Insect senses and preferences

Prof.dr Joop J.A. van Loon

Farewell address upon retiring as Professor of Entomology at Wageningen University & Research on 6 September 2024

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Photo: Hans Smid

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Madam Rector, colleagues, ladies and gentlemen,

Insects are small invertebrate animals that share a number of basic features in morphology and anatomy, the main ones being that adults have six jointed legs and two pairs of wings. Apart from this common body structure, among insects very diverse life styles, food sources, behaviours, and reproductive strategies have evolved over some 480 million years of evolution.
The animal class of Insecta comprises by far the highest number of animal species (currently 1,050,000 taxonomically described) and with the total number of species estimated to be about 4 - 5 times as many[1]: we still may know only 20% of the insect species living on the planet. Out of every 1000 animal species, 800 are insect species.

Ecological significance of insects
Insects fulfil vital functions in natural terrestrial ecosystems, in particular in plant reproduction and in the decomposition of organic matter[2,3]. In agricultural ecosystems predatory and parasitic insects and other arthropods provide natural control of animal organisms that attack plants, animals or humans[2-4]. Some 5000 species are considered to cause damage to agricultural crops and animal and human health, *i.e.* 0.5% of the 1,050,000 insect species.

Food sources utilised by insects
Insects exploit highly diverse food sources that differ in nutritional composition, consistency, and availability. Various types of food source utilised by larval and adult stages of species belonging to 876 insect families are listed in Table 1. Mixed use of food sources is common, *e.g.* seven families of beetles (comprising *ca.* 85,000 species) feed as larvae and/or adults on both fungi and detritus. Some insect taxa are considered food generalists; these are found among earwigs (order Dermaptera), cockroaches (Blattodea), and flies (Diptera).
In particular among plant feeders and parasitoids, a high degree of food specialisation is observed. Among plant-feeding species, ca. 80 % feed from only one or a few closely related plant species belonging to the same plant family or a phylogenetically closely related family producing similar secondary chemicals[2]. The dominance of dietary

specialisation is one of the intriguing features of insect biology and various physiological, ecological, and evolutionary explanations are found in the literature.
Entomologists specialise in the study of insect biology and ask questions such as: how do specialist species find their preferred host plants, hosts or prey? How are physical and chemical features of food perceived by insects? Which sensory organs and receptors respond to these features?

Table 1 – Food sources of larval and adult insects, the terms used for the corresponding insect feeding guilds and the percentages of species utilising these sources (modified after[5]).

Food source	Feeding guild	Larvae (%)	Adults (%)
Plants	Herbivores	35	22
Insects and other animals[1]	Carnivores	30.5	17.5
Decaying organic matter[2]	Detritivores, scavengers	22	18
Fungi[3]	Fungivores	12.5	10
Liquids[4]	Nectivores a.o.	-	25.5
Non-feeding	-	-	7

Notes: 1 - including ectoparasites; 2 - of microbial, plant or animal origin; 3 - living fungi or having a symbiotic relationship with fungi for food digestion; 4 – a.o. and others; nectivores imbibe (extra)floral nectar, other species consume liquid products of decay, honeydew or host hemolymph.

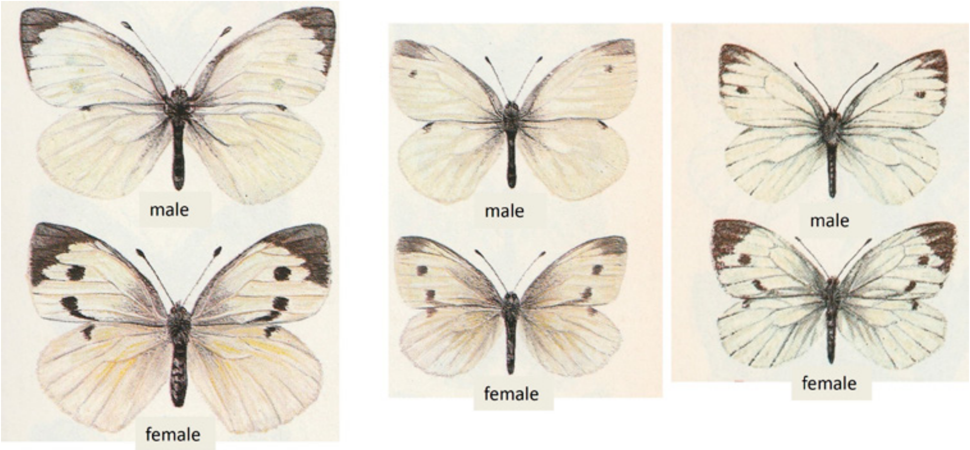
In addition to questions about how insects function in terms of physiological and molecular mechanisms, questions about insect evolution are addressed also, *e.g.*: why is specialism dominant among plant-feeding insects and parasitoids? Which selection forces have driven the strong diversification of insects?
Answers to such fundamental questions are not only nice to know, they are needed to understand how insect preference behaviour is caused and how it evolves[2,3]. Such insights are helpful for developing knowledge-based applications in protection of crops against damage by herbivorous insects and mites and protection of animals and humans against infectious bites of blood-feeding insects.

In this lecture I will focus on insect senses and behaviour. I subdivided the lecture in three sections according to the kind of food used: plants, human blood, and decaying organic matter.

Herbivores – cabbage white butterflies

Host-plant selection of cabbage white butterflies

First I will give an account of our current understanding of the sensory physiology and behaviour of a group of phylogenetically closely related butterflies belonging to the family Pieridae, the cabbage whites (Fig. 1). The life cycle of a cabbage white butterfly has four main stages: adult, egg, larva, which has five instars, and pupa. In the temperate areas of western Europe, cabbage whites eclose as adults from their pupal case in spring.



Large cabbage white
Pieris brassicae L.

Small cabbage white
Pieris rapae L.

Green-veined white
Pieris napi napi L.

Figure 1. Males and females of three cabbage white butterfly species commonly co-occurring in western Europe.

The primary task in adult life is to find a mate to ensure sexual reproduction and the primary sense involved in this is vision. Visual detection of another flying white insect induces approach of a female by a male. In close proximity of each other, in the range of a few centimeters, chemical cues come into play that have a role in sexual selection. These chemical signals are so-called aphrodisiac pheromones, released into the air by the male from specialised plumose scales on its wings, to induce the female, after a phase of spiralling around each other in flight, to settle on a plant after which the male will attempt to mate. Different species of *Pieris* butterflies employ chemically different aphrodisiac molecules that share their biosynthetic origin (Fig. 2). For the identification of these chemical signals a combination of research techniques was used: behavioural bioassays, electrophysiological assays, chemical analysis, and chemical synthesis[6].

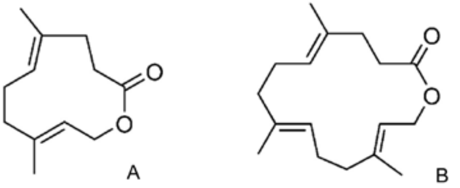


Figure 2. Molecular structures of aphrodisiac pheromones. A: ferrulactone emitted by males of the small cabbage white, Pieris rapae*; B: brassicalactone, emitted by males of the large cabbage white,* Pieris brassicae*.*

Within a day after mating and fertilisation the female starts to search for host plants to deposit her eggs on. The female needs to locate a plant that belongs to the family Brassicaceae, the mustards and cabbages, among which are many important vegetable crops. For egg-laying and larval feeding, cabbage whites do not accept plants belonging to other plant families, except for a few other families that also contain glucosinolates. The interaction between *Pieris* species and its host plants is one of the best-studied examples of specialism on plant family-level[7].

How do female cabbage whites select their preferred host plants in a diverse vegetation?
The female butterfly uses in overlapping sequence optical cues, *i.e.* the colour green of leaves, chemical cues, *i.e.* volatile compounds that are released from leaves and flowers, and after alighting on a leaf, the tactile cues of the leaf surface and compounds present in the leaf cuticle (Fig. 3).

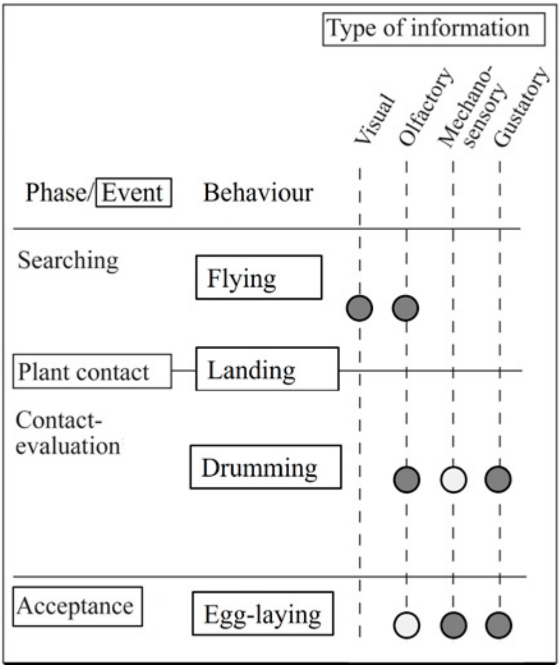
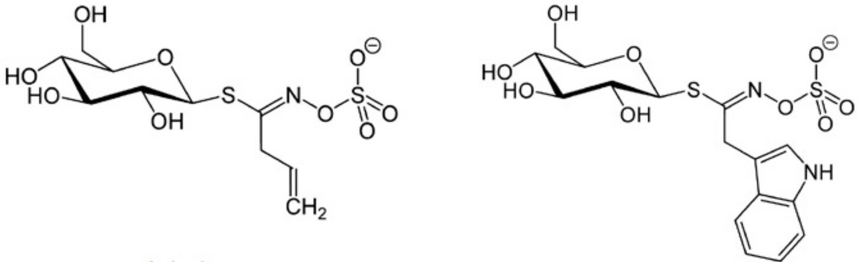


Figure 3. Scheme of host-plant selection behaviour sequence of cabbage white butterflies. Left column: behavioural phase or event. Middle column: corresponding behavioural acts observed. Right column: plant-derived stimuli affecting the behaviour. Dark grey dot = experimentally proved plant cue affecting the behaviour; light grey dot: suggested cue affecting the behaviour.

The flying female is attracted by green objects and detects plant volatiles with olfactory neurons that innervate multiporous hair-shaped sensilla on the antennae.

When a cabbage white female is flying toward plants, it often lands on non-host plants and even when flying over a patch of brassicaceous host plants she may land first on several plants and perform sensory evaluation by so-called ‘drumming’ with the tarsi of the forelegs on the leaf surface before she decides to lay an egg. What is the function of tarsal drumming? The butterfly legs carry sensory hairs that have a single pore at their tip: these are sensilla that contain sensory neurons that are sensitive to dissolved compounds: taste neurons. The legs carry in total 2,100 taste neurons, all of which project to a single large ganglion, situated below the foregut (suboesophageal ganglion) and connected with the brain in the head.

Which plant compounds do these taste neurons detect? A combination of phytochemical fractionation, analysis, and testing their activity in behavioural assays has pinpointed glucosinolates (Fig. 4) as the plant compounds that trigger egg-laying in several species of cabbage white butterflies and other herbivorous insects specialised on Brassicaceae[8,9]. One type of taste neurons in the taste hairs on the legs only responds to these compounds. Glucosinolates are a family of some 120 secondary plant compounds that are characteristic of the Brassicaceae and serve the plant as chemical defenses against plant-feeding animals, bacteria, and fungi. However, a small number of specialised species, such as several cabbage white butterflies (family Pieridae), have evolved biochemical mechanisms to detoxify these defensive molecules[9]. Different *Pieris* species differ in their sensitivity profiles to glucosinolates and also at the sub-species level sensitivity profiles differ significantly[10]. Only a few years ago the molecular receptors in the dendrites of the tarsal taste neurons, seven-transmembrane proteins, for one of the most wide-spread glucosinolates, the



sinigrin

glucobrassicin

Figure 4. Molecular structures of two glucosinolates commonly found in Brassica species. The two compounds differ in the side chain extending from the S-C=N arrangement: a three-carbon aliphatic chain in sinigrin and a tryptophane-derived group in glucobrassicin.

compound sinigrin, responsible for the pungent taste of mustard, has been identified in adults of the small cabbage white *Pieris rapae*[11]. Based on DNA-sequence identity of the genes coding for the receptor protein its evolutionary origin is likely in broad-spectrum molecular receptors that detect secondary plant compounds, so-called bitter receptors that detect a wide variety of secondary plant compounds.

The interactions between *Pieris* butterflies and brassicaceous plants have been, and continue to be, a fruitful model system for specialised insect-plant interactions. The dominance of specialism implies adaptive advantages of specialism. In the literature several adaptive advantages of specialism at plant family, genus or species level are advocated: coping with toxic secondary plant metabolites, the glucosinolates in the case of *Pieris*, avoidance of food competition and reduced mortality from predation.

Thus far I have presented what we know about the recognition of host-plants at the plant family level by a group of specialised butterflies. Host-plant preference behaviour of these butterflies and other insects is more highly evolved than the ability to tell the host-plant family apart from all other plant families: insects can sense subtle differences between chemical blends they encounter in their foraging environment. Based on detailed behavioural studies it is well established that the integration of visual, odour, and taste information enables plant-feeding insects to discriminate among individual plants within a plant species that differ in plant physiological condition as affected by, for example, plant nutrient status, photosynthetic capacity, plant hormone concentrations, past feeding damage and presence of competitors, even of non-feeding stages such as insect eggs [12,13]. Focussing on neural processing of odour information encoded by the hundreds of antennal sensilla harbouring several thousands of odour-sensitive neurons that send their axons to converge into a much smaller number of spherical structures in the antennal lobe called glomeruli; in butterflies and moths there are 50 – 70 glomeruli[14,15]. For comparison, in the antennal lobe in the brain of *Cotesia* parasitoid wasps, the most important natural enemies of cabbage white caterpillars, we found 180 glomeruli[16], a number similar to that found in one of the best studied insects, the honey bee *Apis mellifera*[14]. Such large differences in the number of the neuroanatomical structures involved in primary olfactory processing suggest that the complexity of the chemical information used in behavioural decision-making differs among insect species and is likely associated with the chemical diversity of the food source used and of the environments in which it occurs.

Learning in oviposition behaviour

Insect behaviour is genetically determined, however, it can be modified by experience. Host-plant preferences within the range of accepted plants are not fixed but flexible, they show phenotypic plasticity. The butterfly taste system is involved in associative learning between leaf colour and stimulatory or inhibitory taste cues[17] and between odour detection and taste cues[18]. Recent experiments in our laboratory have demonstrated that the strength of the association between a volatile cue and egg-laying preference is affected by the concentration of the glucosinolate detected by the taste neurons on the legs[18]. What is the adaptive adavantage of associative learning in oviposition behaviour? Time is a major constraint in insect life, most species are short-lived; butterflies for example live just a few weeks. Associative learning reduces the time-investment in selecting a suitable oviposition site. It increases the likelihood of landing on a proper host plant and thereby saves the energy needed to take off from a plant that, after tasting, turns out to be a non-host plant. Associative learning has been demonstrated in many insect species and has been studied in most detail in honeybees and parasitoid wasps; *Pieris* butterflies and parasitoids are still studied in our laboratory[18,19].

Plant responses to insect feeding: herbivore-induced plant resistance

Insect-plant research investigates both partners in the interaction. In this address I focus on the insect side, however, the responses of plants to attack by plant-feeding insects, so-called herbivore-induced responses, is a very productive research field[20].

Insect eggs do not damage the plant yet, nevertheless the plant senses if eggs have been deposited and molecular response cascades are initiated. Internal plant chemistry as well as the odours emitted change[12,13]. In some *Brassica* species a so-called hypersensitivity response against *Pieris* eggs occurs, involving plant tissue necrosis under and around the eggs; this response is specific to *Pieris* eggs and is not observed in response to eggs of other insect species tested[21].

Then the neonate caterpillars hatch from the eggs and start chewing the leaf; plant cells are ruptured, leading to wound reactions. These wound reactions involve dynamic cascades of molecular responses mediated by plant hormones such as jasmonic acid and salicylic acid by which the expression of hundreds to several thousands of genes is changing[22,23]. Transcriptomic analyses of gene expression have become standard in the field and yield a wealth of data on which genes change their expression activity and when. These plant responses do not only occur at the site of damage but occur systemically throughout the plant, endowing leaves, roots or fruits that have not yet been damaged display increased resistance to insect attack.

Metabolomics

Which plant compounds cause increased resistance, and linking to the part on host-plant selection, what is the composition of the blend of chemicals that tells the full message the insect requires to take an optimal behavioural decsision? To answer these kinds of questions metabolomic approaches are very informative. All organic chemical compounds present in plant tissue or emitted as volatiles are quantified[24]. The outcomes are lists of plant compounds, often dozens to hundreds, that differ between intact plants and plants under insect attack, either or not exposed to different environmental conditions such as drought or water stress, soil nutrient levels *etc.* Differential expression of metabolites may be presence/absence, *i.e.* qualitative, and/or concentration, *i.e.*, quantitative, of phytochemicals may explain why an insect species prefers certain plants over others for egg-laying or feeding or why development or growth of larval insects is slowed down compared to that observed on undamaged or non-stressed plants[25].

In practice the number of compounds that differ in presence/absence, in concentration or that remain chemically unidentified is in many cases so high that the necessary next step to pinpoint the main molecules, through formulating a blend that has the full behavioural effect is an unfeasible assignment. In only very few cases the composition of such behaviourally active blends of plant compounds, either volatile or non-volatile, has been unravelled[20, 26,27]. Identification of the main active compounds may also shed light on the question if there are links between the signalling function of a compound and its value as an indicator of host-plant quality. If such links are found this provides insight in the adaptive value of responding to certain types of compounds and not to others, in other words in the evolution of selectiveness of the sensory system[7].

From the greenhouse to the field

Initially we studied non-flowering cabbage in greenhouse conditions. In a first study on a non-cultivated *Brassica*, black mustard (*Brassica nigra* Koch), an abundant plant that flowers early, we discovered that the young caterpillars of the large cabbage white left the leaves and moved to flowers to consume these: it turned from a leaf feeder into a flower feeder[28]. Surprisingly, this behaviour had not been described before. We adopted black mustard as a host plant in our field experiments where attack by insects and other animals, temperature, rainfall, and wind are variable and unpredictable. Mustard plants growing in the field harbour a whole community of plant-feeding insects: other lepidopteran species, leaf-mining fly larvae, flea beetles and aphids, parasitoids, predators and flower visitors: plants are by default under multiple attack[29,30].

Plant-associated insect communities differ between years, and are affected by the species of neighbouring plants in mixed vegetation or crops. An intriguing finding was that the sequence and timing of herbivore attack early in the season has a strong influence on the community of insects that builds up during the remainder of the season[31]. Community ecology of Brassicaceae-insect interactions is a flourishing line of work developed by my colleague Erik Poelman[32-34].

Carnivores: malaria mosquitoes

Among carnivorous insects mosquitoes are notorious due to their feeding on vertebrate blood and in the act may transmit infectious diseases such as malaria, yellow fever, and dengue. Similar questions as asked for herbivores come up when attempting to understand their behaviour: which senses are involved, which cues are detected and are used to find a host to get a blood meal from?

By now it is firmly established that host-seeking mosquitoes respond to carbon dioxide as the primary chemical signal exhaled by their vertebrate hosts, however, at closer distance to the host body, they respond to volatiles emanating from the skin[35,36].

Mosquitoes have olfactory sensilla on antennae and palpi. On the mosquito antenna several types of sensilla are found. Electrophysiological studies on the activity elicited by 44 compounds occurring in human emanations identified over 11 response types among the antennal sensilla of females of the African malaria mosquito *Anopheles gambiae*[37]. For comparison with numbers given above for herbivorous insects, in the antennal lobe of *A. gambiae* 60 glomeruli have been identified[38].

Chemical analysis using gas chromatography coupled to mass spectrometry was employed to identify the blend of volatile compounds released by human hosts; a total of *ca.* 350 compounds has been reported in literature[39]. Early on we found that incubated sweat in which bacteria and other microbes living on the human skin were growing, was highly attractive to the mosquitoes in windtunnel assays without a host present, and the main volatile compounds released were ammonia and lactic acid[40]. Based on odour collections from human volunteers, a series of carboxylic acids were found as predominant compounds in the blend. We then combined ammonia, lactic acid, and single carboxylic acids and systematically tested them at different concentrations in behavioural assays in a windtunnel[41, 42]. In this way we arrived at a basic blend of three compounds, ammonia, lactic acid and, surprisingly, the 14 carbon atoms long tetradecanoic acid as the most attractive mix. When released at proper aerial concentrations the three compounds together showed a synergistic action[41]. We used this ‘basic blend’ to build on further to obtain an expanded attractive blend that could compete with the attractiveness of a human being. Such blends have been evaluated in semi-field set-ups and in African villages[43,44]. As a personal note, I have vivid memories of the visits my colleague Willem Takken and I made to a small village near Lake Victoria in the early evening, when we placed the counter-flow traps just outside houses. Next morning at dawn, when we collected the traps we found that each trap contained hundreds of mosquitoes and very few other insect species (Fig. 5). To tell in a nutshell the outcome of a 20-year quest on finding a maximally attractive blend for trapping malaria mosquitoes: we arrived at a blend of seven compounds, all of which are found in human skin emanations; leaving out any of these seven compounds results in significant loss of attractiveness. Although this blend may still not be the full chemical message eliciting maximal attraction, deploying blends with seven or more compounds that need to be released in a regulated way in the field, would from a practical point of view get technically too complicated and too expensive for people in Africa who would benefit most from these kinds of behavioural interventions.

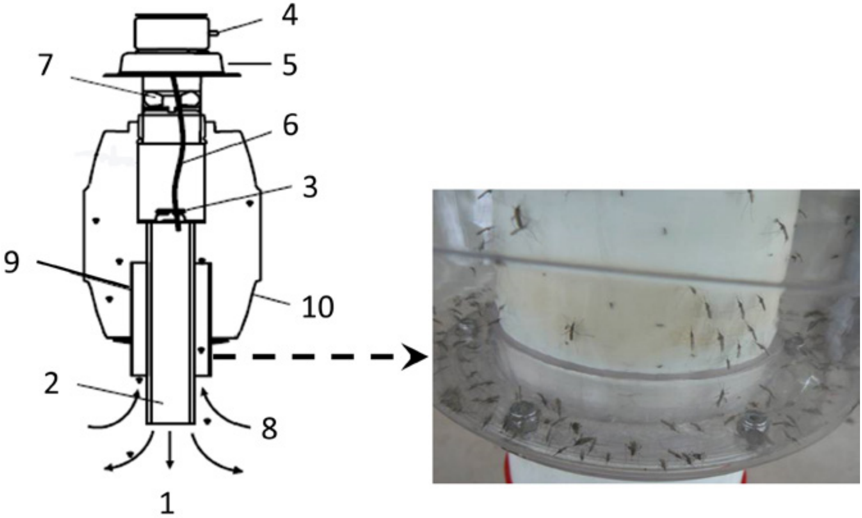


Figure 5. Mosquito trap (sagittal plane) operating according to the counterflow principle: an airstream (1; down- and sideward pointing arrows) flowing out of the central attractant plume tube (2) is generated by a fan (3); to this outflowing air carbon dioxide is added through the gas supply (4) and volatile compounds attractive to mosquitoes are added from slow release materials enclosed in the cap (5) of the trap through the odour tube (6). Simultaneously, an exhaust fan (7) generates suction (8; upward pointing arrows) in a concentric collection tube (9) around the attractant plume tube. When mosquitoes approach the outlet of the attractant plume they are sucked into the collection tube and trapped inside the collection container (10). The stippled arrow points to a photo showing anopheline mosquitoes trapped in the collection container.

The mosquito olfactory system, similar to that of herbivorous species, also responds to volatile compounds that act as repellents, *i.e.*, induce movement away from the source of the volatile, such as a human body, as well as inhibit attraction through interference with host detection and/or biting. Such repellent compounds can be deployed from slow-release dispensing materials and combined with traps baited with attractant blends in so-called push-pull strategies to interfere with mosquito host-seeking behaviour. Such push-pull approaches have been tested on village scale in Kenya and show promise in reducing the number of mosquito bites a person receives[45-48]. Here the challenge is to find strong repellents that escape the development of genetic insensitivity by mosquitoes when deployed on a large scale.

To conclude the first part of this address on insect chemical senses and how they affect preference behaviour, the current understanding is that insects exploit multi-component blends of volatile and non-volatile compounds that they sense with multi-member taste- and odour receptor families expressed in a variety of sensilla on antennae, mouthparts, legs, and ovipositors. Within a fraction of a second they integrate incoming visual, odour, and taste information through designated neural pathways in several brain areas, compare this to memory stored in the mushroom bodies and generate a behavioural decision to lay eggs, to feed or to mate.

Detritivores: insects to convert organic residues to proteins and more

In the last part of this address I would like to focus attention on insect species that evolved to utilise decaying organic matter of microbial, plant or animal origin as food sources; an estimated 200,000 described insect species belonging to various orders use such resources. The reason why we started to study detritivores is that several are edible, *e.g.*, cricket species that are traditionally consumed by indigenous people in Africa, South America, and Asia. A second reason is that they could contribute to nutrient recycling (Fig. 6) and thereby to food security by virtue of their ability to convert decaying organic substrates into high-quality insect proteins, lipids, and other nutrients that they concentrate in their body[49]. Insect proteins are used as efficiently in biosynthesis of human muscle proteins as milk- and egg proteins[50]. Several edible insect species contain appreciable concentrations of minerals such as iron and zinc. Zinc in house cricket tissues is absorbed well in the human gut[51]. Applications in food production are being developed and hold promise to reduce the environmental impact of animal protein production[52].

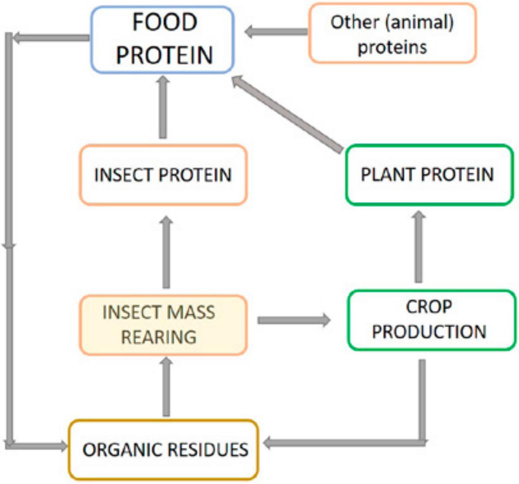


Figure 6. Scheme showing how insect mass-rearing contributes to nutrient production and nutrient recycling. Insects are reared on organic residual material, e.g. from crop production and food (protein) production. Residual material from insect mass-rearing can be fed into crop production as soil amendment.

Decaying organic material has a lower content of essential nutrients than plant material and therefore poses nutritional challenges to insects consuming it as their main food source. Most detritivores have considerably lower growth rates than plant-feeders and carnivores. Among the edible detritivorous insects a few fly species were shown to grow fast compared with crickets and they accept organic residues from a wider variety of origins. By far the most studied detritus-feeding fly species worldwide is the black soldier fly, *Hermetia illucens* L. (Diptera: Stratiomyidae) (Fig. 7). The body of literature on this species has grown strongly over the past decade[53].

Figure 7. Adult black soldier fly, Hermetia illlucens *L.; lateral view. Photo credit Hans M. Smid.*

In nature black soldier fly larvae live in high densities in moist substrates and tend to strongly aggregate. Inside such larval aggregations temperature can rise to 42 °C without lethal effects. Black soldier fly larvae can grow on residues of a diversity of crops, on residues from the food industry, and on manure[54, 55]. Rather than rearing the larvae on a single type of residual stream, several types can be mixed in optimised ratios to improve nutritional suitability of the substrate. Nutritional studies have demonstrated which protein, carbohydrate, and lipid contents of the feed substrate result in maximal growth[56-58]. These larvae display clear preferences for feed *e.g.* when given the opportunity they prefer pig manure over a wheat- and soy-based diet used as starter diet in most commercial rearing facilities[59]. Adult female flies prefer certain substrates for oviposition over others based on the volatiles emitted[60]. Hardly explored compared with herbivorous and hematophagous insect species, chemosensory discrimination abilities seem well-developed in this detritivorous fly.

Insect-microbe symbiosis

A suite of recent studies has demonstrated that the remarkable bioconversion capacity of black soldier fly larvae is achieved in symbiosis with gut microbes and concerted efforts of microbiologists and entomologists are needed to investigate which microbes fulfil which functions in the insect gut[61, 62]. The gut physiology of the fly larvae has evolved to facilitate symbiontic microbes and to kill pathogenic ones. The interactions between microbiomes in the gut and in the feed and detritivorous insects is a rapidly evolving field of study in which genomic and transcriptomic analysis go hand-in-hand with growth, developmental, and behavioural studies to gain insight in how detritivores exploit extremely microbe-rich environments.

From a fundamental perspective the research on the black soldier fly and other edible insect species such as house crickets and mealworms have expanded our insights in insect nutritional biology, immunology, and detoxification capacity[56-58; 63-67] and have revealed a crucial role of microbes in the biology of detritivores[68, 69].

Residues of insect mass-production

After conversion of organic residues by black soldier fly larvae, mealworms or crickets, substantial proportions of the dry matter that was provided to the larvae at the start of mass-rearing remains at the end as ‘residue’, that is a combination of insect faeces, shed insect cuticle, and uneaten feed. To increase the degree of circularity of the conversion process, over the past five years we studied if the residue left after larval rearing could be fed back as fertiliser to crops[70]. Experiments in which we added the residues of insect rearing to soil of cabbage, black mustard, and rape plants resulted in significant improvement of plant growth, improved tolerance to attack by aphids, beneficial effects on attraction of natural enemies of herbivores and pollinators and seed set[71-74]. Changes in the rhizosphere microbiome are observed upon addition of the residue to the soil. First evidence suggests that, apart from mineral nutrition contained in the residue, the microbiome is in part responsible for the favourable effects on plant growth and pollinator attraction (Fig. 8)[73, 74].

Reviewing these encouraging results of soil amendement with residues of insect mass-rearing leads to the notion that during the 20th century, as a consequence of the increasing industrialisation of crop and livestock production, the function of insects as decomposers in agroecosystems has been largely lost; agricultural soil seems deficient in insects, their excreta and their remains. I think it is vital to restore this natural function of insects to increase circularity in agricultural production.

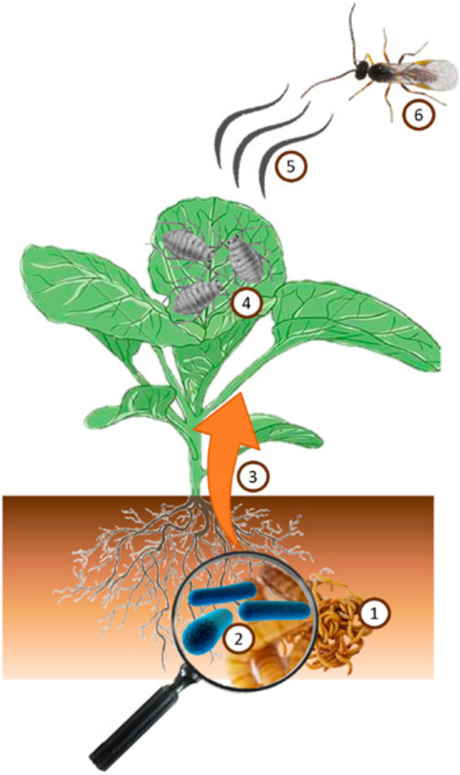


Figure 8. Pictorial representation of the effects of adding insect cuticular material to soil on plant growth and on direct and indirect resistance to herbivorous insects. 1: insect exuviae in soil; 2: bacteria colonise exuviae; 3: stimulated plant growth; 4: induced systemic resistance to herbivores, aphids in this picture; 5: shift in plant volatile production; 6: increased attraction of aphid parasitoids that kill the aphids. Figure credit: Els M. van de Zande.

Decline in insect numbers

Not only in agro-ecosystems but also in natural areas, the number of insects has declined drastically in several geographic areas that are monitored[75-77]. Next to habitat loss, one of the primary causes of this decline is the application of insecticides in agriculture and the side effects this has on neighbouring natural areas. My original motivation for studying biology stemmed from concerns about environmental pollution, among which the detoriating effects of insecticides on wildlife, compellingly put on stage 62 years ago in the book Silent Spring[78]. Three years ago a book was published with the title *Silent Earth, averting the insect apocalypse*[79]. Reading this makes it uneasy for an entomologist to retire as it is evident that the decline of insects is a worrying signal of the continuing detoriation of the natural world.

It is impossible to generalise about "insects", there are friends and foes among them. However, we really need them to pollinate plants and to decompose detritus. Moreover, so many species are really beautiful and have fascinating lifestyles that deserve to be studied, taught, and safeguarded.

Acknowledgements

Madam Rector, nearing the end of this lecture I would like to use the opportunity to say thank you to the many people who contributed to my scientific career and personal development.
I thank my promotor Louis Schoonhoven and my former colleague Freddy Tjallingii whom I met 50 years ago at the Laboratory of Animal Physiology when I followed classes in general and comparative physiology and ecophysiology. I thank you for your continuous support and friendship.
Since 1989 until now I have worked with much pleasure at the Laboratory of Entomology. Early on my colleagues Marcel Dicke and Louise Vet involved me in adopting a common set of insect-plant and tritrophic interactions that we studied jointly, each of us taking approaches based on our own expertise. This has broadened my interest to chemical and behavioural ecology.
Marcel Dicke, thank you for being such a good colleague over the past 35 years. Together we had the opportunity to explore the biology of a diversity of insect species in projects of PhD students whom we jointly supervised, with much pleasure. I thank you also for your energetic leadership as chairholder of Entomology.
Willem Takken, thank you for inviting me to step into mosquito biology, a fascinating topic and so relevant for the health of people in the global south.
Arnold van Huis, thank you for asking me to join the research line on edible insects you started and that sparked research on insect nutrition of crickets, beetles, and flies.
Hans Smid, thanks a lot for always helping out with technical assistance and for making professional photographs and videos that are so important to show the beauty of insects to students and the wider public.

One of the tasks I enjoyed most in my work was the coaching of PhD students to become independent scientists. I have much enjoyed working with each of you. I am grateful to see several of you in the audience today and hope we will keep in touch.

Special thanks to the staff of our Central Insect Rearing, André Gidding, Pieter Rouweler, Kimmy Reijngoudt, Leon Westerd, Leo Koopman and the late Frans van Aggelen. Healthy insect colonies are the basis of our research. Your hard work, also during the weekends, cannot be overvalued. I also thank our secretaries, the skilled personnel of Unifarm for growing plants in greenhouse and field, and the colleagues of the technical services.

Collaboration, both with groups in the university as well as in Wageningen Research, leads to synergy and in my experience WUR colleagues are always willing to discuss joining forces. I have had the privilege to work with colleagues of several chair groups and research institutes. I thank my colleagues Ben Vosman, Roeland Voorrips and Lotte Caarls for their pleasant collaboration in plant breeding for insect resistance and co-supervising joint PhD students. Roland Mumm and Ric de Vos, thanks for the collaboration on metabolomics.

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Alexander Haverkamp, Nina Fatouros, Niels Verhulst, and Alida Melse, many thanks for presenting your work during the mini-symposium earlier this afternoon.

All those other colleagues whom I did not mention by name, rest assured that I have appreciated the various ways in which you have made me enjoy my work.

I thank you all for your attention and will finish with a few last words in Dutch:
Ik wil graag mijn levenspartner José bedanken voor haar voortdurende steun en haar belangstelling voor mijn werk. In de kunst die zij maakt zijn insecten en planten met hun grote diversiteit van vormen en kleuren terugkerende thema’s. Camiel en Martijn, in jullie jonge jaren gingen jullie graag mee naar de insectenkweken die ook tijdens het weekeinde verzorging nodig hadden. Insecten zijn op verschillende manieren ook jullie levens binnengevlogen. Ik hoop dat jullie me foto’s blijven sturen van insecten waarover je meer wilt weten; hoe meer, hoe beter.

Ik heb gezegd.

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Insects exploit very diverse food sources and evolved their specialised lifestyles and behaviours over some 480 million years of evolution. Not only do these small animals display strong preferences among host plants or host animals at the species level, they also discriminate between individuals within a species and change preference through learning. Understanding the neural, behavioural, and ecological mechanisms of food selection is instrumental in developing sustainable strategies for co-existing with insects that fulfil vital ecological functions in plant reproduction, decomposition of organic matter, and natural control.