

INSECT–PLANT RELATIONSHIP – CHANCE AND NECESSITY

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From the early 1920s, Europe was furiously struggling with the invasion of the Colorado potato beetle and then soon took cognisance of its inevitable triumph with resignation. All over Europe, laboratories were established and talented entomologists attempted to discover the “Achilles-heel” of the new pest devastating potato fields and threatening the potato industry.

In 1947, the first scouts of the species were noticed in Western Hungary too. Authorities quickly established a temporary laboratory in the local mansion house at Hédervár and measures were taken to eliminate spots of infestation. The first elementary studies with the species were made by two entomologists who worked while being closely watched by officials of the Hungarian KGB! One of them was TIBOR JERMY.

In spite of the atmosphere of paranoia of those years (the communist authorities insisted that the turn up of the Colorado potato beetle in Hungary was the result of the cover action of the American “war-mongers”), the first connection with the Colorado potato beetle resulted in a lifetime bond and stimulated a research rich in ideas and results. TIBOR JERMY’s special and most important scientific field was born then and there. Although he was a tremendously busy writer on very varied topics at that time (see his complete publication list at the end of this volume), important experimental and theoretical achievements were frequently connected with this particular species. The most important results concerning how insects use host plants, including behavioural and developmental observations, were born by studying the Colorado potato beetle. One cannot also dismiss the idea that the conceptual flourishing of later years must have been rooted in those times.

Based on TIBOR JERMY’s suggestions and plans, a permanent laboratory was opened in Keszthely (West Hungary) in 1958 where quieter atmosphere and fine colleagues helped him to further deepen knowledge about the Colorado potato beetle, as well as basic biology and autecology of several other insect species. Other entomologists, as well as the papers published from this period, univocally prove that he was full of clever ideas, which then were manifested in very simple experiments. His proverbial patience, and endurance under harsh conditions, led to the production of heaps of notebooks full of results, but these were never published; once knowing the outcome of an experiment he was too eager to carry on with the next, instead of writing yet another paper.

Nevertheless, the first major result of the period was a book about the Colorado potato beetle, co-authored with a close colleague, G. SÁRINGER (JERMY & SÁRINGER 1955). In the book, translated into three languages, but unfortunately not into English, a separate chapter deals with the food plants, feeding behaviour and food consumption of various developmental stadia. In the course of detailed investigations the suitability of solanaceous plant species as potential food or as plants supporting maturation and/or the ability to diapause are evaluated and discussed. A similarly detailed study (JERMY & SÁRINGER 1959) further expands the circle of plant species potentially associated with the species. In addition, the book is the first place where simple, but important methods in studying host-plant relations, such as *leaf-disk* and “*sandwich*”-tests are briefly mentioned.

In spite of the very diverse interests (ranging from the Colorado potato beetle’s biological control and sterile male technique to methodology and even to philosophical issues) the central line of TIBOR JERMY’s scientific work has been, and still is, the many facets of insect-plant interactions. If one would like to find the major milestones along this road (although admittedly every classification is subjective), one could distinguish three overlapping and intermingling areas:

(1) the food finding process which includes orientation to host- and non-host-plants, including movement on bare soil surfaces

(2) causes of host-plant specialisation of phytophagous insects, including processes of host recognition, the importance of inhibitory stimuli, as well as how experience modifies host-related behaviour

(3) evolutionary considerations and theories of the relationship between phytophagous insects and plants.

All three areas are embedded into a solid behavioural and ecological matrix. [TIBOR JERMY realized the importance of an ethological approach in entomology very early and the use of behaviour-modifying methods in plant protection entomology in particular (JERMY 1971a). See other chapters in this volume.]

HOST-PLANT FINDING BY PHYTOPHAGOUS INSECTS

Considering the fast spread of the Colorado potato beetle through the European continent, frequently covering large distances, and the remarkable mobility of adults in agricultural habitats, it was self-evident to raise the questions: (a) how does the Colorado potato beetle find its host-plant, and (b) how accurate is its host-finding?

The observations on long distance migration soon provided evidence that there was no connection with host finding, as arrival to a particular area was a ran-

dom event, and even if it terminated on a host, this fact did not negate the conclusion (JERMY & SÁRINGER 1955). It was a very challenging task to understand whether short distance orientation to (host-) plants was governed by stimuli provided by the plant specific to the relationship with the beetle. Evidently, prime candidates for a clue could be chemical factors emanating from the plant. MCINDOO'S (1926) olfactometer experiments and the impetus provided by VINCENT DETHIER'S (1947) important book considerably influenced contemporary thinking, allowing much conceptual space for chemical factors. The general ambition to find compounds responsible for spotting a host-plant has not since died out with phytophagous insects and with the Colorado potato beetle in particular, although results are scanty and support only close range effects.

Assuming that beetles orient to host-plants by the sense of smell, JERMY placed young, vigorously feeding adults (starved for one day prior to the experiment) into a wire mesh tube of 3 m long and 10 cm diam. size closed at both ends. The tube was lying on the soil surface so that one half of its length was among potato plants and the other half on bare ground. The hypothesis was that the beetles would gather at the tube-end placed under the plants. The result was, however, different. The beetles occupied no preferred site and distributed themselves everywhere within the tube. Laboratory tests strengthened these results (JERMY 1954–1956). JERMY not only hinted at his scepticism regarding olfaction-based host-finding for walking and especially for flying insects (JERMY 1954–1956, JERMY & SÁRINGER 1955), but as a corollary of observations he collected, he began experiments on the orientation to host-plant of the Colorado potato beetle. Using SANCHI'S mirror test and in numerous additional ingenious ways he proved (JERMY 1958, 1961a) that keeping directionality by the sun-compass orientation was the most profitable way for walking beetles to encounter a host. Keeping a more or less straight path decreases the likelihood of circular movement in a place. He had also made suggestions for the possible involvement of polarized light and the silhouettes of plants in the orientation of the Colorado potato beetle. His conclusion was that host finding in the beetle was a chance event and the directional movement on bare soil surface or among vegetation provide the highest probability of meeting a potato plant. Upon encountering vegetation numerous contacts are made with individual plants. Thus, close examination and/or possible short-distance olfactory orientation help identify food.

When reading TIBOR JERMY'S papers on this and other subjects one is amazed by the humble simplicity, yet nevertheless strict "Ockhamian logic" of his experiments and conclusions. In addition, from the early works on with insects he noted the high level of inefficiency of (mostly behavioural) functions that phytophagous insects demonstrate, e.g., in host finding. He gradually deepened the idea

that stochastic processes are an important part of insect functioning from genetic to phenotypic levels equally. One can easily agree with him in the importance of accidental events after watching a hungry Colorado potato beetle passing a potato stem within 5 cm. Or recognising that large numbers of eggs, laid by the Colorado potato beetle females, can be collected from totally unsuitable plant species or from objects in a potato stand. There is absolutely no chance for the young larvae to get to the nearby host-plants from these substrates. Then how adaptive is egg-laying with the Colorado potato beetle? These and yet other similar experiences led him to oppose that each phenotypic character is necessarily adaptive.

The conclusions formed from the results of the works on orientation were a guideline for JERMY's understanding of this fundamental step in host finding. Still he re-initiated similar studies in the mid-1980s to obtain results that are even more convincing. The orientation topic was upset by contradictory results from elsewhere and most importantly by the uncritical acceptance and generalisation of results from papers methodologically flawed. The unproven importance of olfactory guidance to the host-plant was still the dogmatic idea in the field of plant-insect interactions, although experiments showed orientation by chemical cues for half a meter at most, in the case of the Colorado potato beetle. The new experiments (JERMY *et al.* 1988) corroborated JERMY's former findings and conclusions. Whereas his earlier works were a collection of observational and experimental mosaics, this study was well planned and coherent enough to serve as a proof of the hypothesis. A "leptodrome" was formed [named by him with a good deal of humour after the ancient circus-arena combined with the genus name (*Leptinotarsa*) of the Colorado beetle] where day-after-day hundreds of adults were allowed to walk towards plants and silhouettes in most varied experimental situations. There were exceedingly hot days also when the temperature put to the test observers and animals alike.

In the results again, a strong directionality showed up with walking beetles that was based on photo-menotaxis, whereas a high turning rate became prevalent once the beetles arrived at a host-plant stand. However, host odour and visual input were not effective from distance greater than 40 cm. Therefore, not only is arrival at a host-plant stand accidental (we do not know of any influential visual factor specific to the potato foliage), but finding a particular host individual in a non-host matrix must also be so.

HOST SPECIALISATION OF PHYTOPHAGOUS INSECTS

Although host finding, recognition, acceptance, rejection of a plant, initiation and maintenance of feeding, and oviposition site selection mean very different actions, they have one thing in common, namely that each represents an event for which inputs are conveyed at the behavioural level. This is an important condition at this level of resolution, although it is assumed that physiological feedback, e.g., experience modifies behaviour.

From experiments with the Colorado potato beetle, it was clear (and it was outlined several times, e.g., in JERMY 1983, 1993) that host-specificity is a behavioural phenomenon and can be influenced and modified also at this level. The realisation gave him possibilities to conduct research in two major directions: (1) conceptual questions of food selection, and (2) practical use of the knowledge so obtained. The first gave him an opportunity to review and re-evaluate dominant theories of food selection and to develop his own idea named the two-way, or as more frequently used later, the asymmetric specialisation of chemoreceptors. The second provided a viable opportunity, attractive to many scientists, to demonstrate the power and usefulness of a scientific idea for the society. [The latter point was a built-in imperative in the Hungarian society at that time, however, flavoured with a schizophrenic thinking, i.e., impeding the realisation of the same idea by all means! This is how science earned a scornfully created picture of uselessness as opposed to values of plain physical work.] The experience that many/most substances present in plants are capable of interfering with or stopping the normal process of feeding has led to the recognition of potential use of *feeding inhibitors*. The idea was not totally new but it did receive very strong support from his experiments.

Stimuli governing host selection

In order to get closer to substances governing host acceptance or rejection three methods were applied (JERMY 1954–1956):

- spraying potato leaves with a substance then cutting out leaf-disks,
- vacuum infiltrating of substances into potato leaf-disks,
- “sandwich test”, for which among two potato leaf-disks a third, the test-plant disk, was pasted.

The usual arrangement of disks for such a test was checkerboard-type or circular, alternating with control disks. Several young and hungry beetles were placed in a dish containing the disks. The most important results were (JERMY 1954–1956, 1958, 1961*b*):

- 1% Bordeaux mixture (a complex compound containing Cu^{2+} ions) sprayed on potato disks inhibited feeding,
- potato disks infiltrated with leaf-sap of the solanaceous plant species *Nicandra physaloides* or the opposite, *Nicandra* disks with potato leaf-sap, were not consumed by the beetles. Thus, *Nicandra* contained compounds capable of masking positive feeding stimuli of potato. Similar effects were experienced when pure alkaloids were used instead of plant saps,
- by the sandwich test the sphere of plant species inhibiting feeding of potato beetles to different extents could be mapped. He named the figure representing the preference distribution of plants the “triangle of food preferences” (see figure in JERMY 1961c). The plant species could be grouped into three categories corresponding to the DE BOER and HANSON’s (1984) classification: (1) host-plants, (2) acceptable non-hosts, and (3) unacceptable non-hosts. The first had feeding stimulants, but no deterrents, the second group contained neither stimulants, nor deterrents, and the third one was dominated by deterrent substances.

Soon extensive laboratory experiments were carried out (JERMY 1961b, c) to find out more about the array of substances, mostly inorganic compounds, capable of influencing feeding of the potato beetle. Besides testing several cations (Cu^{2+} , Mg^{2+} , Fe^{2+} , Na^+ and Ba^{2+}) on feeding, effects of these were also tried out on oviposition behaviour and larval mortality. It turned out that with the exception of Cu^{2+} , other ions did not affect feeding. The copper compound caused a decrease in feeding, and therefore – due to malnutrition of females – egg-maturation depression and lower number of eggs laid, as well as a high level of mortality of young larvae through the process of starvation. Cu^{2+} application on potato foliage resulted in emigration of mobile stadia, mortality of young larvae and decreased egg laying, adding up to a considerable population dynamic effect.

These observations and experiments not only prepared the bases of practical application of feeding deterrents (see following section), but also deeply influenced further development of the food specialisation concept of TIBOR JERMY.

The attempt to form a theory of food specialisation based on the significance of negative (inhibitory) stimuli first evaluated the existing concepts from a historical perspective (JERMY 1961d, 1966, 1972). As relatively more information was available on stimulating substances, the prevalence of (1) *phagostimulatory* concept was inevitable [represented by such authors as LANGERHEIM (1900), VERSCHAFFELT (1910), and THORSTEINSON (1960)] holding the view that food specialisation of phytophagous species is basically determined by the botanical distribution of specific phagostimulants and attractants. Opposing it, DETHIER (1954),

HARLEY and THORSTEINSON (1967) developed the (2) *inhibition* theory, which considered the importance of inhibitory substances in shaping the host-range of polyphagous insects. The last one (3) named *symmetric two-way specialisation* concept was formed on the bases of presence and/or absence of both types of compounds (LIPKE & FRAENKEL (1956)). A modification of the latter is the (4) *asymmetric two-way specialisation*, which can be attributed to TIBOR JERMY's experience gained with inhibitory compounds on oligophagous species (mostly on the Colorado potato beetle). This theory declared that although specialisation depended on the ratio of both positive and negative compounds, it occurred in an asymmetric way, i.e., inhibitory stimuli would always be more powerful and able to block feeding even on the optimal host once applied on it. Secondary plant substances participate in both roles. Stimulatory compounds become sign (token) stimuli for some groups of oligophagous insects indicating proper host.

His arguments ran in this way:

- many oligophagous species can be maintained on diets not containing specific phagostimulatory substances,
- increasing food specialisation results in increased sensitivity to inhibitory substances,
- the two types of stimuli is in an asymmetric relationship,
- most stimulatory substances prove to be simple (primary) plant compounds, which means a limited botanical specificity,
- more inhibitory receptor cells are known than stimulatory ones.

The same concept of asymmetric importance of inhibitory substances was later extended to the then (and unfortunately today also) less known *oviposition* specialisation (JERMY 1965, MUSCHINEK *et al.* 1976, JERMY & SZENTESI 1978) with some reservations. One was the relative autonomy of receptors situated on the ovipositor. They most probably are subordinate to the ones on the palps/antennae. Second, the range of hosts selected by ovipositing insects seemed to be narrower than that of the ones suitable for larval development, at least in some insect species. It is tempting to note that the theory places two basic important behavioural processes into a unified frame.

Simple experimental arrangements, yet an outstanding ability to see much deeper and further than the actual work's periphery, lend the scientific merits to one of his best acknowledged and cited paper (cited well over 100 times) written with professors FRANK HANSON and Vincent DETHIER (JERMY *et al.* 1968). Prior to this paper, JERMY had made one preceding attempt to demonstrate long lasting effects of host plants on the subsequent food choice (JERMY 1961c). He fed 4 larval groups of the Colorado potato beetles to adulthood with tomato and potato leaves in an experimental arrangement (Table 1), and following metamorphosis he tested

Table 1. The effect of larval nutrition on the host selection of young adults (JERMY (1961)). (Number of replicates = 10)

Group	Larval nutrition	Acceptability of tomato leaves to young adults (mean and standard error)
1	L1–L4 tomato leaves	21.1±6.5
2	L1–L2 tomato leaves L3–L4 potato leaves	27.8±12.3
3	L1–L2 potato leaves L3–L4 tomato leaves	8.9±3.9
4	L1–L4 potato leaves	7.9±3.5

the resulting beetles on tomato leaves. Larval feeding had no influence on subsequent host selection of the adults (the difference were not significant), although there was a tendency for accepting tomato at adult stage if larvae had been raised on it either throughout the larval development or during L1 and L2. He called the effect *conditioning* clearly referring to central nervous system processes that would last and be retained through time, as well as substantial physiological changes. Whether the inability to condition the Colorado potato beetle is connected with its oligophagy remains to be demonstrated.

Behavioural observations have always been and still are one of JERMY's most important tools for understanding processes at a given level of complexity. (Among others, the title of his academic doctorate dissertation proves this: "Ethology of food specialisation of phytophagous insects".) In the paper mentioned above (JERMY *et al.* 1968), the authors studied the induction of specific food preferences and demonstrated that in some insect species experience with a given acceptable host plant in a larval stage would generate a long-lasting preference for that food. The induction of preference can be evidenced by choice experiments in later larval stages. Although the phenomenon did not fit into any then known learning processes, its connection with central nervous system events was not denied. It resulted in a narrowing-down of the potential host-range, a sort of "tunnel-vision", sometimes so rigidly formed that larvae died of starvation than accepting any of the alternative host-plants. The many facets of the phenomenon they investigated generated a wealth of further intriguing questions and this paper remained, perhaps, one of the most interesting scientific topics of the field. Extending the area of experience-modified behaviours into the host selection of phytophagous insects TIBOR JERMY reviewed the main phenomena in a succinct paper (JERMY 1987a) published in a book dedicated to VINCENT DETHIER's 70th birthday. This paper discusses the occurrence of and the behaviours involved in the factors influencing the induction process, as well as oviposition induction, habituation to deterrents

and food aversion learning. For the first time it also treats *adaptive significance* of the above-mentioned phenomena. He states that the adaptive advantage of aversion learning and habituation is obvious, as the former prevents consuming deleterious amount of poisonous food, and the second allows utilising unusual, nevertheless still suitable food. It is more difficult to explain the adaptive significance of induced preference. Among the lots of assumptions none is adequate, if one considers the narrowing of food specialisation which is the core event of induction.

The practical use of antifeedants

Steps for practical approaches to utilising information gained about food specialisation soon brought successes. Many reports based on experiments under laboratory conditions (and less frequently performed in the fields) proved the feasibility of application of feeding inhibitors against pests. These were mostly empirical achievements and they supported TIBOR JERMY's asymmetric specialisation theory nicely, though inadvertently. By cooperating with chemists (JERMY & MATOLCSY 1967, MATOLCSY *et al.* 1968, JERMY *et al.* 1981) a wealth of very different compounds showed remarkable inhibitory effects on many phytophagous pest species.

Today it seems that there were basically two types of approach to get efficient antifeedants at that time: (a) testing natural plant substances or synthetics ("sweeping down shelves in chemical laboratories"), and (b) planned selection of structurally related compounds (or designing structures) to catch correlation between phagostimulatory effect and molecular structure. However, only limited successes of the second approach are known, e.g., SZURDOKI *et al.* (1991). None of the ways has given a happy solution for several reasons. Without attempting to list all reasons, JERMY (1971*b*, 1990) highlighted two important ones: (1) it can be *a priori* predicted that a great variety of compounds would play inhibitory roles for any insect species, and (2) it is not likely that one will find a universal antifeedant, active on all insect species.

It was very timely at this point (end of 1970s) to unite two methodologies and attempt to give answers to such questions: (a) whether *behavioural* and *electrophysiological* approaches corroborate each other's findings considering actions of antifeedants, and (b) how, and how widely, inhibitory effects are represented at the receptor level? Of the two approaches (SCHOONHOVEN & JERMY 1977), no doubt, electrophysiology was the younger, and therefore, could hopefully provide different insights. Feeding deterrents could act on the sensory system either by stimulating specialised deterrent receptor cells, or modifying the activity of cells reacting to stimulants. There were some deterrent receptor cells known with a few insect

species, however, no coherent picture of their response range could be formed. The alternative mode of action seemed equally plausible, but even more complex. For instance, although feeding deterrent action of Cu^{2+} ions has been proven behaviourally with the Colorado potato beetle several times, no receptor response could be found. A better understanding of how receptor information is interpreted in the central nervous system of insects would help substantially in conceiving other phenomena accompanying application of feeding deterrents.

One such behaviour-level representation of deterrent-effect was the clear distinction of central excitatory state from *central inhibitory state* (CIS, JERMY 1971*b*). The CIS was evoked by the presence of deterrent, and its decay-time, as well as events accompanying it depended on the type and concentration of substance and on the insect species. The results of a CIS elicited by Cu^{2+} ions with Colorado potato beetle larvae was manifested in cessation of feeding for as long as 30 min, slow backing or total freezing, vomiting then walking away from the site.

As with insecticides, the question of adaptation to and resistance against feeding inhibitors had inevitably to be raised (JERMY 1971*b*, 1983). Considering the low probability of correlated changes in chemoreceptor function and behavioural responses, TIBOR JERMY concluded that it must be an unlikely event. One of the factors he (JERMY 1983) emphasized was the immense diversity of compounds providing an “inhibitory biochemical profile” in plants that would make even less probable adaptive changes at both receptor and behavioural levels. Nevertheless, the possibility of *habituation* to deterrents, as distinct from receptor adaptation, was duly discussed and experimentally demonstrated (SCHOONHOVEN & JERMY 1977). Larvae of at least two oligophagous insect species, *Leptinotarsa decemlineata*, and *Pieris brassicae*, did not decrease “feeding pauses” during repeated presentations of feeding deterrents. However, as information was limited on habituation regarding species number, food specialisation and substances, LIZ BERNAYS and TIBOR JERMY, during the time of a Nairobi conference, agreed on starting an in-depth research into habituation to feeding deterrents. The useful cooperation resulted in a wider perspective about the phenomenon, among others, in obtaining evidence through complicated testing procedures that habituation to feeding deterrents was a more likely event with polyphagous insect species (JERMY *et al.* 1982). Later experiments using a more natural approach, using plant leaves instead of pure and single chemicals with a polyphagous insect species, *Mamestra brassicae*, provided a more sophisticated picture that was difficult to explain (JERMY *et al.* 1987). Nevertheless, the results seemed to strengthen the earlier assumption (JERMY 1983) that insects might be less prone to habituate to the multitude of chemicals present in live plant tissues.

EVOLUTIONARY QUESTIONS OF INSECT PLANT RELATIONSHIPS

Studies of the evolutionary questions of insect plant relationships were a natural consequence of studies on food specialisation. The earliest written version where TIBOR JERMY addresses such questions of insect-plant relationship is a text of oral presentation given in Wageningen (The Netherlands) in 1971 (JERMY 1971c). It is obvious that he knew EHRLICH and RAVEN's (1964) paper by that time, as he refers to it. However, it is remarkable that he detected similar thoughts on evolution (although not named coevolution or meaning reciprocity) with DETHIER (1954) who besides his own treatments referred to PAINTER (1951). JERMY's own idea for the evolution of the relationship is also named differently in comparison with later versions. However, the logic and argument of subsequent papers were already present. The fallacy of the main premise of coevolutionary relations according to which congruent phyletic lines among plants and insects are the dominant case was also clearly stated here. He listed all major important insect-plant relations too, and argued that the other points of the coevolutionary theory, such as competition among phytophagous insects and the role of secondary plant substances also fail to stand firm. The idea of "subsequent evolution" then described and its cardinal theses are listed in eight points. Reading these points one can only conclude with considerable surprise that the core arguments are almost as complete as in the later published versions, although not presented in a as eloquent, elegant and elaborated way as in later papers.

Over the years, the critique of coevolutionary theory between plants and insects became increasingly refined and elaborated (JERMY 1976, 1984a, b, 1991, 1993, 1994, JERMY *et al.* 1990). The essence of the two theories is this: the driving force behind coevolution is the *reciprocal* selective response of (usually) two participants, the plants and insects. Insects exert selective pressure on plants by feeding and forcing them to change, most of all, biochemically. The altered plants, released from the herbivore pressure, however, will soon be recolonised by the adapted insect species once again capable of utilising the new plant species. Then the cycle repeats (EHRLICH & RAVEN 1964). The theory opposing the above scenario (JERMY 1976 and further) is that of *sequential* evolution, which states that, plants change biochemically for reasons other than herbivore pressure, such as climatic, soil, or competitive elements. These changes free them from herbivory momentarily, however, the altered plants will be followed by those insects whose genetic variability were fortunate enough to have mutations from which selection would pick up those capable of utilising the new plant lineage. In other words,

whereas insects do not select new plant lineages, plants select for those of insects' sequentially. This makes the relationship basically asymmetric.

Since the propounding of insect-plant coevolutionary theory, at least two other theories emerged modifying the basic tenets to some extent. The *diffuse coevolution* (VAN VALEN 1973) or *community coevolution* implies that all members of a community affect each other's evolution. The *geographic mosaic theory of coevolution* (THOMPSON 1994) assumes that, due to differences in outcome of interspecific interactions, the nature of relationships can alter through time, space and strength. This creates a mosaic of relationships where levels of intimacy may dynamically change along environmental gradients between the endpoints of mutualism-antagonism.

JERMY gives a very detailed and comprehensive criticism of these and related ideas in SCHOONHOVEN *et al.* (1998). Several factors such as the problem of competition among phytophagous insects, evolution of stenophagy, the importance of attack by herbivores and defence (resistance) by plants in the evolution of the relationship, the palaeobotanical and palaeontomological evidence, alternative hypotheses of oligophagy, the role of secondary plant substances, the reasons for the overdominance of specialized phytophagous species, etc. make the relationship extremely complex. JERMY treats them one-by-one in various papers and to different extents.

One or perhaps the critical point in insect-plant evolutionary considerations is the explanation for the preponderance of specialisation of herbivorous insects (assumed to be at 75–80% of all plant feeding species). According to the co-evolutionary hypothesis, host specialisation is a natural consequence of the coevolutionary process as it promotes niche segregation and decreases interspecific competition. It is also correlated with several environmental and developmental factors (BERNAYS & CHAPMAN 1994). JERMY (1976, 1984a, 1985) has long been dealing with the importance of interspecific competition among herbivorous insects, among others devoted an entire paper to it (JERMY 1985). His major arguments are based on

- the “conspicuous rarity” of most phytophagous insects;
- the almost unlimited availability of plant material as a resource;
- the importance of plant phenology, its patchy distribution, and the specific preference of herbivorous insects for particular plant parts which all contribute to decreased trophic competition;
- the weakness of “evidence” such as “competition past”.

He concluded that interspecific competition was of minor importance in driving evolution of stenophagy. Alternative theories, such as the enemy-free space hypothesis (BERNAYS & GRAHAM 1988 and others) according to which specialisa-

tion in host preference could be the result of predation pressure from generalist predators, seemed also less likely to him (JERMY 1988, 1993, 1994).

In contrast, JERMY (1971c) clearly states that evolutionary changes in host specificity are the result of hereditary changes. In later works, (e.g., JERMY 1993) he emphasizes that it happens as an *autonomous* evolutionary event. JERMY *et al.* (1990) expounded that stenophagy is more frequent than the polyphagous strategy because (1) it reflects the relatively higher rates of speciation and extinction among oligophages, (2) it indicates the evolutionary irreversibility of specialisation (specialists evolve specialists), and (3) it refers to some constraints on the evolution of the insect nervous system.

Most treatments of plant-pollinator systems take for granted that such a relationship can only be the result of reciprocal mutualism. In fact, apart from some very specific cases, such as e.g., fig and fig-wasp mutualism, the overwhelming majority of pollination relationships, as pointed out by JERMY (pers. comm.), SCHOONHOVEN *et al.* (1998) and others, are asymmetric, i.e., it is accompanied by morphological changes only on the plant's side, whereas plants hardly influence evolution of pollinators. In a recent debate over the question of what factors influenced the evolution of the long tongue of hawk moths, and in particular, of *Xanthopan morgani praedicta*, the Malagasy hawk-moth, JERMY (1999 and see references there) again stressed that there was no mutual dependence between the moth and its orchid (*Angraecum sesquipedale*) partner. The long tongue does not imply exclusive specificity for the orchid as shallow flowers are also visited, and long-tongued hawk-moth species are frequent in geographic regions where deep flowers are rare. Thus, the long tongue might be an ancient character, a result of genetic changes of hawk-moth speciation, which can also question its adaptive significance. It seems that the evolutionary relationship between the orchid and its assumed pollinator is one-sided meaning adaptation to the long tongue and not *vice versa*.

Although adaptation is an important element of the evolutionary process, it often creates traps for the evolutionary thinking too (GOULD & LEWONTIN 1979). For instance, JERMY (1987) concluded that induced preference is *nonadaptive* and "...may simply reflect the limited flexibility of the insects' neural systems which might even reduce fitness in certain ecological situations" (p. 154). It is the 1971 Wageningen lecture (JERMY 1971c) which is the first in the series of evolutionary papers that explicitly criticises our inability to get rid of deterministic thinking invoking adaptationism. The sceptical remarks about Nature as being a great destroyer and only a feeble creator, so characteristic of his later papers and discussions also pop up here for the first time: "...evolution is a domino play with the genetic code." (p. 5.) We should, instead, accept Nature where chance events domi-

nate over deterministic ones (JERMY 1998) with many unpredictable and unpurposive events. The sources from where he received support in form of analogous thinking and strengthened his own sceptic view of Nature, and specifically of adaptive evolutionary processes, are the works of two great French scientists, MONOD (1972) and JACOB (1981). JERMY's approach is not enforcing one's imaginations upon Nature, but instead assembling seemingly unrelated facts collected by quiet contemplation. It is aptly described by a sentence of his inauguration speech (JERMY 1987b) that he delivered on the occasion of his election as a member of the Hungarian Academy of Sciences:

“Scientific mentality vigorously resists accepting that Nature is like an engineering product masterminded with mathematical accuracy; instead, it is similar to an artistic object created by evolution with rambling fantasy and largely by random processes. For Man, it is an arduous task to decipher the causality of phenomena; yet, it is Nature's random character that may offer so much aesthetic pleasure for the contemplating Man.” (p. 38, emphasis from the translator.)

POSTSCRIPT

The author of the present account only wanted to be a humble chronicler of a slice of a prosperous scientific life and by no means an evaluator or a critic of TIBOR JERMY's or others' ideas. This should be done by a scientist adequate to the task. All along during TIBOR JERMY's life the classic “one-against-all”-type game has been and still is played. It is still being played at his age of 85. From the most authentic source, from TIBOR JERMY himself, the author knows that he is preparing an even more comprehensive treatise of his evolutionary thoughts in his usual “devil's advocate” manner. This again, there is no doubt, will be fuelling new debates. It is a further personal remark of the author that, although he has tried it, he probably failed to get rid of subjectivism due to the fact that he spent 30 years – it was his good fortune – with TIBOR JERMY sharing his views.

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REFERENCES

- BERNAYS, E. A. & CHAPMAN, R. F. (1994) *Host-plant selection by phytophagous insects*. Chapman & Hall, New York and London.
- BERNAYS, E. A. & GRAHAM, M. (1988) On the evolution of host selection in phytophagous arthropods. *Ecology* **69**: 886–892.
- DE BOER, G. & HANSON, F. E. (1984) 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**: 177–193.
- DETHIER, V. G. (1947) *Chemical insect attractants and repellents*. Blakiston Co., Philadelphia.
- DETHIER, V. G. (1954) Evolution of feeding preferences in phytophagous insects. *Evolution* **8**: 33–54.
- EHRlich, P. R. & RAVEN, P. H. (1964) Butterflies and plants: a study in coevolution. *Evolution* **18**: 586–608.
- GOULD, S. J. & LEWONTIN, R. C. (1979) The Spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. London, B.* **205**: 581–598.
- HARLEY, K. L. S. & THORSTEINSON, A. J. (1967) The influence of plant chemicals on the feeding behaviour, development and survival of the two-striped grasshopper, *Melanoplus bivittatus* (Say), Acrididae: Orthoptera. *Can. J. Zool.* **45**: 305–319.
- JACOB, F. (1981) *Le jeu des possibles*. Fazard, Paris.
- JERMY, T. (1954–1956) A növényevő rovarok táplálékspecializációjának jelentősége a növényvédelem szempontjából. [The importance of host-plant specificity of phytophagous insects in pest control.] *Ann. Inst. Prot. Plant. Hung.* **7**: 45–51.
- JERMY, T. (1958) Untersuchungen über Auffinden und Wahl der Nahrung beim kartoffelkäfer (*Leptinotarsa decemlineata* Say). *Entomol. Exp. Appl.* **1**: 197–208.
- JERMY, T. (1961a) Fitofág rovarok tájékozódása a fény iránya alapján. [Orientation of phytophagous insects based on the perception of light direction.] *Állatt. Közl.* **48**: 57–63.
- JERMY, T. (1961b) Néhány szervetlen só rejektív hatása a burgonyabogár (*Leptinotarsa decemlineata* Say) imágóira és lárváira. [The rejective effect of some inorganic salts on Colorado potato beetle (*Leptinotarsa decemlineata* Say) adults and larvae.] *Ann. Inst. Prot. Plant. Hung.* **8**: 121–130.
- JERMY, T. (1961c) On the nature of the oligophagy in *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae). *Acta zool. hung.* **7**: 119–132.
- JERMY, T. (1961d) Über die Nahrungsspezialisation phytophager Insekten. *Proc. Conf. Sci. Problems Plant Prot.*, Budapest, pp. 327–332.
- JERMY, T. (1965) The role of rejective stimuli in the host selection of phytophagous insects. *Proc. XIIIth Int. Congr. Entomol.*, London, 1964, p. 547.
- JERMY, T. (1966) Feeding inhibitors and food preference in chewing phytophagous insects. *Entomol. Exp. Appl.* **9**: 1–12.
- JERMY, T. (1971a) Az ökológiai és etológiai kutatások helyzete és problémái. [Conditions and problems of ecological and ethological research.] *Állatt. Közl.* **58**: 66–70.
- JERMY, T. (1971b) Biological background and outlook of the antifeedant approach to insect control. *Acta Phytopathol. Acad. Sci. Hung.* **6**: 253–260.
- JERMY, T. (1971c) Insect-foodplant relationships. Coevolution or subsequent evolution. Manuscript with the remark “Wageningen, 1971”.
- JERMY, T. (1972) A növényevő rovarok táplálékspecializációjának etológiája. [Ethology of food specialisation of phytophagous insects.] Doktori értekezés tézisei. [Thesis of D.Sc.] Budapest.

- JERMY, T. (1976) Insect–host–plant relationship – co-evolution or sequential evolution? *Symp. Biol. Hung.* **16**: 109–113.
- JERMY, T. (1983) Multiplicity of insect antifeedants in plants. Pp. 223–236. In WHITEHEAD, D. L. & BOWERS, W. S. (eds) *Natural products for innovative pest management*. Pergamon Press, Oxford.
- JERMY, T. (1984a) On the evolution of insect/host plant systems. *Verh. SIEEC X*, Budapest, 1983, 13–17.
- JERMY, T. (1984b) Evolution of insect/host plant relationships. *Am. Nat.* **124**: 609–630.
- JERMY, T. (1985) Is there competition between phytophagous insects? *Syst. Evolutionsforsch.* **23**: 275–285.
- JERMY, T. (1987a) The role of experience in the host selection of phytophagous insects. Pp. 143–157. In CHAPMAN, R. F. *et al.* (eds) *Perspectives in chemoreception and behavior*. Springer Verlag, New York.
- JERMY, T. (1987b) Gondolatok a koevolúcióról. [Thoughts on coevolution.] In TOLNAI, M. (ed.) *Értekezések, emlékezések*. Akadémiai székfoglaló, 1986. március 11. Akadémiai Kiadó, Budapest, 44 pp.
- JERMY, T. (1988) Can predation lead to narrow food specialization in phytophagous insects? *Ecology* **69**: 902–904.
- JERMY, T. (1990) Prospects of antifeedant approach to pest control – a critical review. *J. Chem. Ecol.* **16**: 3151–3166.
- JERMY, T. (1991) Evolutionary interpretations of insect–plant relationships – a closer look. *Symp. Biol. Hung.* **39**: 301–311.
- JERMY, T. (1993) Evolution of insect–plant relationships – a devil’s advocate approach. *Entomol. Exp. Appl.* **66**: 3–12.
- JERMY, T. (1994) Hypotheses on oligophagy: how far the case of the Colorado potato beetle supports them. Pp. 127–139. In JOLIVET, P. H. *et al.* (eds) *Novel aspects of the biology of Chrysomelidae*. Kluwer Acad. Publ., Dordrecht.
- JERMY, T. (1998) The major transitions in evolution: what has driven them? *Trends Ecol. Evol.* **13**: 199–200.
- JERMY, T. (1999) Deep flowers for long tongues: a final word. *Trends Ecol. Evol.* **14**: 34.
- JERMY, T. & SÁRINGER, GY. (1955) *A burgonyabogár*. [The Colorado potato beetle.] Mezőgazdasági Kiadó, Budapest.
- JERMY, T. & SÁRINGER, GY. (1959) A burgonyabogár magyarországi tápnövényei. [The food plants of the Colorado potato beetle in Hungary.] *Kísérletügyi Közl.* **52/A**: 95–116.
- JERMY, T. & MATOLCSY, GY. (1967) Antifeeding effect of some systemic compounds on chewing phytophagous insects. *Acta Phytopathol. Acad. Sci. Hung.* **2**: 19–22.
- JERMY, T. & SZENTESI, Á. (1978) The role of inhibitory stimuli in the choice of oviposition site by phytophagous insects. *Entomol. Exp. Appl.* **24**: 458–471.
- JERMY, T., HANSON, F. E. & DETHIER, V. G. (1968) Induction of specific food preference in lepidopterous larvae. *Entomol. Exp. Appl.* **11**: 211–230.
- JERMY, T., BUTT, B. A., MCDONOUGH, L., DREYER, D. L. & ROSE, A. F. (1981) Antifeedants for the Colorado potato beetle. I. Antifeeding constituents of some plants from the sagebrush community. *Insect Sci. Appl.* **1**: 237–242.
- JERMY, T., BERNAYS, E. A. & SZENTESI, Á. (1982) The effect of repeated exposure to feeding deterrents on their acceptability to phytophagous insects. *Proc. 5th Int. Symp. Insect–Plant Relationships, Wageningen, 1982*. Pudoc, Wageningen, pp. 25–32.

- JERMY, T., HORVÁTH, J. & SZENTESI, Á. (1987) The role of habituation in food selection of lepidopterous larvae: the example of *Mamestra brassicae* L. (Lepid., Noctuidae). Pp. 231–236. In LABEYRIE, V. *et al.* (eds) *Insects–plants*. Junk Publishers, Dordrecht.
- JERMY, T., SZENTESI, Á. & HORVÁTH, J. (1988) Host plant finding in phytophagous insects: the case of the Colorado potato beetle. *Entomol. Exp. Appl.* **49**: 83–98.
- JERMY, T., LÁBOS, E. & MOLNÁR, I. (1990) Stenophagy of phytophagous insects – a result of constraints on the evolution of the nervous system. Pp. 157–166. In VIDA, G. & MAYNARD-SMITH, J. (eds) *Organizational constraints on the dynamics of evolution*. Manchester Univ. Press, Manchester.
- LANGERHEIM, G. (1900) Zur Frage der Schutzmittel der Pflanzen gegen Raupenfrass. *Entomol. Tidskr.* **21**: 209–232.
- LIPKE, H. & FRAENKEL, G. (1956) Insect nutrition. *Annu. Rev. Entomol.* **1**: 17–44.
- MATOLCSY, G., SÁRINGER, G., GÁBORJÁNYI, R. & JERMY, T. (1968) Antifeeding effect of some substituted phenoxy compounds on chewing and sucking phytophagous insects. *Acta Phytopathol. Acad. Sci. Hung.* **3**: 275–277.
- MCINDOO, N. E. (1926) An insect olfactometer. *J. Econ. Entomol.* **19**: 545–571.
- MONOD, J. (1972) *Chance and necessity. An essay on the natural philosophy of modern biology*. Vintage Books, New York.
- MUSCHINEK, G., SZENTESI, Á. & JERMY, T. (1976) Inhibition of oviposition in the bean weevil (*Acanthoscelides obtectus* Say, Col., Bruchidae). *Acta Phytopathol. Acad. Sci. Hung.* **11**: 91–98.
- PAINTER, R.H. (1951) *Insect resistance in crop plants*. Mcmillan Co., New York.
- SCHOONHOVEN, L. M. & JERMY, T. (1977) A behavioural and electrophysiological analysis of insect feeding deterrents. Pp. 133–146. In MCFARLANE, N. R. (ed.) *Crop protection agents – their biological evaluation*. Academic Press, London.
- SCHOONHOVEN, L. M., JERMY, T. & VAN LOON, J. J. A. (1998) *Insect-plant biology. From physiology to evolution*. Chapman and Hall, London.
- SZENTESI, Á. & JERMY, T. (1990) The role of experience in host plant choice by phytophagous insects. Pp. 39–74. In BERNAYS, E. A. (ed.) *Insect-plant interactions. Vol. 2*, CRC Press, Boca Raton.
- SZURDOKI, F., SZENTESI, Á., ABDEL-AAL, M. T., SZÉKÁCS, A., HORVÁTH, J., BAUER, K., MATOLCSY, G. & T. JERMY, T. (1991) Novel feeding deterrents against the Colorado potato beetle. Pp. 251–254. In HRDY, I. (ed.) *Insect chemical ecology*. Academia, Praha. (Proc. Conf. Insect Chem. Ecol., Tabor, 1990)
- THOMPSON, J. N. (1994) *The coevolutionary process*. Univ. Chicago Press, Chicago.
- THORSTEINSON, A. J. (1960) Host selection in phytophagous insects. *Annu. Rev. Entomol.* **5**: 193–218.
- VAN VALEN, L. (1973) A new evolutionary theory. *Evol. Theory* **1**: 1–30.
- VERSCHAFFELT, E. (1910) The cause determining the selection of food in some herbivorous insects. *Proc. K. Ned. Akad. Wet.* **13**: 536–542.

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