.
205. **Takata, N.**, Studies on the host preference of common cabbage butterfly, *Pieris rapae crucivora* (Boisduval). XII. Successive rearing of the cabbage butterfly larva with certain host plants and its effect on the ovipositional preference of the adult, *Jpn. J. Ecol. (Nippon Seitai Gakkaishi)*, 11, 147, 1961.
206. **Thibout, E., Auger, J., and Dakkouni, M.**, Conservation à court terme de l'information chimique issue de la plante-hôte lors de la ponte chez la Teigne du Poireau (Lépidoptère), *C. R. Séances Acad. Agric. Fr.*, 300, 489, 1985.
207. **Thompson, R. F. and Spencer, W. A.**, Habituation: a model phenomenon for the study of neuronal substrates of behaviour, *Psychol. Rev.*, 173, 16, 1968.
208. **Thon, B.**, Acquisition and retention of habituation as a function of intertrial interval duration during training in the blowfly, *Behav. Proces*[illegible], 47, 1987.
209. **Thon, B. an**[illegible]**uzle, A.**, Differential sensitization, retention, and generalization of habituation in two response systems in the blowfly *(Calliphora vomitoria), J. Comp. Psychol.*, 98, 119, 1984.
210. **Thorpe, W.H.**, Further studies on pre-imaginal olfactory conditioning in insects, *Proc. R. Soc. London, Ser. B.*, 127, 424, 1939.
211. **Thorpe, W. H.**, *Learning and Instinct in Animals*, Methuen and Co. Ltd, London, 1963.
212. **Thorpe, W. H. and Jones, F. G. W.**, Olfactory conditioning and its relation to the problem of host selection, *Proc. R. Soc. London, Ser. B*, 124, 56, 1937.
213. **Tinbergen, L.**, The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds, *Arch. Neerl. Zool.*, 13, 265, 1960.
214. **Ting, A. Y.**, The Induction of Feeding Preference in the Butterfly *Chlosyne lacinia*, Unpublished thesis, University of Texas, Austin, 1970.
215. **Traynier, R. M. M.**, Long-term changes in the oviposition behaviour of the cabbage butterfly, *Pieris rapae*, induced by contact with plants, *Physiol. Entomol.*, 4, 87, 1979.
216. **Traynier, R. M. M.**, Associative learning in the ovipositional behaviour of the cabbage butterfly, *Pieris rapae, Physiol. Entomol.*, 9, 465, 1984.
217. **Traynier, R. M. M.**, Visual learning in assays of sinigrin solution as an oviposition releaser for the cabbage butterfly, *Pieris rapae, Entomol. Exp. Appl.*, 40, 25, 1986.
218. **Traynier, R. M. M.**, Learning without neurosis in host finding and oviposition by the cabbage butterfly, *Pieris rapae*, in *Insects-Plants, Proc. 6th Int. Symp. on Insect-Plant Relationships*, Pau, Labeyrie, V., Fabres, G., and Lachaise, D., Eds., W. Junk, Dordrecht, 1987, 243.
219. **Tully, T. P.**, Behavior-genetic Analysis of the Black Blowfly, *Phormia regina*, Using the Central Excitatory State (CES), Unpublished doctoral dissertation, University of Illinois at Urbana-Champaign, 1981.
220. **Tully, T.**, *Drosophila* learning: behavior and biochemistry, *Behav. Genet.*, 14, 527, 1984.
221. **Tully, T.**, Measuring learning in individual flies is not necessary to study the effects of single-gene mutations in *Drosophila:* a reply to Holliday and Hirsch, *Behav. Genet.*, 16, 449, 1986.
222. **Vargo, M. and Hirsch, J.**, Central excitation in the fruit fly *(Drosophila melanogaster), J. Comp. Physiol. Psychol.*, 96, 452, 1982.
223. **Vet, L. E. M. and van Opzeeland, K.**, 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, 1984.
224. **Visser, J.H. and Avé, D. A.**, General green leaf volatiles in the olfactory orientation of the Colorado beetle, *Leptinotarsa decemli-*

neata, Entomol. Exp. Appl., 24, 738, 1978.

225. **Volkonsky, M.,** Observations sur le comportement du Criquet Pèlerin (*Schistocerca gregaria* Forsk.) dans le Sahara algéro-nigérien, *Arch. Inst. Pasteur Alger.*, 20, 236, 1942.
226. **Waldbauer, G. P. and Bhattacharya, A. K.,** Self-selection of an optimum diet from a mixture of wheat fractions by the larvae of *Tribolium confusum, J. Insect Physiol.*, 19, 407, 1973.
227. **Waldbauer, G. P., Cohen, R. W., and Friedman, S.,** Self-selection of an optimal nutrient mix from defined diets by larvae of the corn earworm, *Heliothis zea* (Boddie), *Physiol. Zool.*, 57, 590, 1984.
228. **Waldbauer, G. P. and Friedman, S.,** Dietary self-selection by insects, *Proc. Int. Conf. Endocrin. Frontiers Physiol. Insect Ecol.*, Szklanska Poreba, Poland, Sept. 1987, in press.
229. **Wallace, R. A.,** *Animal Behavior. Its Development, Ecology and Evolution,* Goodyear Publishing Co., Santa Monica, 1979, 590.
230. **Walsh, B. D.,** On phytophagic varieties and phytophagous species, *Proc. Entomol. Soc. Phila.*, 3, 403, 1864.
231. **Walsh, B. D.,** On the phytophagic varieties of phytophagous species, with remarks on the unity of coloration of insects, *Proc. Entomol. Soc. Phila.*, 5, 194, 1865.
232. **Wasserman, S. S.,** Host-induced oviposition preferences and oviposition markers in the cowpea weevil, *Callosobruchus maculatus, Ann. Entomol. Soc. Am.*, 74, 242, 1981.
233. **Wasserman, S. S.,** Gypsy moth *(Lymantria dispar)* induced feeding preferences as a bioassay for phenetic similarity among host plants, in *Proc. 5th Int. Symp. Insect-Plant Relationships,* Wageningen, Visser, J. H. and Minks, A. K., Eds., PUDOC, Wageningen, 1982, 261.
234. **Wehner, R. and Raeber, F.,** Visual spatial memory in desert ants, *Cataglyphis bicolor,* (Hymenoptera: Formicidae), *Experientia,* 35, 1569, 1979.
235. **Whelan, R. J.,** Response of slugs to unacceptable food items, *J. Appl. Ecol.*, 19, 79, 1982.
236. **Wiklund, C.,** Host plant suitability and the mechanism of host selection in larvae of *Papilio machaon, Entomol. Exp. Appl.*, 16, 232, 1973.
237. **Wiklund, C.,** Oviposition preferences in *Papilio machaon* in relation to the host plants of the larvae, *Entomol. Exp. Appl.*, 17, 189, 1974.
238. **deWilde, J., Sloof, R., and Bongers, W.,** A comparative study of feeding and oviposition preference in the Colorado beetle (*Leptinotarsa decemlineata* Say), *Meded. Landbouwhogesch. Opzoekingsstn. Staat Gent,* 25, 1340, 1960.
239. **Wiseman, B. R. and McMillian, W. W.,** Feeding preferences of *Heliothis zea* larvae preconditioned to several host crops, *J. Ga. Entomol. Soc.*, 15, 449, 1980.
240. **Wright, R. H.,** Housefly memory, *Can. Entomol.*, 106, 223, 1974.
241. **Yamamoto, R. T.,** Induction of host plant specificity in the tobacco hornworm, *Manduca sexta, J. Insect Physiol.*, 20, 641, 1974.
242. **Yamamoto, R. T. and Fraenkel, G.,** The physiological basis for the selection of plants for egg-laying in the tobacco hornworm, *Protoparce sexta* (Johan.), *Verh. XI. Int. Kongr. Entomol., Wien,* 3, 127, 1960.
243. **Zahorik, D. M. and Houpt, K. A.,** Species differences in feeding strategies, food hazards, and the ability to learn food aversions, in *Foraging Behaviour. Ecological, Ethological and Psychological Approaches,* Kamil, A. C. and Sargent, T. D., Eds., Garland STPM Press, New York, 1981, 289.