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- 3 R.J. Britten and J. Smith, *Carnegie Inst. Wash. Yearb.* 68, 378 (1970).
- 4 D.A. Wilson and C.A. Thomas, Jr, *J. molec. Biol.* 84, 115 (1974).
- 5 C.A.G. Haasnoot, J.H.J. den Hartog, J.F.M. de Rooij, J.H. van Boom and C. Altona, *Nucleic Acids Res.* 8, 169 (1980).
- 6 N. Hardman, A.J. Bell and A. McLachlan, *Biochim. biophys. Acta* 564, 372 (1979).
- 7 M. Brabic and M.J. Fraser, *Biochim. biophys. Acta* 240, 23 (1971).
- 8 C.W. Schmid, J.E. Manning and N. Davidson, *Cell* 5, 159 (1975).
- 9 P.J. Dott, C.R. Chuang and G.F. Saunders, *Biochemistry* 15, 4120 (1976).
- 10 H.J. Lin and C.L.H. Lee, *Analyt. Biochem.* 96, 144 (1979).
- 11 H.L. Klein and S.K. Welch, *Nucleic Acids Res.* 8, 4651 (1980).
- 12 T.J. Kelly, Jr, and H.O. Smith, *J. molec. Biol.* 51, 393 (1970).
- 13 A.M. Maxam and W. Gilbert, *Proc. natl Acad. Sci. USA* 70, 3581 (1973).
- 14 W.R. Jelinek, *J. molec. Biol.* 115, 591 (1977).
- 15 W.R. Jelinek, G. Molloy, R. Fernandez-Munoz, M. Salditt and J.E. Darnell, *J. molec. Biol.* 82, 361 (1974).
- 16 D. Drahovsky, T.L.J. Boehm and W. Kresis, *Biochim. biophys. Acta* 563, 28 (1979).
- 17 M.H. Schneiderman and D. Billen, *Biochim. biophys. Acta* 308, 352 (1973).
- 18 G.R. Wyatt, in: *The Nucleic Acids*, vol. 1, p. 243. Ed. E. Chargaff and J.N. Davidson. Academic Press, New York 1955.
- 19 G.H. Beaven, in: *The Nucleic Acids*, vol. 1, p. 493. Ed. E. Chargaff and J.N. Davidson. Academic Press, New York 1955.
- 20 A. Razin and J. Sedat, *Analyt. Biochem.* 77, 370 (1977).
- 21 J.W. Drake and R.H. Baltz, *A. Rev. Biochem.* 45, 11 (1976).
- 22 J.H. Taylor, in: *Molecular Genetics*, part 3, p. 89. Ed. J.H. Taylor. Academic Press, New York 1979.
- 23 J.E. Gill, J.A. Mazrimas and C.C. Bishop, Jr, *Biochim. biophys. Acta* 335, 330 (1974).

### Location of a lure by the drumming insect *Pimpla instigator* (Hymenoptera, Ichneumonidae)

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**Summary.** Females of the parasitoid *Pimpla instigator* (Hymenoptera, Ichneumonidae) are able to locate a lure hidden in a paper sheath. The lure is located without having been touched or sighted, and without any olfactory stimuli. We propose that the ability to locate the lure is linked with the drumming behavior of the females.

Most studies on host invasion by hymenopteran endoparasites have been concerned with its 1st step, host selection<sup>1</sup>. The general conclusion is that olfactory, visual and tactile stimuli may all be involved in the process. Some additional information has been obtained by Carton<sup>2-5</sup>, working on *Pimpla instigator*, a large ichneumonid which parasitizes the pupae of Lepidoptera. *Pimpla* females were shown to be attracted by protruding objects, and they tend to perforate any cylindrical object with a diameter close to that of a pupa. Also, they can locate a *Pieris brassicae* pupa even when it is hidden behind sheet of paper.

Under these conditions, host selection is likely to have involved the interaction of several sensorial functions. We have attempted to evade this obstacle by replacing the pupal host by a substitute as neutral as possible. Cigarette filter-tips are actively perforated by *Pimpla* females (fig. 1): we tried to find out whether this lure could be located as

well as a pupa. (It should be noted that eggs were never laid into the filter.)

In a 1st experiment (fig. 2, A), the filter was placed in the middle of a sheath made of thin paper (32 g/m<sup>2</sup>). Most perforations were observed to be associated with the filter. The next series of tests (fig. 2, B) involved 2 filters, each of them at a distance of 4 cm from 1 extremity of the sheath. Most perforations were again found to be associated with the lures. So the females were able to locate the filter whatever its position was in the sheath.

In a 3rd experiment, females were presented with a sheath made of thick paper (80 g/m<sup>2</sup>) which had a filter in the middle (fig. 2, C). The perforations were now observed to be uniformly distributed along the sheath (the females utilized were checked both before and after these experiments, and found to be fully able to locate the lure when it was hidden behind thin paper).

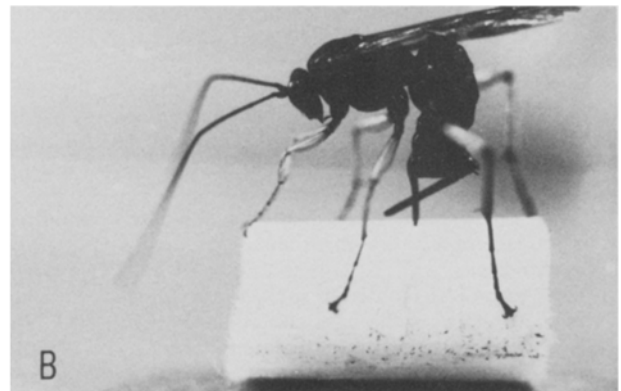
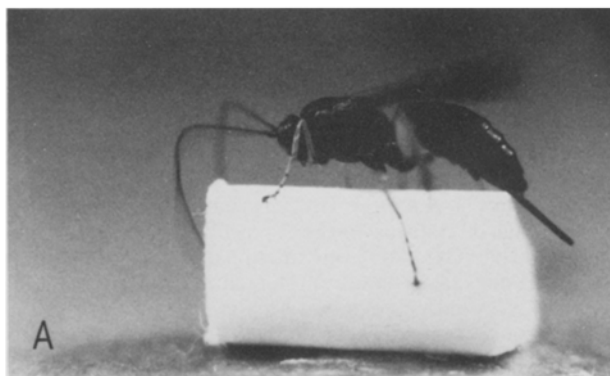


Figure 1. 2 behavioural elements of *Pimpla instigator*. A *Pimpla* female explores (A) and perforates (B) a cigarette filter.

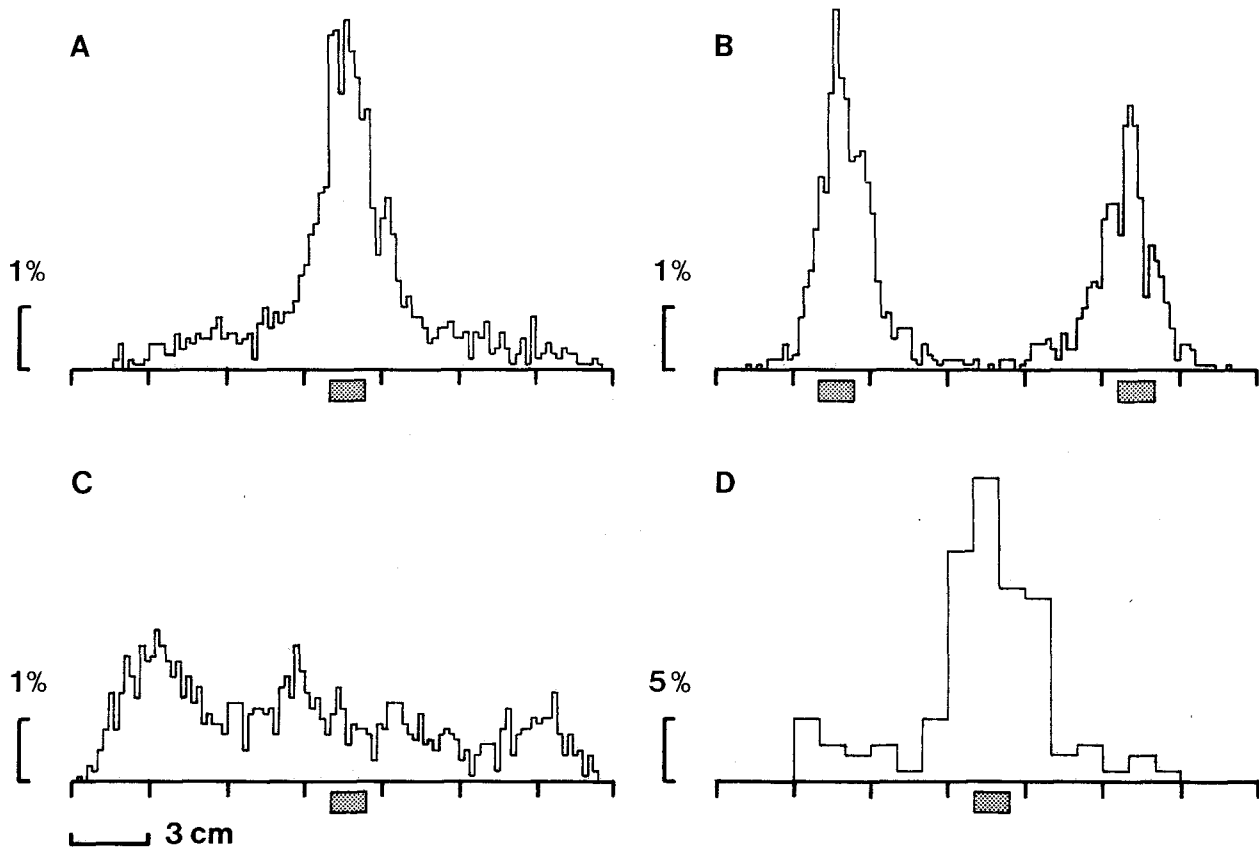


Figure 2. Measurements of the ability of *Pimpla instigator* females to locate a lure. A cigarette filter RIZLA (length 14 mm, diameter 8 mm) was introduced into a paper sheath (length 210 mm, diameter 8 mm). Sheaths were exposed to groups of 14 females in a plastic box of 30 × 30 × 25 cm. Females originated from the laboratory breeding stock<sup>8</sup>. Time of exposure was 24 h in figures A, B and C. This time allows each female to make in average 93 perforations. The test was repeated 10 times for each. The repetitions were homogeneous for each experimental condition. In figure D, the sheath and filter were changed after each perforation and the test was repeated 103 times. After exposure, lines 2 mm apart were ruled on the sheaths, and perforations counted in each section. [shaded box] filter; A light paper, 1259 perforations. B light paper, 1600 perforations. C heavy paper, 1204 perforations. D light paper, 103 perforations. The ordinate represents percent of the total number of holes. The abscissa represents the dimensions of the paper sheath.

The comparison between this result and experiment 2A excludes the possibility that the lure is first encountered by accident and that females find it again either by memorizing its whereabouts, or making direct contact with their antennae through already existing perforations. The same conclusion may also be reached in a more direct way by removing both filter and sheath after each perforation (using thin paper, with the filter placed in the middle, as in fig. 2, A). By repeating this test (fig. 2, D) we have checked that females perforate in the right place from the outset, without there being any preexisting perforation. The lure is thus located without having been touched or sighted. It is very unlikely that olfactory stimuli exist for cigarette filters. Since none of the sensory functions usually invoked for the natural prey can account for our observations, how then was the lure located? Some clues to the answer may be obtained by watching the exploratory behaviour of females. When moving along the sheath, they may be observed to tap the paper gently with their antennae, which are held at right angles to the surface.

From time to time the insect comes to a standstill and the drumming rate then increases, a sequence that often results in the paper eventually being perforated. We have recorded the drumming of the antennae. We have systematically explored its frequency spectrum and found it to vary, depending on the object being probed, which means that part of it must consist of vibrations of the substratum (data to be published elsewhere).

We therefore propose that *Pimpla instigator* females identify the whereabouts of the lure during their antennae drumming activity through the spot sounding 'solid'. Experiment 2C may be accounted for by the paper being heavy enough to hinder perception of the additional muffling brought about by the filter.

Insects are known to be highly sensitive to vibrations transmitted by solids<sup>6</sup>. Some arthropod species are even known to rely exclusively on the vibrations emitted by their prey in order to spot it<sup>7</sup>. Antennae drumming activity has been described in other insect species, and especially among hymenopteran parasites whose hosts dwell in a capsule, a gall or behind the bark of trees, and those which attack eggs<sup>1</sup>. We propose, as a working hypothesis, that insects showing drumming behavior generate a noise in order to gain information about the object on which they are resting. Such a sensory function might be called 'acoustic probing' by analogy with its industrial counterpart.

- 1 S.B. Vinson, A. Rev. Ent. 21, 109 (1976).
- 2 Y. Carton, Entomophaga 16, 285 (1971).
- 3 Y. Carton, Entomophaga 18, 25 (1973).
- 4 Y. Carton, Entomologia exp. appl. 17, 265 (1974).
- 5 Y. Carton, Entomophaga 23, 249 (1978).
- 6 J. Schwartzkopf, in: 'The Physiology of Insecta', vol. 2, chapter 6, p. 273. Ed. Rockstein. Academic Press, New York 1974.
- 7 P. Brownell and R.D. Farley, Anim. Behav. 27, 185 (1979).
- 8 J. Guerdoux and M. Masselot, Entomophaga 25, 389 (1980).