

Pest Control: from Chemical Ecology to Evolution. A Hungarian Perspective

T. JERMY, Á. SZENTESI, M. TÓTH and G. SZÓCS*

Plant Protection Institute, Hungarian Academy of Sciences,
H-1525 Budapest, P.O. Box 102, Hungary

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From 1880, the year of funding the National Phylloxera Research Station, the predecessor of the present Department of Zoology of the Plant Protection Institute, the main thrust of entomological research was towards solving practical problems in agriculture, which mission governs our recent activity and guides our plans for the future.

Our studies on the behaviour of herbivorous insects have shown that oligophagy is mainly due to the sensitivity of the insects' chemosensory system to deterrent chemicals occurring in the non-host plants. This enables the use of antifeedants in pest control. In field experiments the insects found their hosts largely by chance, which has implications for crop rotation. The ability of learning in some herbivorous insect species has been demonstrated. It may result in induced preference for some otherwise avoided plants. Ecological studies indicated that predispersal seed predators do not necessarily affect plant population dynamics and that there is no interspecific competition among them. Studying the presumable processes that drive the evolution of insect-plant associations resulted in elaborating the theory of sequential evolution instead of the theory of coevolution.

In course of 30 year studies, female-produced sex pheromones were evidenced in behavioural studies, isolated, and chemically identified in cooperations with organic chemical laboratories, for a few dozens of lepidopterous species. Related sex attractants were established by means of field trappings for further dozens of species. Based on these results, the role of sex pheromones in maintaining reproductive isolation between taxonomically closely related, sympatric species, as well as the chemotaxonomical value of sex attractants in higher taxa of Lepidoptera are discussed.

As a result of our studies on Elateridae (Coleoptera) we developed and optimized pheromone baits and traps for catching males of all important pest *Agriotes* click beetles in Central and Western Europe. The most effective pheromone combinations for each species were tested in a Europe-wide comparative effort, giving information on the probable importance of the respective species in the respective area.

In Scarabaeidae (Coleoptera) we discovered sex attractants for 3 species of the genus *Anomala*, and floral attractants for 4 species of the subfamily Cetoniinae, all orchard pests damaging fruits or flowers. Traps were developed for these scarabs taking into consideration the optimal visual and chemical cues for each respective species. The trap and bait combinations show preliminary evidence that their use for direct control through mass trapping is possible.

Among chrysomelid beetles, new trap types were developed for the western corn rootworm *Diabrotica v. virgifera*. These trap types are widely used in Europe for the detection and monitoring of the pest. Most recent results concern the relationships between host-plant related and pheromonal communication in flea beetles (*Phyllotreta* spp.).

* Corresponding author

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The National Phylloxera Research Station, founded by the Hungarian Government in 1880 in Budapest, was the predecessor of the present Department of Zoology of the Plant Protection Institute. Although the main task of the Station was developing methods of control against phylloxera that threatened at that time to devastate the vineyards of the country, the scientific staff of the Station began soon to deal with other problems of agricultural and forest entomology. From the first years on the main thrust of research was towards solving practical problems. This trend continued throughout the succeeding institutions such as the Hungarian Royal Entomology Station and finally the present Department of Zoology. It turned out, however, very early that on the one hand, applied entomology research is successful only if it is based on insect taxonomy, ecology, physiology, and behaviour; and that on the other hand, these theoretical branches of science may gain significantly by the results of applied research.

The following annotated list of publications provides a brief review of the main results of the staff members of the Department of Zoology in insect behaviour, ecology, and evolution, obtained during the last decades.

Insect – host plant relationships

Factors determining the relation between herbivorous insects and their host-plants are actually the basic subjects of agricultural entomology. Revealing the nature of these factors help developing new control measures against pest species, but it enables also answering more general biological questions. The publications reviewed below present the results of mainly theoretical studies on behavioural, ecological and evolutionary aspects of insect-plant relations.

Behavioural aspects

The ultimate factor governing plant-insect interactions is plant chemistry. Plants possess a wealth of compounds produced in the process of secondary metabolism whose one of the several roles is to provide resistance to plants against insect consumption. This fact makes possible to modify host seeking and acceptance behaviours by the application of chemicals of plant or of synthetic origin.

Approximately 80% of phytophagous insect species have restricted host-range (Schoonhoven et al., 1998), i.e. they feed on a limited number of plant species within a plant family. Inhibitors of feeding (Jermy, 1958, 1961a,b) or oviposition (Jermy and Szentesi, 1978) of oligophagous herbivorous insects were demonstrated and their practical application explored theoretically (Jermy, 1966, 1971, 1983, 1990; Schoonhoven and Jermy, 1977; Szentesi and Jermy, 1985).

Behavioural modification of responses by insects to substances negatively affecting feeding is possible through experience. Although insects are usually considered as organ-

isms of limited capabilities to change behaviour due to learning, a surprisingly rich repertoire is available for them (Szentesi and Jermy, 1990). Among such responses habituation to feeding deterrents (Jermy et al., 1982, 1987; Szentesi and Bernays 1984) and induced preference (Jermy et al., 1968) to a particular host can substantially alter host-related behaviour. It is further assumed that the above behaviours coupled with alleles whose spread in a population confers advantage to an insect population might change responses to resistant crops.

Besides feeding and oviposition, the study of a couple of other complex behavioural patterns might provide perspectives for future pest control manipulations. With such ideas in mind we made investigations on the sex-related behaviour (Szentesi, 1985; Jermy and Butt, 1991), on spatial orientation to host plants (Jermy et al., 1988), on oviposition deterring pheromones (Szentesi, 1981), on difference in feeding behaviour among populations (Szentesi and Jermy, 1993), on visual stimuli affecting orientation to food or to sexual partners (Szentesi et al., 1996a, 2002), and on clutch size determination (Szentesi, 2003).

Among the results of the studies on insect behaviour three are highlighted that have been studied for the first time in the field of plant-insect interactions in the Plant Protection Institute: (1) The importance of inhibitory stimuli in determining host range of herbivorous insects. The idea that host specialisation is asymmetric at the sensorial level, i.e. herbivorous insects confer greater significance to chemicals negatively affecting acceptance and feeding (or oviposition), has since gained general acceptance. (2) Induced preference that is capable to restrict host range of some herbivorous insects to a particular plant species and might cause “starvation-to-death-at-Lucullian-banquet” (Jermy, 1987). (3) Habituation to deterrents that enables herbivorous insects to tolerate feeding inhibitory substances. Its role in the host selection process among natural vegetation might be equally important.

Ecological aspects

Insect ecology research of the last decade was concerned with the ecology of pre-dispersal seed predators. We found that seed shape of leguminous plant species and bruchid body size were fairly good predictors of bruchid infestation patterns at plant tribe, species and sample (locality) levels. It was also concluded that the evolution of the seed size of plant species studied is not likely driven by bruchids or by other seed predators (Szentesi and Jermy, 1995). Pre-dispersal seed predators consume developing seeds on the host-plant and might cause substantial decrease of individual plant fitness (Szentesi, 1999). However, the cause of low levels of recruitment in a plant population can be limitation not only in seed number, but in the availability of micro-sites suitable for seed germination. In a field experiment (Szentesi and Jermy, 2003) it was shown that recruitment in a *Vicia angustifolia* population was determined by seed limitation, however, not caused by pre-dispersal seed predators. Perennial host plants provide predictable food sources for guilds of pre-dispersal seed predator insects (Szentesi et al., 1996b). A null-model approach indicated the lack of interspecific competition among pre-dispersal seed predators either at the species- (bruchids) or at the family-level (bruchids, curculionids and lepidopterous insects) and suggested a different assembly rule for the guild (Szentesi et al., 2006).

Evolutionary aspects

Coevolution of plants and herbivorous insects based on an ‘arms race’ between the two partners has long been the generally accepted explanation of the evolution of insect-plant associations. Our theoretical analyses of extant insect-plant relations have questioned the overall validity of the coevolutionary theory and have proposed instead the theory of sequential evolution the main points of which are as follows. (1) Host specificity is primarily a behavioural trait of herbivorous insects governed by the nervous system. It means specificity in plant recognition that is based on the information provided mainly by the chemoreceptors. Therefore the non-host plant species are not necessarily ‘resistant’ to or ‘defended’ against the insect species that avoid them rather they are not recognised by the insects. (2) The evolution of a new insect-plant association, i.e. a host shift, is propelled by a hereditary change of the insects’ nervous system that results in a change of the plant recognition trait. If repeated host shifts occur to A, B, C, etc. plant species that are congeners of the parental plant species, congruent insect-plant phylogenies would be the outcome. The more distant the relation of the plant species involved the more incongruence would result. The former case has been called *sliding host shift*, the latter *jumping host shift*. (3) Plant evolution provides an immense variety of specific resources that are sequentially occupied by the radiating herbivorous insects while the herbivorous insects do not affect plant evolution (Jermy, 1976, 1984, 1988, 1993; Jermy et al., 1990; Jermy and Szentesi, 2003; Schoonhoven et al., 1998).

Pheromonal communication of insects

If disciplines had birthday, insect chemical ecology surely dated it from the identification of the first insect sex pheromone (silkworm, *Bombyx mori*) (Butenandt, Z. Naturforsch., 14B, 283, 1959), although the term of “chemical ecology” itself was much later introduced (Ritter, Chemical Ecology. Elsevier, Amsterdam, 1979). However, the fascinating progress in chemical ecology happened only many years later, as a result of mutually stimulating interactions of various disciplines, such as ultra-micro analytical chemistry of insect-derived, behaviour-mediating components, insect’s behaviour, -ecology and evolution. This changing international scenario posed the questions to us: “*Shall Hungary simply adopt ready-made results produced abroad, or initiate his own, original basic research?*” Hungary answered this question by actively joining to the international trend: chemical ecology, as a new discipline was launched at the Department of Zoology. Rooting in long tradition of taxonomical and ecological studies, insect chemical ecology soon started to flourish. We resume below some of our most significant results in studying pheromone-mediated communication of Lepidoptera and Coleoptera.

LEPIDOPTERA

Pheromone studies were initiated on Lepidoptera, however, even in the seventies, when we joined to this line of research, the scope of this field waited for discovery. Our key to progress was fruitful, multidisciplinary collaboration with chemical and ecological

laboratories around the World, and establishment of instrumentation totally new at that time to traditional Hungarian entomological laboratories (gas chromatograph linked to electroantennographic detector, insect flight tunnel). Grouping of our results illustrates the manifold facets of this field of research.

Identification of pheromones of lepidopterous species

It was only in the late seventies when the number of publications reporting on pheromone identifications slowly started to increase in the world-leading entomological journals. Therefore it was an important break-through for the Hungarian entomological research, when we managed to evidence the presence of a female-produced sex pheromone in the cabbage armyworm, *Mamestra brassicae* L. (Noctuidae) (Szentesi et al., 1975), followed by the chemical identification (Novák et al., 1979). Studying the pheromone-mediated mating system and performing the extraction and chemical analyses hand-in-hand resulted in success first in species belonging to the family Noctuidae (an example, the silver-y-moth, *Autographa gamma* L.: Szőcs and Tóth, 1979; Tóth et al., 1983), soon followed by publications on members of other, neglected families, such as Geometridae (Szőcs and Tóth, 1978). This epoch is highlighted by pioneering results in identifying the structure of pheromones in some lepidopteran families, studied by us among the firsts, and also by the novel chemical structures identified by us in international cooperation. One of the first identification in Geometridae revealed a diunsaturated hydrocarbon with a ketone group for the first time (Buser et al., 1985), in Old-World Sesiidae a new octadecadienal was first found (Szőcs et al., 1985), while in the ancient family of Nepticulidae a secondary alcohol, a completely new structure of the that time known Lepidopteran pheromones, was revealed (Tóth et al., 1995). Field screenings of series of trap baits consisting of new mixtures of known pheromone components, allowed us to describe powerful sex attractants for males of a number of lepidoperous species (Szőcs et al., 1981).

Intraspecific geographic variation: rule or exception in the pheromone systems of lepidoptera?

While the pheromone system of insects should be highly conservative to ensure mate finding and reproduction, evolutionary processes certainly take place on a long-term time scale. Pheromone-polymorphism within geographically isolated populations of a species can be taken as a sign of this phenomenon. However, this is well documented only by extremely few cases. We contributed to these examples by demonstrating in the turnip moth, *Agrotis segetum* Den. et Schiff. (Noctuidae) that whereas there are only subtle differences between the populations in Europe and Asia and in Africa North to the Equator, the populations South to the Equator in Africa are markedly different (Tóth et al., 1992). In the currant borer, *Synanthedon tipuliformis*, Cl. (Sesiidae) we found that its populations in Europe, which fell into the original distribution area of the species, are fairly uniform. Similarly, the populations in Canada and New Zealand, to which places this pest was incidentally introduced, are similar to those in Europe (Szőcs et al., 1991a; Szőcs et al., 1998). In contrast to this, the population in Tasmania, which was established also as a result of an introduction, represent a different pheromone-strain (Szőcs et al., 1990).

Reproductive isolation by pheromones between closely related lepidopterous species

The sibling pair of sympatric *Diachrysia chrysitis* L. and *D. tutti* Kostrowicki (Noctuidae) use the same two components, chemically positional isomers of monounsaturated decyl acetate, in different ratios, as their respective sex pheromone. However, as for the males captured in traps baited with these components in various ratios, we found some overlapping, reflecting an early evolutionary stage of split (Löfstedt et al., 1994).

The sympatric feathered thorn moth, *Colotois pennaria* L. and mottled umber moth, *Erannis defoliaria* Cl. (Geometridae, Ennominae), both flying in November, use opposite enantiomers of (3Z),(9Z)-6,7-epoxynonadecadiene, as their respective main pheromone component (Szőcs et al., 1993). Moreover, their isolation is corroborated by a reciprocal inhibition by the opposite enantiomers (racemic mixture hardly attracts males of these species). A third closely related, sympatric species, *Agriopsis (Erannis) marginaria* F. is isolated from the two above-mentioned species by its flight period in March. Whereas both *E. defoliaria* and *A. marginaria* use the same enantiomer, the latter species can equally well be trapped also by the racemic mixture (Szőcs et al., 1993), showing that there is no evolutionary pressure on *A. marginaria* to be discriminating in the lack of other species which would use the other enantiomer. Males of *E. tiliaria* Harr., the New-World sibling pair of *E. defoliaria*, exhibit a similar enantiomeric preference and attraction-inhibition, as *E. defoliaria* (Szőcs et al., 2001), showing that geographic isolation and not the chemical structure of the pheromone serves as a barrier between these species.

The reproductive isolation between the co-flying northern winter moth, *Operophtera fagata* Scharf. (Geometridae, Laretiinae) and the common winter moth *O. brumata* L., which share a pheromone component, is maintained by a minor pheromone component of the former species, essential for attraction of conspecific males, but inhibitory for males of the other species (Szőcs et al., 2004).

Taxonomic, faunistic and chemotaxonomic relevance in lepidoptera

Systematic field screenings with new combinations of known pheromone components allowed us to describe a powerful male sex attractant for an unknown tineid species, that was later described exclusively from male specimens collected by pheromone traps as a genus and species new to science, under the name of *Matratinea rufulicaput* Sziráki et Szőcs (Sziráki, 1990). Some species new to the Hungarian fauna were also found (Sziráki and Szőcs, 1989). Chemotaxonomic relationships between tineids and sesiids, based on sex attractants newly discovered by us, are discussed by Szőcs et al. (1989), while the chemotaxonomic value of sex pheromones and -attractants on the level of subfamilies of Geometridae is discussed by reviewing literature data by Szőcs et al. (1991b).

COLEOPTERA

Based on our experience and methods developed for the study of Lepidopteran pheromones, our laboratory started to study the chemical communication of selected beetle pests (Coleoptera) in the early nineties.

Elateridae

Wireworms, the larvae of click beetles, rank among the most important soil-dwelling agricultural pests worldwide. In most countries insecticides are applied to soil on a schedule, without actual risk assessment of wireworm damage, mostly because of the clumsiness and labor-intensiveness of conventional methods of population sampling and density estimation for these pests. Trapping the adults could assist in making long-term forecast decisions (more than a year) on the need for soil insecticide treatments in the area in question. Similar to other groups of insect pests, sex pheromone baited traps would be ideal monitoring tools (Furlan et al., 1996, 1997).

In the course of our studies we identified the pheromonal composition of *Agriotes brevis* Candèze and *A. sordidus* Illiger, and defined powerful new sex attractants for *A. rufipalpis* Brullé and *A. proximus* Schwarz (Furlan et al., 2004, Tóth et al., 2002a, b). In the cases of *A. lineatus* L., *A. ustulatus* Schaller, *A. sputator* L. and *A. litigiosus* Rossi our laboratory improved the performance of previously described pheromone compositions (Tóth et al., 2003d) or corrected false identifications by other authors. In *A. obscurus* L. our results confirmed pheromone compositions described earlier, and as a consequence we developed pheromone baits and traps for catching males of all important pest click beetles in Central and Western Europe (Furlan et al., 2001, 2002; Tóth et al., 2003d). Finally, the most effective pheromone combinations for each species were tested in a Europe-wide comparative effort, giving information on the probable importance of the respective species in the respective area (*Fig. 1*) (Tóth et al., 2003e; Tóth and Furlan, 2005).

Scarabaeidae

There are several European scarab pests which may cause significant damage to orchard cultures or vineyards. In case of some of these damage caused by adult beetles is more important than larval damages. Our laboratory started to study the chemical communication of such scarab pests in order to develop semiochemical-baited traps for the capture of the adults. In contrast to the widely used pheromone traps for moth spp., in this case, since the traps are capturing the damage-causing life stage, we hoped that opportunities may evolve for the application of such traps beyond detection and monitoring also for directly decreasing the damage levels through mass trapping.

A large capture capacity, modified funnel trap design codenamed “VARb3” has been developed which proved to be highly effective for the capture of scarabs in the course of tests with several species (Imrei and Tóth, 2002; Schmerra et al., 2004).

Powerful male attractants have been discovered as (*E*)-2-nonen-1-ol for *Anomala vitis* Fabr. and *A. dubia* Scop. (Tóth et al., 1994), and as (*R,Z*)-5-(*–*)-(oct-1-enyl)-oxacyclopentan-2-one for *A. solida* Er. (Tóth et al., 2003a) (Coleoptera, Scarabaeidae, Rutelinae). All three species are known to cause leaf damage in orchards and vineyards. More recently, *A. vitis* has been reported also to feed on ripening peaches, making the fruit non-marketable (Voigt and Tóth, 2000). Preliminary perimeter trapping experiments against *A. vitis* and *A. dubia* showed promise in keeping the fruit damage levels below the economic threshold in peach orchards (Voigt and Tóth, 2002). In sour cherry nurseries perimeter trapping on its

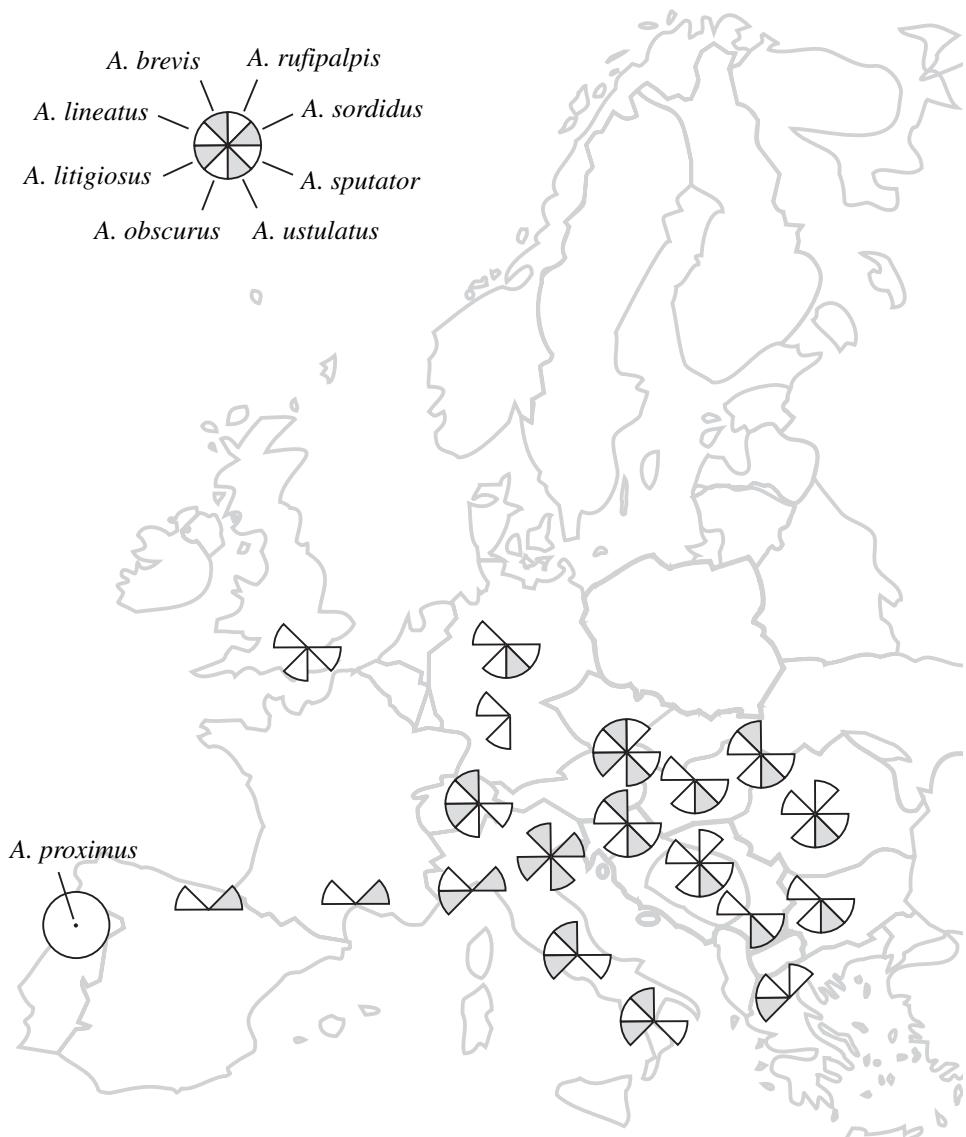


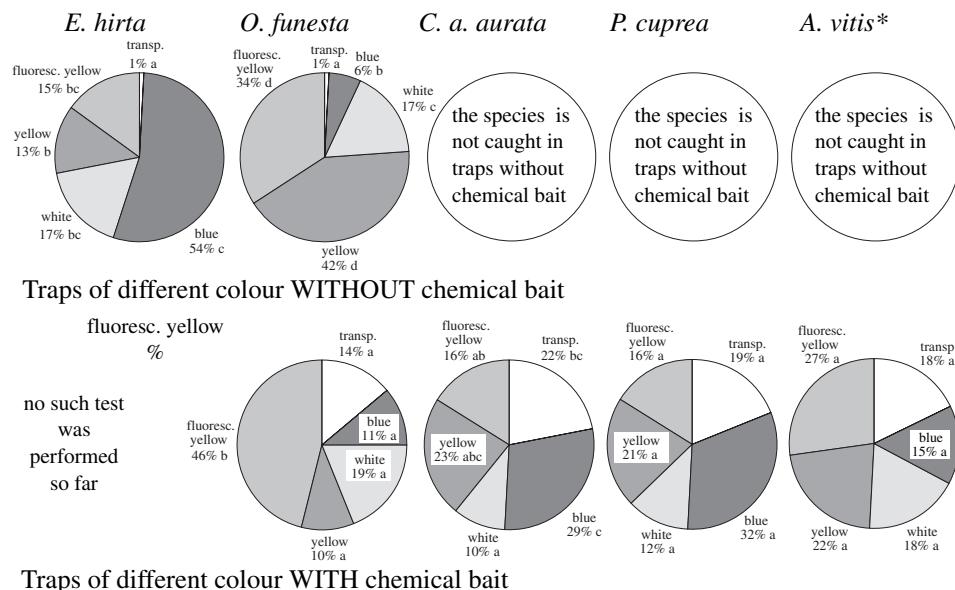
Fig. 1. Catches of click beetle spp. in traps baited with their respective pheromone baits in parallel tests of all pheromone compositions at experimental sites in different countries of Western and Central Europe. Data from Tóth and Furlan (2005)

own did not give sufficient reduction, but it may be possible to significantly reduce the amount of insecticide used through treating only the close vicinity of attractant dispensers (lure and kill) (Voigt and Tóth, 2004).

A synthetic floral attractant has been developed for catching *Epicometis (Tropinota) hirta* Poda (Coleoptera, Scarabaeidae, Cetoniinae), as the mixture of cinnamyl alcohol and (*E*)-anethol (Tóth et al., 2003b, 2004). The adults of *E. hirta* may cause significant damage to blossoming orchard trees, to ripening strawberries and similar berry fruits. The adults of *E. hirta* are sensitive also to bright colours. We optimized a trap combining the optimal visual cue (light blue) and the chemical attractant (Schmera et al., 2004). Preliminary results show promise for its use as a mass trapping tool in strawberries.

A ternary floral attractant was defined and optimized for *Cetonia a. aurata* L. and *Potosia cuprea* Fabr. (Coleoptera, Scarabaeidae, Cetoniinae), consisting of (*E*-anethol, 3-methyl eugenol and 1-phenethyl alcohol (Imrei et al., in preparation). These cetonins are known flower devastators and may cause in draught years also severe fruit damage to ripening fruits (i.e. peaches) (Voigt et al., 2005).

It is of high interest that colour preference of these scarabs may be different in the absence or presence of a synthetic floral attractant (Fig. 2). *E. hirta* never goes to the transparent traps in the absence of the attractant, but it shows a very strong visual response to blue, and quite strong responses to other colours tested, too. The closely related *Oxythyrea funesta* Poda clearly prefers yellow colour hues when a chemical bait is not present. When traps are with floral bait, outstanding responses are recorded in fluorescent yellow traps. *C. a. aurata* and *P. cuprea* do not show any response to any of the colours when there is no chemical bait. When traps are baited, however, these latter spp. also show a



Traps of different colour WITH chemical bait

Fig. 2. Distribution of catches of some scarabs in VARb3 traps of different colour, with or without synthetic floral bait optimized for the respective species. Segments with same letter within one diagram do not differ at $P=5\%$ by ANOVA, Games-Howell (after Tóth et al., 2006).

* in this case the *A. vitis* pheromone bait was used as bait

slight preference for blue. For comparison, in *Fig. 2* we include also responses of another daytime-active scarab, *A. vittis* to traps of different colours baited with the sex pheromone. In this case responses do not show significant preference to any of the colours. (Naturally, traps without the pheromone bait do not capture any *A. vittis*.) The lack of colour sensitivity in *A. vittis* could be explained by the fact that in this case we deal with sexual communication, where probably visual cues have only short-range importance if any, while in the other cetonians orientation towards feeding sites (i.e. flowers) may be significantly affected by processing visual information from the environment, which is supplemented by chemical information from floral scents (Tóth et al., 2006).

Chrysomelidae

Our investigations on chrysomelids were triggered by the unexpected introduction of the western corn rootworm (*Diabrotica v. virgifera* LeConte) into Europe in the early nineties near Belgrade, Yugoslavia. Baited with dispensers containing the already known sex pheromone (Guss, J. chem. Ecol., 8, 545, 1982), we developed and optimized a sticky trap design codenamed "PAL", which proved to be highly sensitive for the detection of the corn rootworm (Tóth et al., 1996, 2003c). The EU-research project DIABROTICA (QLK5-CT-1999-01110) recommended to use PAL traps baited with pheromone as the standard detection tool for *D. v. virgifera* in Europe. Since sticky traps are not suitable for the study of quantitative aspects due to the fact that their efficiency constantly changes over time, our laboratory developed the non-sticky, high capture capacity modified funnel trap type "VARs+" (Tóth et al., 2000a, b), which, when baited with pheromone plus an already known floral attractant (Metcalf, J. chem. Ecol., 21, 1149, 1995) catches both sexes of the corn rootworm in the natural sex ratio (Imrei et al., 2002, Tóth, 2005). In 2005, our laboratory introduced a female-targeted non-sticky trap of novel design, the KLP ("hat") trap, which, when baited with the floral bait caught females in the highest percentage among all other corn rootworm trap designs tested (Tóth et al., 2005a).

One of our most recent projects on chrysomelids include studies on chemical communication of cabbage flea beetles (*Phylloptreta* spp., Chrysomelidae) (Csonka and Tóth, 2005). Already the first results demonstrated that there was a connection between pheromone-related and host-plant related communication in these beetles (Tóth et al., 2005b), which phenomena deserve further scrutiny.

Pest control: from new pheromone traps to improved IPM stategies

Methodology of how to best use pheromone traps in monitoring pests is dealt by Farag et al. (1985) and by Szőcs et al. (1995). In the frame of biological control projects, we developed sex attractant traps for monitoring the spread of beneficial biocontrol agents, such as *Agapeta zoegana* Haw. (Cochylidae) introduced against the knapweed, *Centaurea diffusa* Lam. and *C. maculosa* Lam. in Canada (Tóth et al., 1985), and for *Agonopteryx ulicitella* Stainton (Oecophoridae) against *Ulex europaeus* L. in New Zealand

and Hawaii (Suckling et al., 2000). However, the major benefit of our knowledge has been put into practice by providing farmers complete set of pheromone traps and advisory materials, which can be ordered from our institute on a non-profit base, under the aegis of our extension service “CSALOMON®” (www.julia-nki.hu/traps). This activity includes continuous chemical and biological quality control of lures. As a result of development of the design of trap bodies, large-capacity funnel traps, suitable for precise quantitative monitoring, are available for a number of pests. Broadening our basic studies towards plant volatiles (allomones and kairomones) enabled us in some cases to develop traps attracting also female insects. The more farmers incorporate our traps into the monitoring system, the safer the product and healthier our environment will be.

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