Close range interactions between a parasitoid and its leafmining host mediated by substrate vibrations

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CLOSE RANGE FORAGING BEHAVIOUR

The foraging behaviour of parasitoids has found much attention during the last decades. Most studies focus on the efficiency of the parasitoids’ foraging behaviour at the long range where chemical cues seem to play a major role (see Vinson, 1985 for a review). Interactions on the close range have been proved to be more diverse, and are guided by several different stimuli (see Schmidt 1991 for a review). Visual, contact chemical, as well as physical stimuli function as information source for the foraging parasitoid once it approaches a prospective host. But these close range stimuli generally bear a special feature: most of them cannot be sensed by the parasitoid unless it gives away information to the approached host on its part. The parasitoid e.g. may need to come so close to its target that it accidentally emits various stimuli itself. These stimuli might provide information for the alert host larva that tries to avoid contact with its antagonist. Therefore studying close range stimuli in a host parasitoid-system usually means to deal with a two-way relationship of sensory modalities and cues of both opponents.

Casas (1989) hypothesized that the foraging behaviour of the parasitoid Sympiesis sericeicornis Nees (Hymenoptera, Eulophidae) is influenced on the close range by mechanical stimuli triggered by the leafmining host larva, Phyllorycter malella Ger. (Lepidoptera, Gracillariidae). Not only the host larva but also the foraging parasitoid probably triggers vibrational signals while foraging on the leaf lamina. The stimuli are transmitted by way of the leaf lamina in both cases. Therefore the investigation of the role of vibrational stimuli in the close range interactions between parasitoid and leafmining host larva requires a two step set-up: (1) characterisation of vibrational stimuli triggered by the host larva and those triggered by the foraging parasitoid and (2) characterisation of behavioural interactions between both species as influenced by vibrational signals.
CHARACTERISING THE VIBRATIONAL STIMULI

Substrate vibrations were measured with a laser vibrometer on a single leaf in a cantilever set up. This technology allows non contact point measurements. The signals were characterised in the time and the frequency domain (Meyhöfer et al. 1994b).

The analysis of the measured data shows that vibrational signals triggered by the host larva are stage and activity specific. During the foraging behaviour of the larva inside the mine vibrational signals with a maximum frequency of 5 kHz are triggered. These results contrast with vibrational signals triggered by a wriggling larva or a wriggling pupa where frequencies of up to 16 kHz can be measured. Both signal types differ in their temporal pattern. During the foraging activity, the larva triggers short vibrational signals in a more or less regular time course; i.e. frequencies of 3 kHz occur with a probability of 20% in a 5ms time interval (Meyhöfer et al. 1994a). On the other hand a wriggling larva or pupa triggers longer vibrational signals which only occur spontaneously and therefore are unpredictable. The variance in the information content of these vibrational signals is high and can be explained in both cases by three factors: location of the sender in the mine relative to the location of the receiver, location of the mined area on the leaf, and by the impact force of the activity on the leaf.

Vibrational signals triggered by the foraging parasitoid were characterised by Bacher et al. (1996). The parasitoid displays three different foraging activities: moving, standing, and probing. During the probing behaviour dominant frequencies of up to 5.6 kHz are observed, while the maximum frequency is found above 20 kHz. Vibrations triggered during moving and standing have a lower frequency and occur only scarcely. Bacher et al. (1996) proposed that probing provides a reliable and detectable source of information for the host and could therefore account for evasive behaviours of the host larva.

BEHAVIOURAL INTERACTIONS

The specific role of vibrational signals in the interspecific relationship between parasitoid and leafmining host was verified by a behavioural analysis of the interactions between both species (Meyhöfer et al. 1997). For this analysis we designed an observation set-up that allowed us continuous recording of both insects on a mined apple leaf on the same video frame using a video camera and a mirror system.

The behaviour of the parasitoid was classified in three states (searching, pausing, and ovipositor insertion), the behaviour of the host larva in four states (feeding, moving, wriggling, and still). Transition probabilities were calculated between behavioural states of both insects during a foraging bout. By doing so we could compare behavioural reactions in situations where vibrations were present (i.e. behavioural reactions of the parasitoid when the host larva was moving) with those situations where vibrational signals were absent (i.e. when the host larva was...
standing still). The analysis was done separately for the parasitoid and the host. Behavioural reactions might change significantly after the first physical contact between both insects, when the parasitoid’s ovipositor touches the host larva. Therefore the behavioural sequences were divided into two phases: Phase 1 starts when the parasitoid entered the mine for the first time and ends with the first physical contact between the parasitoid and the host larva. Phase 2 starts after the first contact and ends with the final paralysis of the host. By discriminating these two phases behavioural interactions triggered by vibrational signals transmitted through the leaf lamina could be separated from those triggered at least partly by a physical contact.

The results of this analysis show that the behavioural response of both species, the parasitoid and the host larva, are affected by the presence of vibrational signals triggered by each one’s opponent. Before the first physical contact (phase 1) the moving host influences the behavioural transitions of *S. sericeicornis* from searching to ovipositor insertion (and vice versa) and from searching to pausing. These transition probabilities are significantly reduced when the host is moving compared to when it remains still.

The parasitoid chooses spots for ovipositor insertions very carefully. A reduced transition probability from searching to ovipositor insertion is observed in cases where the larva is triggering vibrational signals. This observation allows the hypothesis that the parasitoid to some extent receives spatial information about the larva’s location. The vibrational signal seems to tell the parasitoid that its current location is not close enough to the larva that it would be worthwhile to insert the ovipositor.

The behaviour of the host larva is strongly influenced by vibrations triggered by ovipositor insertions of the foraging parasitoid whereas the parasitoid’s searching activity does not seem to account for special behavioural reactions of the host larva. Ovipositor insertions of the parasitoid lead to increased transition probabilities of the host larva from moving to still and vice versa. The transition probabilities, especially for the parasitoid, becomes independent of the larva’s activity after the first physical contact between the two opponents, indicating a specific role of this key element for the ensuing behavioural sequence.

Evasive behavioural manoeuvres of the host larva are very effective. A host without escape possibilities (i.e. surface mines on leaves) would normally be stung by the first ovipositor insertion of the parasitoid near the host which would correspond with the end of phase 1 of *S. sericeicornis*. Since the leafminer *P. malella* produces tentiform mines it is able to prolong the time until paralysis by performing escape manoeuvres as a reaction to the parasitoid’s attack (phase 2). This is shown by the time budget of the foraging parasitoid: Phase 1 alone lasted 25.3 s (median of *n*=41) while the escape behaviour of the larva added additional 62.6 seconds (duration of phase 2) until the parasitoid finally is able to paralyse the larva (Fig. 1). As a function of time the parasitoid’s motivation may decrease...
depending on its physiological state and could lead to abandonment of the host larva.

![Figure 1: Notched box plots of the time budget of the foraging parasitoid: amount of time from entering the mine until the first physical contact with the host (phase 1) and from the first physical contact until injection of the venom and paralysis of the host larva (phase 2) (tested using the Mann-Whitney U-test; p<0.001).](image)

CONCLUSION AND NEXT STEPS

The overall results of this case study indicate that vibrational signals play an important role for the close range interactions between the parasitoid *S. sericeicornis* and its host larva *P. mallela*. Undoubtedly behavioural reactions to vibrational signals should be advantageous for both insects. The parasitoid may use vibrational signals for effective host location when performing either a kinetic or a taxis reaction. The host larva on the other hand is not able to spatially escape parasitism because it is confined to the mine. But the results show that 35% of the hosts can escape parasitism (Casas, 1989), most likely by the performance of evasive manoeuvres. The integration of these behavioural results in an individual based model will address the importance of single events for the progress of the foraging sequence.

For the confined host larva vibrational stimuli may be the only source of information to detect the presence of an foraging parasitoid. But behavioural transitions of the parasitoid are only partly influenced by vibrations which indicates that it does not exclusively rely on vibrational stimuli for host location. Chemical
signals as well as visual stimuli may also play a role for the orientation and decision when and where to insert the ovipositor. Future research should include these stimuli and focus on multisensory orientation.

REFERENCES


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