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Are host plants important in pheromone-mediated mating systems of Lepidoptera?

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Summary. The role of host plants in the synthesis and release of lepidopteran sex pheromones is examined. Females synthesise pheromones de novo and pheromone quality is not markedly influenced by larval food sources. However, host plants may have a significant effect on different physiological and behavioural parameters associated with pheromone production. Males in some species of Nymphalidae and Arctiidae use secondary plant compounds, such as pyrrolizidine alkaloids, as a pheromone precursor. In such cases these plant compounds serve an additional role, such as protection against predation, and may reflect potential male reproductive investment. In the one instance where the effect of larval host plants on the de novo synthesis of a male sex pheromone was examined, larval nutrition did not alter either the quality or quantity of the hairpencil contents.

Key words. Lepidoptera; semiochemicals; sex pheromones; host plants; secondary plant compounds; calling behaviour; mate choice; *Homoeosoma electellum; Pseudaletia unipuncta.*

Introduction

Plant semiochemicals play an important role in the selection of oviposition sites by adult Lepidoptera[15], as well as in subsequent larval feeding activity[21], and considerable effort has been invested in both fundamental and applied research in this field. In comparison, research on the importance of host plants with respect to the production and emission of lepidopteran sex pheromones has received very little attention, despite the potential of these semiochemicals in integrated pest management programmes. The objective of this brief review is to demonstrate that host plants may play an important role in the pheromone-mediated communication of Lepidoptera, for even when host plants are not the direct source of pheromone precursors their presence or absence may induce physiological and/or behavioural changes that markedly influence mating.

Female pheromones: synthesis and release

Hendry et al.[23] reported that many compounds, known to be insect sex pheromones, were present in a wide variety of plant species and suggested that females may use chemicals obtained directly from the host plant as a source of pheromone. They based this hypothesis on data obtained in a study of the oak leaf roller moth, *Archips semiferanus* Walker (Tortricidae). They observed that a) at least 21 isomeric tetradecenyl acetates were found in the female sex pheromone, b) cis-10-tetradecenyl acetate, one of the most active isomers in field trapping trials, was present in high quantities in black oak, a major host plant in the study area, c) females reared on black oak or wheat germ diet containing oak leaves contained (Z)-10-tetradecenyl acetate, while those reared on unmodified wheat germ or alfalfa synthetic diets did not, and d) males exhibited mating behaviour in the presence of damaged oak leaves. They concluded that if females obtained sex pheromone directly from the host and if males 'imprinted' to the odour of the host plant on which they had completed larval development then this could, in some cases, be a mechanism leading to speciation as the chemical composition varied between different host plant species. Miller et al.[28] re-examined the sex pheromone of the oak leaf roller and found that it was always a specific blend (67:33) of trans-11 and cis-11-tetradecenyl acetate and that it did not differ quantitatively or qualitatively when females were reared on three oak species or on an artificial diet containing no host plant compounds. They concluded that the chemical composition of the sex pheromone was not influenced by larval nutrition as Hendry et al.[23] had initially suggested.

While Miller et al.[28] rejected the idea that pheromone composition would be influenced by larval nutrition they did not rule out the possibility that major changes in diet may influence different aspects of pheromone production. To examine this we studied the effect of larval diet on both calling behaviour[36] and pheromone production[10] in the polyphagous armyworm *Pseudaletia unipuncta* (Haworth) (Noctuidae), testing different host plants as well as different phenological stages of the same plant. Larval nutrition significantly influenced pupal weight, the age at which the females initiated calling behaviour (release of pheromone) for the first time following emergence, and the time of calling during the scotophase (table). However, there was no dietary effect on the quantity of cis-11-hexadecenyl acetate, the major female pheromone component[25], extracted from glands of virgin females (table). In light of our findings, it is possible that the absence of pheromone in oak leaf roller females reared on artificial diet by Hendry et al.[23] was due to the age of females used for pheromone analysis. If there was a delay in the onset of calling and pheromone synthesis related to food quality, and if only glands from young females were analysed, no pheromone would have been detected.

While Hendry et al.[23] only addressed the direct utilization of plant compounds as female sex pheromones they stated that host plants may "function in more subtle ways, such as causing physiological changes in the insect concomitant with the 'induction' of pheromone biosynthesis." Riddiford and Williams[31] reported that mating of the polyphemus moth, *Antheraea polyphemus* (Cram.) (Saturnidae) only occurred in the presence of volatiles

Effect of larval diet on pupal weight (mg), the age (days) at which females initiated calling, as well as the mean onset time of calling (expressed as the number of minutes after lights-off) and the pheromone gland content (ng) at the end of the second night of calling in *Pseudaletia unipuncta* virgin females.

Larval[1] diet	N	Pupal weight[2]	Calling age[2]	N	MOTC[3]	Pheromone[4] content
Corn I	44	374.6 ± 5.7 ab	4.7 ± 0.2 b	15	388.7 ± 7.2 ab	21.1 ± 3.9 a
Corn II	47	373.2 ± 7.2 ab	4.6 ± 0.2 b	15	406.9 ± 7.9 a	25.6 ± 5.8 a
Oats I	29	338.6 ± 10.6 bc	4.4 ± 0.3 b	15	378.9 ± 8.4 ab	39.5 ± 5.3 a
Oats II	39	367.5 ± 8.3 ab	5.4 ± 0.3 ab	14	379.2 ± 9.4 ab	31.9 ± 6.9 a
Wheat I	8	357.5 ± 24.3 ab	6.6 ± 0.9 a	7	358.6 ± 12.8 b	20.0 ± 6.5 a
Wheat II	40	373.6 ± 8.2 ab	5.4 ± 0.3 ab	12	397.5 ± 7.2 a	25.3 ± 6.4 a
Timothy I	36	320.5 ± 9.4 c	5.4 ± 0.3 ab	8	396.3 ± 9.1 a	38.3 ± 4.5 a
Diet	40	390.3 ± 6.6 a	5.1 ± 0.2 ab	15	402.9 ± 9.1 a	32.9 ± 5.1 a

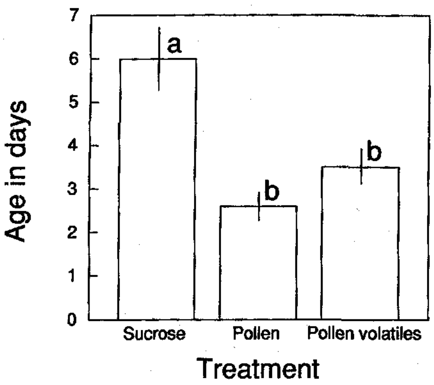
[1] The second rearing was started 21 days after the first, using plants from the same field plot. [2] Values followed by the same letter do not differ significantly ($p > 0.05$, Kruskal-Wallis followed by SNK). [3] Values followed by the same letter do not differ significantly ($p > 0.05$, Anova followed by SNK).

from oak leaves or alcoholic oak leaf extracts, but not in the presence of other larval host plants. One host plant volatile, subsequently identified as trans-2-hexenal[30], was found to affect only females. It was suggested that females were stimulated to release sex pheromone when in the presence of volatiles from a suitable host plant. The lack of host plant stimulation by species other than oak, despite the ubiquity of trans-2-hexenal in green leaves, was attributed to either higher release rates from oak or to the presence of masking odours in other hosts[30]. In a subsequent study of the polyphemus-oak interaction Cardé and Taschenberg[5] demonstrated that host plant volatiles were not required for either the expression of calling behaviour or for successful mating in this system. While they concluded that host plant volatiles were not essential in the reproduction of the polyphemus moth, they did not eliminate the possibility for other species and postulated that "such a kairomonal interaction [sic] would be most likely among monophagous or oligophagous species (perhaps with a patchy host distribution) and especially among species that are long-lived as adults and that are not reproductively mature upon adult eclosion, in which case the host cue might exert an effect on ovarian development."

Herrebout and van der Water[24] suggested that host plant volatiles affected pheromone production in the small ermine moth, *Yponomeuta cagnagellus* Hubner (Yponomeutidae), a long-lived species that reaches sexual maturity about one week after emergence. This conclusion was based on the higher number of males captured by 'experienced' female moths (those that had been held in the presence of host plant volatiles prior to the field trial) when compared with 'inexperienced' (no previous contact with host plant odours) individuals. However, in both experiments 'inexperienced' moths were held at 5 °C for longer periods than 'experienced' ones and a cold-induced delay in the age at which females initiated calling[9, 37], could have resulted in lower captures by 'inexperienced' females. Subsequent experiments have demonstrated that the age at which females initiate calling is influenced by the presence or absence of suitable host plants and thus hosts may play an important role in speciation within the genus *Yponomeuta*[22]. Recently Raina[29] has shown that host plant volatiles were not only essential for the expression of calling behaviour but also for pheromone synthesis in *Heliothis zea* (Boddie) and *H. phloxiphaga* G. and R. (Noctuidae) females that were collected as larvae from their respective host plants in the field.

It is also possible that a very specific part of the host plant may influence female calling behaviour. The sunflower moth, *Homoeosoma electellum* (Hulst.) (Pyralidae), oviposits preferentially in newly-opened flowers[12, 35] and we have recently shown that sunflower pollen contains an oviposition stimulant for the sunflower moth[11]. Following anthesis the availability of free pollen, an essential dietary resource for neonate larvae[32], will be limited in space by the distribution of acceptable host plants and in time on any given plant by the action of pollinators and meteorological conditions such as wind and rain. As this species is a known migrant[1], and since it has been hypothesized that the calling behaviour of migratory species may differ from that of non-migratory ones[27], we undertook studies to determine if pollen availability influenced the calling behaviour of virgin *H. electellum* females. The age at which calling behaviour was initiated varied considerably; the presence of pollen and sucrose stimulated females to initiate calling at a significantly younger age than sucrose alone (fig.). However, the observed differences in calling age could have resulted from differential adult nutrition. Gilbert[19] previously demonstrated that adults of certain neotropical *Heliconius* (Nymphalidae) species fed on pollen and that the nutrients obtained markedly affected fecundity. However, there was reason to believe that sunflower moths did not actually feed on pollen. Adults exhibit no distinct pollen collecting behaviour and possess no structures, such as the pronounced papillae on the proboscis that could serve as a pollen-collecting brush. Furthermore, *Heliconius* adults obtain nutrients by wetting pollen with nectar (pollen incubated in a sucrose solution rapidly releases free amino acids[26] and proteins[34]) and agitating it for several hours. No such behaviour was noted for sunflower moths.

To confirm that changes in calling behaviour of *H. electellum* were due to the presence of semiochemicals in pollen we compared females that had direct access to pollen with those that were exposed only to pollen odour. As seen in the figure there was no significant difference in the mean age at which females in the two groups called, clearly indicating that volatiles from the pollen are involved. Whether the chemicals that serve as oviposition stimulants, detected principally by receptors on the antennae[11], also act as semiochemicals to initiate the onset of calling behaviour remains to be determined. This ability to modify reproductive behaviour could enable the



The age at which *Homoeosoma electellum* virgin females initiated calling for the first time following emergence when in the presence of sucrose only, pollen and sucrose, or pollen volatiles and sucrose at 25 °C, 65 ± 5% R.H. under a 16L:8D photoperiod.

sunflower moth to adjust to the presence or absence of an essential but unpredictable resource.

Male pheromones

Lepidopteran male sex pheromones have not been studied to the same extent as those of females, most probably due to their limited use from an applied perspective. However, published works clearly show the importance of plants for the production of male pheromones. Males in the Nymphalidae (Danainae and Ithomiinae) and Arctiidae use pyrrolizidine alkaloids (PA) obtained from plants either during larval development or through adult feeding, as precursors of the male pheromone found in the scent organs or coremata[2,14].

Females of the arctiid *Utetheisa ornatrix* emit a sex pheromone[7] and during the subsequent close-range pre-copulatory interaction males evert the coremata[8]. However, males reared on PA-free diet exhibited normal mating behaviour but had a lower courtship success than control males[8]. It was suggested that male pheromone content might provide the female information concerning the males ability to sequester PAs[8] which, if heritable, could influence the fitness of her progeny as these compounds may provide considerable protection from predation[4,13,14]. More recently it has been shown that *U. ornatrix* spermatophores contain PAs and that these compounds are incorporated into eggs, thus affording some degree of protection against predation[13]. Thus, females could assess potential male investment through pheromone content and thereby select the most suitable mates, given that the level of pheromone present in the coremata closely reflects the systemic alkaloid load, which in turn influences the amount transferred in the spermatophore[13]. The ability to select suitable males may be further facilitated if, as noted for *Creatonotos gangis* and *C. transiens*, the size of the coremata was always directly related to the quantity of PAs ingested[3,33].

In some species male sex pheromones are synthesized de novo[6] rather than being derived from secondary plant compounds. However, to our knowledge the possible effects of larval nutrition in such species have not been examined. True armyworm males synthesize both benzaldehyde[20] and acetic acid[18] de novo (Miller et al., unpublished data) and these compounds, when released in close proximity to calling females, facilitate acceptance of the courting male[16]. We therefore determined the pheromone titre of males[17] reared on a variety of larval host plants and found that larval food had no significant effect on the quantity of either compound in the hairpencils (Fitzpatrick and McNeil, unpublished data). Thus, in the case of *P. unipuncta*, where both sexes synthesize their sex pheromones de novo, host plants do not influence the quality or quantity produced. Whether aspects of male receptivity to the female sex pheromone, such as the age of first response[38], are affected by larval nutrition in the same manner as female pheromone emission (table) remains to be determined.

Conclusion

In Lepidoptera it appears that host plants are only used as a source of sex pheromone precursors when these plant-derived compounds serve an additional purpose, such as a deterrent against predation, and there is a relationship between pheromone content and subsequent parental investment. To date this situation has only been observed in males but, if such a case were found in females, one might expect males to be the choosy sex and the female pheromone to be an indicator of female fitness.

In species where sex pheromones are synthesized de novo the precursors could be obtained, directly or indirectly, from a wide variety of host plants. As a result, given that pheromone blends are species-specific over a wide range of ecological conditions, one would not expect the quality or the quantity to vary when individuals were reared on different host plants. However, as seen in the Noctuidae[29], Pyralidae (see above), and Yponomeutidae[22], host plant volatiles may influence pheromone synthesis and/or calling behaviour. Therefore, additional studies examining the influence of host plants on different behavioural and ecological aspects of pheromone-mediated mating systems should prove to be a fruitful area of research in the field of chemical ecology.

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The chemical ecology of Diabroticites and Cucurbitaceae

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Summary. The coevolutionary association between plants of the family Cucurbitaceae and beetles of the tribe Luperini (Coleoptera: Chrysomelidae; Galerucinae) is mediated to a large extent by chemicals of the host plants. The kairomones involved in host selction by the rootworm beetles are the oxygenated tetracyclic triterpenoid cucurbitacins that act as arrestants and feeding stimulants and a number of volatile cyclic plant blossom components that act as long-range orientation cues. The complex ecological and evolutionary factors regulating the chemical ecology of host-plant selection are discussed.

Key words. Chrysomelidae; Diabroticites; attractants; cucurbitacins; host-plant selection.

Introduction

Utilization of suitable hosts by phytophagous insects is considered to involve a chain of internally programmed behaviors that are initiated, maintained and modified by the interaction of excitatory and inhibitory inputs from the host, internal state of the herbivore, and the environment[13]. Although insect-plant relationships can not be