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Mini review

## Vibratory stimuli in host location by parasitic wasps

R. Meyhöfer<sup>a,\*</sup>, J. Casas<sup>b</sup>

<sup>a</sup> Institute of Plant Diseases and Plant Protection (IPP), University Hanover, Herrenhäuser Str. 2, D-30419 Hanover, Germany

<sup>b</sup> IRBI CNRS ESA 6035, Faculté des Sciences, Université de Tours, F-37200 Tours, France

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### Abstract

Parasitic wasps use a broad spectrum of different stimuli for host location and host acceptance. Here we review the published evidence for the use of mechanical stimuli, i.e. substrate born vibrations which are invariably regarded as vibrotaxis. We propose a set of criteria to class behavioural reactions as vibrotaxis or vibrokinesis and characterize 14 studies reporting the use of host-associated vibrations by parasitoids. The studies are compared concerning (i) experimental design; (ii) characterisation of vibrational signals; and (iii) progress of the parasitoid towards the host.

The recent experimental development based on new measurement techniques shows the growing body of evidence that host-associated vibrations are exploited by parasitic wasps. Nevertheless a definite proof for vibrotaxis is still lacking. To assess the exact mechanisms by which parasitoids use vibrations bioassays comparing reactions to natural and artificially generated signals are needed. Vibrotaxis as well as vibrokinesis are both helpful host location strategies for parasitoids foraging in a multimodal environment. At the community level they may lead to niche differentiation. © 1999 Elsevier Science Ltd. All rights reserved.

**Keywords:** Experimental design; Parasitoid; Vibrotaxis; Vibrokinesis; Host location

### 1. Introduction

Host location and host acceptance in parasitic wasps is a very active field of research, much of which is centred around the identification of stimuli and the characterisation of behavioural responses (for reviews see Godfray, 1994; Quicke, 1997). Apart from chemical and visual stimuli, mechanical stimuli from the host also provide valuable information for the foraging parasitoid. Vibrations emanating from hosts which are feeding or moving have been reported to induce a behavioural response in a number of parasitoid species. Such behaviour was invariably regarded as vibrotaxis.

The aim of this work is to review the literature reporting the use of host-associated vibrations by parasitoids and to examine the validity of this assertion. The following sections will focus on the definitions of the types of behaviours which vibrations elicit in parasitoids, a review of the current literature on the subject, and dis-

cuss the conditions under which the use of vibrations can be characterised clearly.

### 2. Definitions of vibrotaxis and vibrokinesis

A *taxis* is a behavioural reaction where an animal moves directly towards (positive taxis) or away (negative taxis) from the source of the stimulus (Fraenkel and Gunn, 1961; Dusenbery, 1992). A *kinetic* reaction is defined as the behavioural response of an animal to a stimulus that is proportional to the intensity of the stimulation, but independent of the spatial properties of the stimulus (Fraenkel and Gunn, 1961; Dusenbery, 1992). Kinetic reactions do not result in directed movement towards the source, but keep the animal in the vicinity to the target. The response of the animal can increase (positive kinesis) or decrease (negative kinesis) relative to the intensity of the stimulus.

To rank the behavioural response of a parasitoid as vibrotaxis or vibrokinesis, three criteria need to be met:

1. Characterisation of the vibratory signal (spatial and temporal transduction, frequency).

\* Corresponding author. Tel.: +48-511-762-3096; fax: +49-511-762-3015.

E-mail address: meyhoefer@mbox.ipp.uni-hannover.de (R. Meyhöfer)

2. The position of the signal source and the progress of the parasitoid towards it.
3. The intensity of the signal and the behavioural response of the parasitoid which results, in terms of speed (orthokinesis) or degree of turning (klinokinesis).

In all cases there should be conclusive evidence that the behavioural reaction of the parasitoid is modulated directly by the vibrational signal. Only if the vibrational signal triggered by the movement of the host results in the parasitoid approaching the location of the host can it be concluded that the parasitoid shows a vibrotactic response. If the signal influences the turning angles or speed of movement of the parasitoid, but does not result in a net progress towards the target, then the behaviour is classed as vibrokinesis.

### 3. Literature review

The work reviewed here is characterised according to (i) experimental design, (ii) characterisation of the emitted vibrations, (iii) progress of the parasitoid towards the host and (iv) the classification as taxis or kinesis (see Table 1). We discuss the first two aspects in more detail below.

#### 3.1. Experimental design

Anecdotal descriptions of the behaviour of parasitoids as they approach their hosts are insufficient to give

a clear indication of the mechanisms which are used by the parasitoid in host location. Experiments which seek to examine the role of vibrations in host location should, therefore, exclude other potential stimuli e.g. semiochemicals from the host or host habitat. Parasitoids are sensitive to chemicals originating from their hosts e.g. saliva or faeces and as a result of damage to plants (see reviews by Godfray, 1994; Quicke, 1997). In addition, immobilized hosts are often used in a choice test, to study behavioural reactions of the parasitoid in situations with and without vibrations. But this does not necessarily provide conclusive evidence for vibrotaxis. As an example, Glas and Vet (1983) presented alternatively paralysed and non-paralysed *Rhagoletis pomonella* (Walsh) (Diptera, Tephritidae) larvae in a hawthorn fruit to the parasitoid *Diachasma alloeum* Muesebeck (Hymenoptera, Braconidae). The immobile larvae had been paralysed by a heterospecific parasitoid. Similarly, Sokolowski and Turlings (1987) used a *Drosophila* strain which becomes immobile above a threshold temperature of 30°C. The method by which the host is immobilized, e.g. by dipping in hot water (Prince, 1976; Cheah and Coaker, 1992), inserting a needle (Sugimoto et al., 1988a), or freezing (Prince, 1976), may also effect the cues emanating from it. A major impediment to the use of dead hosts or hosts which are immobilized artificially is, therefore, that they may produce chemicals which differ in composition and abundance from those of a healthy host. Furthermore, their metabolic rate is usually altered (decreased or non-existent), which affects heat- and CO<sub>2</sub>-radiation (Dusenbery, 1992). Since a parasitoid may be influenced by these stimuli as well,

Table 1

Current literature on the use of vibrations by parasitoids: (1) experimental design in a way that other stimuli are excluded, with cases where the evidence is suggestive but not conclusive marked with ±, (2) characterisation of the signal in time and frequency components, (3) recording of the progress of the parasitoid to the host, (4) classification of the behavioural reaction as vibrotaxis or vibrokinesis. (exp. = experimental results, obs. = observational results).

Author	Type	Parasitoid	Host	(1)	(2)	(3)	(4)
Cheah and Coaker, 1992	exp.	<i>Diglyphus isaea</i>	<i>Chromatomyia syngenesiae</i>	±	no	no	host detection
De Leon, 1935	obs.	<i>Coeloides dendroctoni</i>	<i>Dendroctonus monticolae</i>	no	no	no	host detection
Glas and Vet, 1983	exp.	<i>Diachasma alloeum</i>	<i>Rhagoletis pomonella</i>	±	no	no	taxis
Lathrop and Newton, 1933	obs.	<i>Opius melleus</i>	<i>Rhagoletis pomonella</i>	no	no	no	taxis
Lawrence, 1981	exp.	<i>Biosteres longicaudatus</i>	<i>Anastrepha suspensa</i>	±	no	no	taxis
Meyhöfer et al., 1994a,b <sup>a</sup>	exp.	<i>Sympiesis sericeicornis</i>	<i>Phyllonorycter malella</i>	yes	yes	yes	kinesis
Prince, 1976	exp.	<i>Phaenocarpa persimilis</i>	<i>Drosophila melanogaster</i>	±	no	no	taxis
Quednau, 1967	obs.	<i>Chrysocharis laricinellae</i>	<i>Coleophora laricella</i>	no	no	no	host detection
Ryan and Rudinsky, 1962	obs.	<i>Coeloides brunneri</i>	<i>Dendroctonus pseudotsugae</i>	no	no	no	taxis
Sokolowski and Turlings, 1987	exp.	<i>Asobara tabida</i>	<i>Drosophila Melanogaster</i>	yes	no	no	taxis
Sugimoto et al., 1988a <sup>b</sup>	exp.	<i>Dapsilarthra rufiventris</i>	<i>Phytomyza ranunculi</i>	yes	yes	no	–
Van Alphen and Drijer, 1982 <sup>c</sup>	exp.	<i>Asobara tabida</i>	<i>Drosophila melanogaster</i>	±	no	yes	taxis
Van den Assem and Kuenen, 1958	obs.	<i>Choetospila elegans</i>	<i>Sitophilus granarius</i>	no	no	no	taxis
Van Dijken and van Alphen, 1998	exp.	<i>Leptopilina longpipes</i>	<i>Drosophila</i> spp.	yes	no	no	taxis

<sup>a</sup> Meyhöfer et al., 1997.

<sup>b</sup> Sugimoto et al., 1988b.

<sup>c</sup> Van Alphen and Janssen, 1982; Vet and Alphen, 1985; Vet and Bakker, 1985.

the compounding effects may mask the true role of any vibrations. Meyhöfer et al. (1997) suggested an alternative experimental approach where other stimuli were not excluded, but compared with and without vibrational signals within a single foraging sequence. This approach requires a record not only of the behaviour of the parasitoid, but also of that of the host.

### 3.2. Characterising vibrational signals

To determine which behavioural activities in the host give rise to vibratory signals that can be exploited by the parasitoid, the qualitative and quantitative characteristics of the vibrations which are emitted have to be quantified. Appropriate recording and analysis of vibratory signals enables the observer to assess whether:

1. vibrations are occurring during the interaction.
2. the host-emitted vibrations can be detected by the parasitoid.
3. the resultant behaviour of the parasitoid is a function of the vibrations.

Only two studies have so far characterised vibrational signals triggered by the host of a parasitoid. In pioneering work, Sugimoto et al. (1988a) inserted a needle into leaf tissue, attached it to a speaker membrane, and recorded the vibrational signals emitted by the leafminer *Phytomyza ranunculi* Schrank (Diptera, Agromyzidae). In a more recent study, Meyhöfer et al. (1994a,b) used laser vibrometry, a non-contact optical method, to characterise vibrational signals triggered by the tentiform leafminer *Phyllonorycter malella*. Besides laser vibrometers accelerometers provide nowadays a second commercially available measurement system. The advantages and disadvantages of the different techniques for recording vibratory signals in host-parasitoid interactions have been reviewed by Casas (1994).

### 3.3. Analysis of published evidence

Vibrations are reported to play a major role in determining the foraging success of 13 species of parasitoids (Table 1). The majority of the parasitoids that were studied belong to the Braconidae, Eulophidae, and Pteromalidae and attack endophytic hosts of the Diptera or the Lepidoptera. These hosts live hidden in the substrate, mining in leaves or feeding in fruits, inside grains, underneath the bark of trees or in decaying fruit substrates. That stem borers have not been included in this group is most likely due to the difficulty in observing the host experimentally. Parasitoids usually attack the mobile larval stages, rather than the pupa. It is suggested that, as these hosts are concealed, visual and chemical stimuli might be less important for foraging parasitoids

and hence vibrations would therefore be the main stimuli used.

While observational studies such as the ones by Van den Assem and Kuenen (1958) on *Choetospila elegans* Westw. (Hymenoptera, Calcidae) and Ryan and Rudinsky (1962) on *Coeloides brunneri* Viereck (Hymenoptera, Braconidae) provide some information for the design of laboratory studies, their results cannot be used to assess the importance of vibrations in host location and acceptance. More recently, a series of experimental studies on the host location behaviour of different *Drosophila* parasitoid species has provided more useful information on the importance of host-associated vibrations in host location (Van Alphen and Drijer, 1982; Sokolowski and Turlings, 1987; Van Dijken and van Alphen, 1998). In these studies a strain of drosophilid larvae was used that becomes immobile above 30°C. This work indicated that the parasitoids *Asobara tabida* Nees (Hymenoptera, Braconidae) and *Leptopilina longipes* (Hymenoptera, Eucoilidae) failed to locate immobile *Drosophila* larvae in the substrate. This observation suggests that movement of the host is important in the host location behaviour of these *Drosophila* parasitoids. Whether vibrotaxis is used by these parasitoids has not, however, been confirmed.

Similar results were found in other experimental studies, where a number of parasitoid species also failed to locate immobilized hosts (e.g. Glas and Vet, 1983; Lawrence, 1981; Cheah and Coaker, 1992). These 'missing' reactions were interpreted as an indication of the use of vibrotaxis by the parasitoid.

Papers by three other groups have markedly increased our understanding of the use of vibrations by parasitoids. Firstly, the braconid *Biosteres longicaudatus* Ashmead (Hymenoptera, Braconidae) was found to respond to movement by the larvae of its host the tephritid *Anastrepha suspensa* Lowe (Diptera, Tephritidae) by Lawrence (1981). The parasitoid was unable to locate a host in a hawthorn fruit if the larva was etherized or paralysed by a conspecific female. In a subsequent experiment, the author simulated vibrational signals of host larvae by scratching the interior of the fruit with a pin. The parasitoid responded to this signal which suggested that vibratory information did not have to be of host origin.

Secondly, in two studies, Sugimoto et al. (1988a,b) reported that patch location behaviour of the leaf miner parasitoid *Dapsilarthra rufiventris* (Nees) (Hymenoptera, Braconidae) was influenced by acoustical signals emitted by the larva of the host. The parasitoid landed less frequently on leaves that were mined or contained a dead larva (killed with a dissecting needle) or a larva showing reduced feeding activity. When given a choice between leaflets with and without an accompanying playback of the sound of the active larvae, the parasitoid landed more often on those leaflets where sound was provided. It is not clear whether the

parasitoid responded to acoustical stimuli or avoided leaflets without vibrational signals. This study also did not distinguish between substrate vibrations and air particle movements. Given the paucity of behavioural studies which assess the perception of acoustic signals by parasitoids, it would be useful to compare vibrational signals transmitted via the substrate and those transmitted via air particle movement (as done in Casas et al., 1998) and thereby identify those signal components that trigger the behavioural response.

Thirdly, in a series of studies, Meyhöfer and co-workers characterised the signal quality (Meyhöfer et al., 1994a) and quantity (Meyhöfer et al., 1994b) emitted by the leafminer *Phyllonorycter malella*, as well as the behavioural interactions between the parasitoid *Sympiesis sericeicornis* and the leafmining host larva (Meyhöfer et al., 1997). They were able to observe the behaviour of the host and the parasitoid with respect to their relative positions to each other simultaneously. The results showed that the parasitoid was not able to detect the host by vibrotaxis, however, higher rates of ovipositor insertions close to the host indicated that vibrokinesis might be involved. These studies also showed that *S. sericeicornis* did not rely exclusively on vibrational information provided by the host larva, but also used other cues from the habitat of the leafminer (e.g. chemical or visual cues).

In future work on the use of vibrotaxis by parasitoids it is important that the quality and quantity of the vibrational signal should be investigated. In addition, a behavioural bioassay is required to assess the response of the parasitoid to vibrational signals isolated from the host larvae. Such a bioassay should determine the progress of the parasitoid towards the source of the signal, a criterion that is necessary for a proper identification of vibrotaxis. This would be particularly useful where the hosts have been immobilized artificially and would show whether the method of immobilization influenced the reaction of the parasitoid (see Experimental design).

#### 4. Conclusions

There is a growing body of evidence which indicates that host-associated vibrations are exploited by parasitoids in host location. The exact mechanisms by which parasitoids use vibrations produced by hosts will be determined only through detailed studies such as those for other cues such as semiochemicals (e.g. Vet and Dicke, 1990; Murlis et al., 1992; Pickett et al., 1992). This will require bioassays to assess natural and artificially generated signals following work done on other arthropods e.g. spiders (Schüch and Barth, 1990) or leaf-mining lepidopteran larvae (Bacher et al., 1997). This is confounded by the inherent difficulty in producing a

bioassay which allows vibrotaxis to be assessed directly. The relevant information concerning signal quality, quantity and behavioural response needed to conduct such biotests is available at present for only one system (Meyhöfer et al., 1994a,b, 1997). Studies on wave propagation from the sender to the receiver will also be necessary to understand the influence of the in most cases heterogenous substrate (path geometry, properties of the material) on the signal properties and the subsequent behavioural response.

Setting aside the issue of quantifying vibrations it is clear that these signals are an useful source of information for a foraging parasitoid, whether they induce a vibrotactic reaction or as source for vibrokinesis. A distinction between the two ways in which vibrations may be used is important, not only in neuroethological terms, but also in the context of population biology of host-parasitoid systems. As vibrations differ as a function of host behaviour and host instar, the parasitoid may use this information to assess host quality, the probability of successfully ovipositing in the host or to estimate the optimal patch leaving time (giving-up time). In the presence of several hosts a parasitoid using vibrotaxis may behave differently from a parasitoid searching with vibrokinesis. This is because vibrational signals from different hosts may produce vibrational patterns which interfere with the orientation behavior of the parasitoid. In this respect, the use of *vibrotaxis* is a good strategy at low host densities while *vibrokinesis* is a better strategy at high host densities. At the community level different host location strategies may lead to niche differentiation (Van Dijken and van Alphen, 1998).

It is clear that vibrations are only one type of cue which parasitoids may exploit to find a host. There is evidence that the use of a series of cues may lead the parasitoid towards its host e.g. the leafminer parasitoid *Sympiesis sericeicornis* uses visual cues to define the contours of the mine and hence restrict the size of the area of search (Casas, 1988). Vibrations can then be used to assess that a suitable host is present and alive in a mine (Casas, 1989; Meyhöfer et al., 1997). The impact of exploiting vibratory cues on this process can now be examined using new technologies such as non-contact laser vibrometers and vibration controllers. This will enable us to develop a fuller understanding of the role of physical cues in the evolution of host location strategies.

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## References

- Bacher, S., Casas, J., Wäckers, F.L., Dorn, S., 1997. Substrate vibrations elicit defensive behaviour in leafminer pupae. *Journal of Insect Physiology* 43, 945–952.
- Casas, J., 1988. Analysis of searching movements of a leafminer parasitoid in a structured environment. *Physiological Entomology* 13, 373–380.
- Casas, J., 1989. Foraging behaviour of a leafminer parasitoid in the field. *Ecological Entomology* 14, 257–265.
- Casas, J., 1994. The functional response of parasitoids: Probability models and sensory ecology. In: *Proceeding of the 6th European Workshop on Insect Parasitoids*, vol. Supplement. Norwegian Journal of Agricultural Sciences, Biri, Norway, pp. 233–241.
- Casas, J., Bacher, S., Tautz, J., Meyhöfer, R., Pierre, D., 1998. Leaf vibrations and air movements in a leafminer-parasitoid system. *Biological Control* 11, 147–153.
- Cheah, C.A., Coaker, T.H., 1992. Host finding and discrimination in *Diglyphus isaea* a parasitoid of the chrysanthemum leaf miner *Chromatomyia syngenesiae*. *Biocontrol Science and Technology* 2, 109–118.
- De Leon, D., 1935. The biology of *Coeloides dendroctoni* Cushman (Hymenoptera-Braconidae) an important parasite of the mountain pine beetle (*Dendroctonus monticolae* Hopk.). *Annals of the Entomological Society of America* 108, 411–424.
- Dusenbery, D.B., 1992. *Sensory Ecology*. W. H. Freeman and Company, New York.
- Fraenkel, G.S., Gunn, D.L., 1961. *The Orientation of Animals*. Dover Pub. Inc, New York.
- Glas, P.C.G., Vet, L.E.M., 1983. Host-habitat location and host location by *Diachasma alloenum* Musebeck (Hym.: Braconidae), a parasitoid of *Rhagoletis pomonella* Walsh (Dipt.: Tephritidae). *Netherlands Journal of Zoology* 33, 41–54.
- Godfray, H.C.J., 1994. *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton, Princeton University Press.
- Lathrop, F.H., Newton, R.C., 1933. The biology of *Opius melleus* Gahan, a parasite of the blueberry maggot. *Journal of Agricultural Research* 46, 143–160.
- Lawrence, P.O., 1981. Host vibration—a cue to host location by the parasite *Biosteres longicaudatus*. *Oecologia* 48, 249–251.
- Meyhöfer, R., Casas, J., Dorn, S., 1994a. Host location by a parasitoid using leafminer vibrations: characterizing the vibrational signals produced by the leafmining host. *Physiological Entomology* 19, 349–359.
- Meyhöfer, R., Casas, J., Dorn, S., 1994b. Host location using vibrations by a leafminer's parasitoid: interpreting the vibrational signals produced by the leafmining host. In: *Proceeding of the 6th European Workshop on Insect Parasitoids*, vol. Supplement. Norwegian Journal of Agricultural Sciences, Biri, Norway, p. 407.
- Meyhöfer, R., Casas, J., Dorn, S., 1997. Vibration-mediated interactions in a host-parasitoid system. *Proceedings of the Royal Society London: Biological Sciences* 264, 261–266.
- Murlis, J., Elkinton, J.S., Cardé, R.T., 1992. Odor plumes and how insects use them. *Annual Review of Entomology* 37, 505–532.
- Pickett, J.A., Wadhams, L.J., Woodcock, C.M., Hardie, J., 1992. The chemical ecology of aphids. *Annual Review of Entomology* 37, 67–90.
- Prince, G.J., 1976. Laboratory biology of *Phaenocarpa persimilis* Papp (Braconidae; Alysiinae) a parasitoid of *Drosophila*. *Australian Journal of Zoology* 24, 249–264.
- Quednau, F.W., 1967. Notes on mating behaviour of *Chrysocharis laricinella* (Hymenoptera: Eulophidae), a parasite of the larch case-bearer (*Coloephora laricinella*). *Canadian Entomologist* 99, 326–331.
- Quicke, D.L.J., 1997. *Parasitic Wasps*. Chapman and Hall, London.
- Ryan, R.B., Rudinsky, J.A., 1962. Biology and habitats of the Douglas-fir beetle parasite, *Coeloides brunneri* Viereck (Hymenoptera: Braconidae), in Western Oregon. *Canadian Entomologist* 94, 748–763.
- Schüch, W., Barth, F.G., 1990. Vibratory communication in a spider: Female response to synthetic male vibrations. *Journal of Comparative Physiology A* 166, 817–826.
- Sokolowski, M.B., Turlings, T.C.J., 1987. *Drosophila* parasitoid-host interactions: Vibrotaxis and ovipositor searching from the hosts perspective. *Canadian Journal of Zoology* 65, 461–464.
- Sugimoto, T., Shimono, Y., Hata, Y., Nakai, A., Yahara, M., 1988a. Foraging for a patchily-distributed leaf miners by parasitoid, *Dapsilarthra rufiventris* (Hymenoptera: Braconidae). III. Visual and acoustic cues to a close range patch-location. *Applied Entomology and Zoology* 23, 113–121.
- Sugimoto, T., Ichikawa, T., Mitomi, M., Sakuratani, Y., 1988b. Foraging for a patchily-distributed leaf miners by parasitoid, *Dapsilarthra rufiventris* (Hymenoptera: Braconidae). IV. Analysis of sound emitted by a feeding host. *Applied Entomology and Zoology* 23, 209–211.
- Van Alphen, J.J.M., Drijver, R.A.B., 1982. Host selection by *Asobara tabida* Nees (Braconidae; Alysiinae) a larval parasitoid of fruit inhabiting *Drosophila* species. *Netherlands Journal of Zoology* 32, 215–231.
- Van Alphen, J.J.M., Janssen, A.R.M., 1982. Host selection by *Asobara tabida* Nees (Braconidae; Alysiinae) a larval parasitoid of fruit inhabiting *Drosophila* species. II. Host species selection. *Netherlands Journal of Zoology* 32, 194–214.
- Van den Assem, J., Kuenen, D.J., 1958. Host finding of *Choetospila elegans* Westw., a parasite of *Sitophilus granarius* L. *Entomologia Experimentalis et Applicata* 1, 174–180.
- Van Dijken, M.J., van Alphen, J.J.M., 1998. The ecological significance of differences in host detection behaviour in coexisting parasitoid species. *Ecological Entomology* 23, 265–270.
- Vet, L.E.M., Dicke, M., 1990. Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology* 37, 141–172.
- Vet, L.E.M., Alphen, J.J.M.V., 1985. A comparative functional approach to the host detection behaviour of parasitic wasps. 1. A qualitative study on Eucolidae and Alysiinae. *Oikos* 44, 478–486.
- Vet, L.E.M., Bakker, K., 1985. A comparative functional approach to the host detection behaviour of parasitic wasps. 2. A quantitative study on eight eucoilid species. *Oikos* 44, 487–498.