# Catching Ariadne by her thread: how a parasitoid exploits the herbivore's marking trails to locate its host

Thomas S. Hoffmeister[1], Bernard D. Roitberg & Robert G. Lalonde[2]
*Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby,
B.C., Canada (Fax: ++49-(0)431-8804368; E-mail: thoffmeister@zoologie.uni-kiel.de);* [1]*Current address: Zoologisches Institut, Ökologie, Christian-Albrechts-Universität, Am Botanischen Garten 1-9, D-24098 Kiel, Germany;*
[2]*Current address: Department of Biology, Okanagan University College, 3333 College Way, Kelowna, B.C.
V1V 1V7, Canada*

## Abstract

Chemical signals that can be associated with the presence of a host insect often work as arrestants in close range
host location by parasitoids, leading to longer searching times on patches where such signals are present. Our
current view of parasitoid host location is that by prolonging the search times in patches, randomly searching
parasitoids enhance their chance of detecting host insects. However, prolonged search times are not necessarily
the only modification in parasitoid behaviour. In this study, we examine the exploitation of host-fruit marking
pheromone of rose-hip flies, *Rhagoletis basiola* Osten-Sacken (Diptera: Tephritidae) by the specialized egg-larval
parasitoid *Halticoptera rosae* Burks (Hymenoptera: Pteromalidae). We provide evidence that the instantaneous
probability that a host egg will be located by a searching parasitoid wasp differs markedly between pheromone-
marked and unmarked fruits. The arresting response to the marking pheromone, i.e., the prolonged time a wasp
is willing to search on marked fruits, can only account for a small fraction of the difference in successful host
location on marked and unmarked fruits. We further demonstrate that the time wasps require to locate the host
egg is independent of the size of the rose-hip harbouring the fly egg, and thus is independent of the area the wasp
potentially has to search. A comparison of our findings with results of different search algorithms for parasitoid
wasps suggests that wasps use the fly's pheromone marking trail as a guide way to the fly's oviposition site and
thus the host egg.

Reproduction in insect parasitoids depends on the successful search for hosts, usually immature insects, into or onto which female parasitoids lay eggs. The parasitoid offspring subsequently kills these insect hosts and utilizes them for larval development. Consequently, successful host location is a major component of a parasitoid's fitness. Usually, parasitoid foraging for hosts takes place in complex and structured environments, where the patchy distribution of hosts makes successful host location a major obstacle. Consequently, cues revealing the presence of hosts can act as strong selective forces in parasitoids. Cues which reliably indicate the presence of an insect host may emanate from damaged plant tissue and frass of the host and may serve as kairomones for parasitoid host location (Weseloh, 1981; Vet & Dicke, 1992; Agelopoulos & Keller, 1994; Potting et al., 1995; Suiter et al., 1996; Rose et al., 1997). However, when hosts are concealed or inactive, such cues may not be readily available. Under such conditions, parasitoids may use an infochemical detour and spy on the chemical communication of adult stages of the host species (Prokopy & Webster, 1978; Vinson, 1984; Noldus, 1989; Roitberg & Lalonde, 1991; Wiskerke et al., 1993; Aldrich, 1995; Hoffmeister & Gienapp, 1999). Often, such cues are exploited during short

range host location and act as arrestants, increasing the time a parasitoid female invests into searching the patch (e.g., Waage, 1978; Galis & van Alphen, 1981; Dicke et al., 1985; van Alphen & Vet, 1986; Noldus et al., 1988). This increase in residence time on the kairomone containing patch usually stems from an inverse orthokinetic response (i.e., a decrease in walking speed or actual stopping) on the area contaminated with kairomone and a klinotaxic response (i.e., a directed turn back to the area contaminated with kairomone) when contact with the kairomone is lost (Waage, 1978). Thus, the currently held view is that arrestant chemicals do not provide directional information, but reveal the possible presence of a host in the near vicinity and thus lead to localized and prolonged search (Lewis et al., 1976; Vinson, 1976; Godfray, 1994). Congruent with this view, theory for parasitoid foraging behaviour predominantly assumes random search for hosts in parasitoid wasps (see Godfray, 1994, for a recent review). If arrestant chemicals facilitate directed search for hosts, this would perhaps change our view of host-parasitoid interactions and require that we test the importance of non-random search to host-parasitoid theory (see, e.g., Green, 1987 for the effect of non-random search on optimal patch leaving rules).

In tephritid fruit flies, host eggs are laid into the larval feeding site and few, if any, direct cues may be available that parasitoids can associate with the presence of a host egg or young larva. Here, parasitoids evidently exploit the communication of adult fruit flies, wherein many of the fruit infesting species use contact pheromones to mark exploited oviposition sites (Roitberg & Prokopy, 1987). Such host marking pheromones (HMP) facilitate oviposition decisions in tephritid fruit flies, because they allow females to discriminate between unexploited and egg-infested fruits and thus avoid potentially lethal competition among fly offspring (Roitberg & Mangel, 1988). These pheromones are deposited on the fruit by the female immediately after oviposition. Typically, a female fly will lift her ovipositor from the oviposition puncture and walk across the fruit while dragging her ovipositor across the fruit surface leaving criss-crossing trails of HMP behind (Hoffmeister, unpubl.; Prokopy, 1972; Averill & Prokopy, 1981; Roitberg & Prokopy, 1987; Averill & Prokopy, 1988). Since the marking pheromone persists on the marked fruit for a couple of days (see, e.g., Averill & Prokopy, 1987b), both flies and parasitoids may potentially use the HMP as an information source. Three parasitoid species attacking the eggs or young larvae of tephritid fruit fly hosts have been reported to respond to the fly's HMP as a kairomone for host location by searching longer on pheromone marked than on unmarked fruits (Prokopy & Webster, 1978; Roitberg & Lalonde, 1991; Hoffmeister & Gienapp, 1999). However, it has hitherto remained untested whether the prolonged search times on HMP-marked fruits can explain the much higher success rates in host location on marked compared with unmarked fruits. We here provide two lines of indirect evidence that *Halticoptera rosae* wasps, which attack the eggs of *Rhagoletis basiola* rose-hip flies, exploit the host fly's HMP to locate the oviposition site of the adult fly directly and subsequently parasitize the egg.

The rose-hip fly *Rhagoletis basiola* is a univoltine tephritid fly that is widely distributed across North-America and develops in the fruit of at least 13 species of rose bushes (*Rosa* spp.) (Bush, 1966). It was recently found to attack apples at low frequency in Oregon (Westcott et al., 1985). In western British Columbia, Canada, its main host plants are *Rosa nutkana* and hybrids of *R. nutkana* and *R. pisocarpa* (Roitberg & Mangel, 1997). Females lay single eggs into the hypanthium of rose-hips and subsequently mark the fruit with a contact host marking pheromone which allows flies to recognize prior infestation of rose-hips (Averill & Prokopy, 1981) and thus avoid situations of lethal competition among fly larvae. Hatching maggots feed within the hypanthium for about three weeks where they cause necrosis, yet do not destroy the seeds (Roitberg & Mangel, 1997). Upon maturity, larvae drop from the fruits and burrow into the soil, where they pupate and hibernate (Roitberg & Mangel, 1997). Although four species of parasitoids are reported as attacking *R. basiola* (Hoffmeister & Vidal, 1994), the specialized egg-larval parasitoid *Halticoptera rosae* was the only parasitoid species found in more than eight years of collections at natural stands of rose bushes in the lower Fraser Valley and on Vancouver Island, British Columbia, Canada. *Rhagoletis basiola* is the only host for this parasitoid recorded so far (Herting, 1982). The wasp, like its host, is univoltine and the adult occurs simultaneously with host fly adults in the field, where it searches rose-hips for fly eggs and exploits the fly-host's marking pheromone for host location (Roitberg & Lalonde, 1991). *Halticoptera rosae* is a koinobiotic parasitoid and thus parasitoid larvae kill and consume the host only after the formation of the fly puparium in the soil.

In this study, we re-analyse data from an earlier experiment (Roitberg & Lalonde, 1991) to elucidate how search time affects the probability of detecting a host's oviposition site on unmarked vs. marked fruits. Furthermore, we test for the effect of fruit size on the time a wasp needs to locate the host's oviposition site. Taken together, the evidence suggests that we should modify the way that we view parasitoid response towards contact kairomones. There may be more instances where such kairomones not only increase the time a wasp is willing to search in a patch, but allow directed search for the host (e.g., Doutt, 1964; Vinson & Lewis, 1965; Klomp, 1981).

## Methods

*Experimental procedure.* To obtain flies and parasitoids, rose-hips infested with fully grown fly larvae were collected the year prior to the experiment. Fly puparia were overwintered at 3–4 °C for nine months, and then incubated at 21 or 25 °C for the two experiments. Upon emergence, *Rhagoletis basiola* flies and *Halticoptera rosae* wasps were transferred to separate cages. The flies were fed yeast hydrolysate, sugar, and water (Prokopy & Boller, 1970); parasitoid wasps were fed honey and water (Peterson, 1964). To obtain fruits for experiments, rose-hips of natural hybrids of *Rosa nutkana* and *Rosa pisocarpa* were collected from a natural stand on Barnston Island in the lower Fraser Valley (British Columbia, Canada). All fruits used in experiments were kept in gauze bags in the field from late June onwards to prevent infestation by local populations of *R. basiola*.

In the first experiment, individual wasps were presented with either an infested but unmarked fruit (flies were allowed to oviposit but were removed from the fruit before they could start marking) (N = 14), or an infested + marked fruit (flies were allowed to oviposit and mark the fruit with HMP until they stopped marking and either left the fruit or started preening) (N = 21). A test fruit was held over a vial containing a single wasp until the wasp hopped onto the fruit, after which the vial was removed. If the wasp did not remain on the fruit for at least 10 s that trial was excluded from further analysis. Wasps were only used once and for each wasp, it was noted whether or not she located the host egg, and how long she needed to locate the host or, if she did not detect the fly's oviposition site, how long she searched before she would give up searching and leave the fruit. Note that times given

in this paper reflect search times (i.e., times parasitoids performed other kinds of behaviour like resting or preening were excluded from analysis, because information about the presence and location of hosts can only be obtained while searching) and differences between treatments can only be attributed to different success rates per unit search time. A problem with estimating a host's probability to be found as a function of a wasp's search time accrues from the fact that some wasps give up searching before they detect the host. This leads to censored data (the event of host detection did not occur) that should not be excluded from analysis, because they contain the information that at least to the point where the wasp left the fruit, the search time was insufficient to detect a host. Consequently, the effect of fly-HMP on success in wasp host location was analyzed using Cox regression (SPSS 6.0) which allows one to analyze time series data with censored observations, i.e., where the host was not detected, and to compute a host's propensity to be detected as a function of wasp searching time.

In the second experiment, individual wasps were presented with infested and HMP-marked rose-hips of different sizes. Fruits (and thus fruit sizes) used in the experiments represented a random sample from the bagged fruits brought into the laboratory. The rose-hips were presented to rose-hip flies in a population cage and a female that started probing into a fruit was transferred to a vial, where it could finish oviposition and mark the rose-hip with pheromone. The rationale underlying this experiment was to demonstrate that search success of wasps is not due to chance alone. If *H. rosae* wasps would search randomly for host eggs, we would expect that average search time required to detect a host on a given fruit should increase with increasing fruit size. Again, wasps were only used once, and the search time a wasp needed to locate the host's oviposition site was recorded along with the diameter of the fruit (i.e., the maximum width of the fruit, measured by using a hand-held micrometer, as a proxy for searchable fruit surface, which is the variable of interest in this experiment). All experiments were run in a climatized room at 20 ± 2 °C, 50 to 60% r.h., and L16:D8 light regime.

*Algorithms to generate expected values for search times needed for host location with different search mechanisms.* In order to elucidate whether *H. rosae* wasps locate hosts through (1) random search on rose-hips, or (2) exploiting the fly's HMP by directly following the trail, or (3) systematic search, algo-

rithms were developed that generate expected values for the time parasitoids need for host location on fruits of various sizes for each of the three search mechanisms. In all models the searchable fruit surface is represented by a two-dimensional grid, where the three-dimensionality of fruits was restored in that wasps which leave the grid at one side would re-enter the grid from the opposite side. Wasps produce search paths of 1.177 mm width (i.e., the average width of a wasp's head which we assume to represent the lateral area she can cover with her antennae while searching) and thus search an area of 1.385 mm$^2$ per time instant, i.e., one cell of the grid.

Randomly searching wasps in models (1) and (2) perform a constrained random walk, i.e., the wasp has the choice to walk straight or to turn 45° or 90° to either side into a neighbouring cell at each time instant, and she does this with equal probabilities. However, she cannot walk backwards in a given time instant and thus is constrained from a true random walk. Grids searched by model-(2) wasps are marked with a HMP trail. This trail is of identical length on fruits of all sizes. (Note, however, that whether the trail is of constant length, increases in proportion to fruit circumference or to fruit surface does not alter the general findings of the model.) It originates at the fly's oviposition site and leads in four circles around the fruit. As soon as a wasp walks onto the HMP-trail, she will follow this trail to the fly's oviposition site.

Search times needed to locate the host were modelled for six different fruit sizes (with surface areas of 554, 670.34, 797.76, 936.26, 1085.84, and 1246.5 mm$^2$). For models (1) and (2), 5000 replicates of simulations were run, where the location of the host and the starting point of the wasp, i.e., the cell on the grid, were randomly chosen.

Model-(3) wasps search systematically for the host. Thus, every cell of the grid is visited only once, and the probability $P$ to detect the host in one time instant is

$$P = N^{-1}, \tag{1}$$

where $N$ is the number of cells on the grid, i.e., an area of $N$ times 1.385 mm$^2$. Every increase in fruit size, accompanied by an increase in the area $\Delta A$ of fruit surface a wasp might search, leads to a increase of cells which a wasps has to search
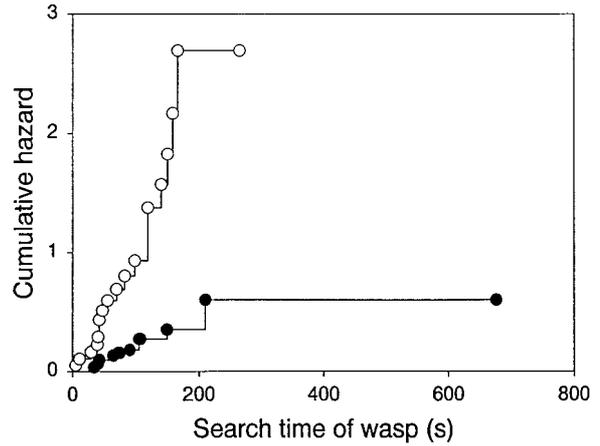
$$\Delta N = \Delta A / 1.385 \tag{2}$$



*Figure 1.* The search-time dependent hazard that a host egg will be detected by a searching parasitoid wasp, expressed as cumulative hazard functions of the Cox proportional hazard model for hosts on HMP-marked rose-hips (open circles) and unmarked fruits (filled circles). Note that the hazard function is not a probability but gives the death rate of host eggs per unit of parasitoid search time, and thus need not be less than unity. The hazard function thus gives information how likely a host will be detected at time t, given it was not detected until time t (Norusis, 1994). The circles represent the cumulative hazard at the search times found in the first experiment for the respective treatments.

and a decrease in the probability to find the host per time instant

$$\Delta P = 1/\Delta N. \tag{3}$$

Consequently, there is a linear relationship between the average time $\bar{T}$ a wasp needs to locate the host and the surface area $A$ of the fruit

$$\bar{T} = 0.5A/1.385 \tag{4}$$

(Figure 3).

## Results

Analysis of the search-time dependent hazard to a host egg on infested + marked vs. infested but unmarked fruits (Figure 1) indicates that search time alone cannot account for the difference in success in host location on infested + marked vs. infested but unmarked fruits. The presence of the HMP-trails on egg-infested fruits has a significant positive effect on the probability per unit of parasitoid search time that a host will be detected (Cox regression: coefficient $\beta = 1.4941$, Test statistic = 5.6107, df = 1, P = 0.0179, N = 33). Thus, host eggs on marked fruits faced a much higher probability of detection per unit search time of wasps than on unmarked fruits
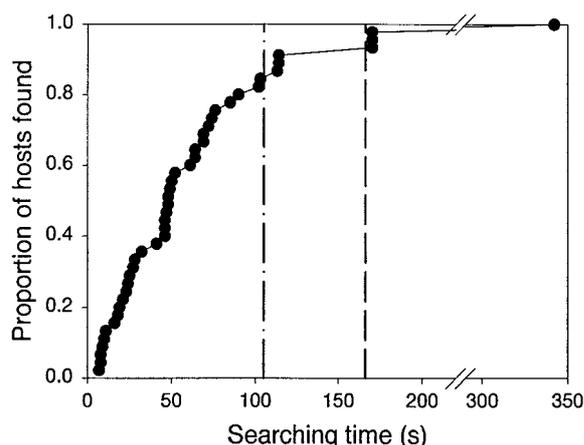
*Figure 2.* Cumulative success in host location as a function of search time (filled circles and solid line) (from the second experiment) superimposed on the search times before *Halticoptera rosae* wasps gave up searching on egg-infested, but unmarked rose-hips (dash-dotted line) and on egg-infested and HMP-marked rose-hips (dashed line) (data from the first experiment).

(Figure 1). Parasitoid wasps located the host's oviposition site on HMP-marked fruits in 95% (N = 21) and 100% (N = 45) of trials in the first and second experiment, respectively. If success in host location is solely a function of the search time wasps are willing to invest before they give up the search, we could predict the proportion of hosts that wasps could detect on infested but unmarked fruits from the relation between search time and success in host location on HMP-marked fruits (Figure 2). If the time that wasps search on marked fruits before giving up (i.e., median $\pm$ SE = 166 $\pm$ 12.29 s) is sufficient to detect 93% of hosts (the intersection of the graph for the proportion of hosts found with the giving up time on infested and marked fruits, represented by the dashed line in Figure 2), then the search time wasps invest on infested but unmarked fruits (median $\pm$ SE = 105 $\pm$ 16.74 s) should allow the detection of 85% of hosts (the intersection of the graph for the proportion of hosts found on infested and marked fruits with the giving up time on infested but unmarked fruits, represented by the dash-dotted line in Figure 2). However, wasps actually found only 29% of hosts on infested but unmarked fruits (in N = 4 of N = 14 trials) in our first experiment.

In the second experiment, we tested what effect fruit size, and thus the area a parasitoid has to search to locate the host, has on the time the parasitoid needs for host location. To be able to relate observed search times needed for host location to a

search mechanism of parasitoids, we generated expected values for the search time until host location using algorithms for parasitoids engaging in (1) random search, (2) random search until contact with the host's HMP after which the parasitoid exploits the HMP directly by following the trail towards its origin, i.e., the fly's oviposition site, and (3) systematic search on fruits. When parasitoids engage in random search for hosts the search time needed for host location is expected to increase linearly with the surface of the fruit (Figure 3A, $y = 0.446A - 39.835$; $r^2 = 0.091$, $F_{1,34998} = 3503.8$, P < 0.001; with $A$ = fruit surface [mm$^2$]). Similarly, when parasitoids search systematically and avoid repeated search of portions of the fruit surface, the search time needed for host location is expected to increase linearly with the surface of the fruit, although the increase in search time needed per unit increase in fruit surface is less than with random search (i.e., the slope of the function is shallower, with $y = 0.130A$, Figure 3A). When parasitoids engage in random search only until they contact the fly's marking trail and engage in directed search by following the marking trail to the fly's oviposition site, an extremely shallow increase in the search time needed for host location is expected as a function of increasing fruit surface (i.e. the slope is more than an order of magnitude shallower than in systematic search: $y = 0.008A + 49.189$; $r^2 = 0.105$, $F_{1,34998} = 4084.2$, P < 0.001, Figure 3A).

When *H. rosae* wasps searched for hosts on rose-hips of different size, no relationship between fruit size and the search time needed for locating the fly's oviposition site was found (filled circles in Figure 3B; regression of search time vs. fruit diameter $y = 0.02A + 40.198$, $r^2 = 0.007$, $F_{1,42} = 0.281$, P = 0.599, one extreme value, $t > 300$ s, excluded from the analysis; however including this data point does not alter the insignificant pattern, $y = 0.004A + 60.86$, $r^2 < 0.001$, $F_{1,42} = 0.005$, P = 0.945).

**Discussion**

Chemical substances exploited for close range host location by parasitoid wasps are often contact kairomones that usually work as arrestants (van Alphen & Vet, 1986). Such substances often elicit behavioural changes such as reduction in walking speed or an increase in the rate of turning (Waage, 1978; van Alphen & Vet, 1986) and thus reinforce
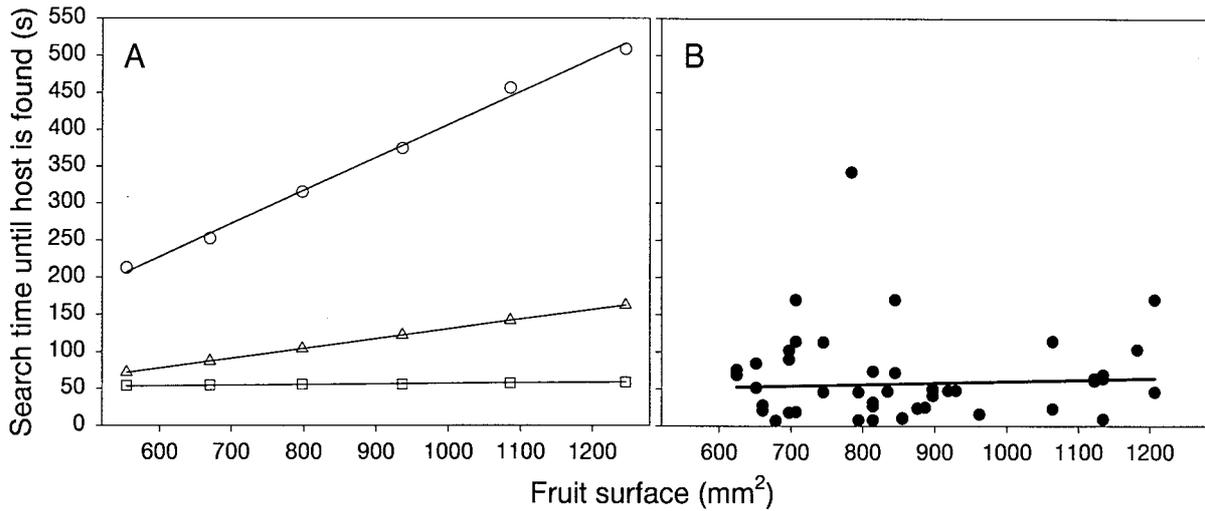
*Figure 3.* (A) Expected values for the search time wasps need to locate a fly host's oviposition site when engaging in (1) random search (open circles) and (2) random search with exploitation of HMP trails where, upon contact with the marking trail, wasps follow the trail until they encounter the host at the origin of the trail (open squares), and (3) systematic search (open triangles) (see Methods for details). (B) The search time *H. rosae* wasps needed to locate the fly host's oviposition site on fruits of different size and thus searchable fruit surface (the bold line represents the best fit for the data). Note that fruit surface for all fruits is assumed to be $4\pi(0.5 \text{ fruit-diameter})^2$, since hybrids of *R. nutkana* and *R. pisocarpa* are almost spherical.

an intensified searching behaviour in areas where the kairomone is present rather than allowing a directed search for the host (Lewis et al., 1976; Vinson, 1976, but see Doutt, 1964; Vinson & Lewis, 1965 and Klomp, 1981 for exceptions). For the three parasitoid wasp species exploiting the HMP of their tephritid fruit fly hosts, prolonged search times have hitherto been reported (Prokopy & Webster, 1978; Roitberg & Lalonde, 1991; Hoffmeister & Gienapp, 1999). In contrast, there have been no reports of direct exploitation of marks that would facilitate directed search for the host's oviposition site. For one of these species, search directed by the marking trail would be impossible, because the host stage attacked (the first instar larvae which feeds in the centre of the fruit) cannot be found through the fly's oviposition site (Hoffmeister & Gienapp, 1999). In the remaining two species the host is attacked in the egg stage, and therefore marking trails could at least potentially guide a wasp to the oviposition site. However, Prokopy & Webster (1978) argued that apple maggot flies (*Rhagoletis pomonella*) lay down the marking trail in apparently random fashion, repeatedly crossing itself, and it would therefore be impossible that the parasitoid *Opius lectus* would follow such trails to the fly's oviposition puncture.

Yet, our finding that *R. basiola* hosts face a much higher probability of detection per unit of parasitoid search time on HMP-marked than on infested but un-

marked fruits strongly suggests that *H. rosae* wasps directly exploit the HMP of *R. basiola* flies for location of host eggs on rose-hips, despite of the fact that marking trails sometimes cross. The longer time that wasps are willing to search on marked vs. unmarked fruits can only account for a small fraction of the difference in successful host location on infested + marked vs. infested but unmarked fruits. Consequently, the presence of HMP leads to non-random search for host eggs, and other potential sources of information like, e.g., odour emanating from the fly's oviposition puncture can be ruled out as cue exploited for non-random search. In another line of argument, our experiments with fruits of different sizes provide strong inference for the direct exploitation of the HMP. Search algorithms for wasps that do not exploit the HMP trail as a guide way to the fly's oviposition site produce a linearly increasing relationship between the time needed to locate the host and host fruit surface, irrespective of whether they represent random search or systematic search (Figure 3A). The only algorithm that explains the pattern found in our experiments suggests that the parasitoid directly exploits the HMP trail upon encounter and follows the trail to the fly's oviposition site (see Methods for details). Such an algorithm produces an extremely shallow elevation for the regression between the search time until host location and fruit surface that is comparable to the elevation which

gives the best fit with the experimental data. However, to obtain search times that are more or less independent of the fruit size requires the marking trail to be spread across a sufficient portion of the fruit surface in such a way that wasps commencing to search on a fruit will encounter the trail after spending only a short time on small as well as large fruits. As *R. basiola* flies mark the fruit while circling it for about 2 minutes ($\bar{x} \pm SE = 123.94 \pm 15.37$ s, N = 63; Hoffmeister unpublished) this condition should be met. Sensitivity analyses with trail length that are independent of fruit size or increase proportional to the circumference of the fruit (as suggested by Averill & Prokopy, 1987a for *Rhagoletis pomonella*) revealed that the extremely shallow increase of searching time needed for host location with increasing fruit size holds for a broad range of trail lengths that includes the range of values found so far for tephritid flies (Averill & Prokopy, 1989): when assuming trail length to be independent of fruit size, the slope of regressions for the time needed for host location as function of the fruit surface varied between $b = 0.028$ for short trails (where the trail circles medium sized fruits with 936 mm$^2$ surface twice) and $b = 0.002$ for long trails (where the trail circles medium sized fruits with 936 mm$^2$ surface eight times), respectively; when assuming trail length to increase with fruit circumference, the slope of regressions for the time needed for host location as function of the fruit surface varied between $b = 0.031$ for short trails (where the trail circles fruits of all sizes twice) and $b = 0.057$ for long trails (where the trail circles fruits of all sizes eight times), respectively. For comparison, the slope for a randomly searching wasp that does not exploit the marking trail is one order of magnitude higher with $b = 0.446$ (Figure 3A).

The suggestion that *H. rosae* wasps directly exploit the host's HMP furthermore is in line with our observations that wasps approaching the fly's oviposition puncture display a lower rate of turning (i.e., decreased klinotaxis) than observed on unmarked fruits and seldom miss the oviposition puncture, which is inconsistent with random search. Yet, since fly marking trails are invisible on the fruit and flies cannot be forced to lay down marking trails in a manipulated fashion, the best evidence we can obtain to date is the indirect evidence for the direct exploitation of HMP trails by *H. rosae* wasps presented here. Marking trails can be made visible with copy toner powder, but this method cannot be used in combination with searching wasps, since wasps stop searching and engage in preening upon getting in contact with powdery sub-stances. Moreover, substances that adhere to marking trails might interfere with recognition of the marking pheromone. Nevertheless, our experiments provide clear evidence for non-random search for hosts in *H. rosae*.

In conclusion, our results suggest that parasitoids may engage in non-random, rather than localized random search whenever a contact kairomone, or any other host-induced change in the quality of the substrate provides a perceivable trail leading to the host. Best candidates for an exploitation of chemical cues for directed host location are parasitoids of immobile host stages like eggs that are laid into small resources which are subsequently marked by the ovipositing female (e.g., herbivores infesting and marking fruits, flower heads, seeds, cones, or producing leaf-mines and marking the leaves, Prokopy, 1981; Quiring & McNeil, 1987; Averill & Prokopy, 1989; Straw, 1989; Quiring et al., 1998). Alternatively, vibrotaxis may lead to directed search for hosts (e.g., Sugimoto et al., 1988a; van Dijken & van Alphen, 1998) or optical cues of leaf-mines (e.g., Sugimoto et al., 1988a, b). Additionally, as Klomp (1981) has demonstrated, exposed feeding larvae may also be found through chemical trails they leave behind. A relevant issue here is to what extent search on patches becomes non-random as a consequence of exploitation of host associated cues. If, for example, parasitoids recognize small resource items like fruits as patches and detect host kairomones that facilitate directed search shortly after arrival on a patch, search within patches will be non-random to a large extent. This, in turn, should affect other aspects of parasitoid foraging behaviour like patch leaving decisions and might even affect our theoretical concepts which are based on an assumption of random search in parasitoids (see Godfray, 1994, for a recent review). For example, non-random search by individual parasitoids may have profound negative effects on local persistence and density of host populations.

# References

Agelopoulos, N. G. & M. A. Keller, 1994. Plant-natural enemy association in tritrophic system, *Cotesia rubecola – Pieris rapae* – Brassicaceae (Cruciferae). III: collection and identification of plant and frass volatiles. Journal of Chemical Ecology 20: 1955–1967.

Aldrich, J. R., 1995. Chemical communication in the true bugs and parasitoid exploitation. In: R. T. Cardé & W. J. Bell (eds), Chemical Ecology of Insects 2. Chapman and Hall, New York, pp. 318–363.

Alphen, J. J. M. van & L. E. M. Vet, 1986. An evolutionary approach to host finding and selection. In: J. K. Waage & D. J. Greathead (eds.), Insect Parasitoids. Academic Press, London, pp. 23–61.

Averill, A. L. & R. J. Prokopy, 1981. Oviposition deterring fruit marking pheromone in *Rhagoletis basiola*. Florida Entomologist 64: 222–226.

Averill, A. L. & R. J. Prokopy, 1987a. Intraspecific competition in the tephritid fruit fly *Rhagoletis pomonella*. Ecology 68: 878–886.

Averill, A. L. & R. J. Prokopy, 1987b. Residual activity of oviposition-deterring pheromone in *Rhagoletis pomonella* (Diptera: Tephritidae) and female response to infested fruit. Journal of Chemical Ecology 13: 167–177.

Averill, A. L. & R. J. Prokopy, 1988. Factors influencing release of host-marking pheromone by *Rhagoletis pomonella* flies. Journal of Chemical Ecology 14: 95–111.

Averill, A. L. & R. J. Prokopy, 1989. Host-marking pheromones. In: A. S. Robinson & G. Hooper (eds), Fruit Flies. Their Biology, Natural Enemies and Control. Elsevier, Amsterdam, pp. 207–219.

Bush, G. L., 1966. The taxonomy, cytology, and evolution of the genus *Rhagoletis* in North America. Bulletin of the Museum of Comparative Zoology 134: 431–562.

Dicke, M., J. C. van Lenteren, G. J. F. Boskamp & R. van Voorst, 1985. Intensification and prolongation of host searching in *Leptopilina heterotoma* (Thomson) (Hymenoptera: Eucoilidae) through a kairomone produced by *Drosophila melanogaster*. Journal of Chemical Ecology 11: 125–136.

Dijken, M. J. van & J. J. M. van Alphen, 1998. The ecological significance of differences in host detection behaviour in coexisting parasitoid species. Ecological Entomology 23: 265–270.

Doutt, R. L., 1964. Biological characteristics of entomophagous adults. In: P. DeBach (ed.), Biological Control of Insect Pests and Weeds. Chapman & Hall, London, pp. 145–167.

Galis, F. & J. J. M. van Alphen, 1981. Patch time allocation and search intensity of *Asobara tabida* Nees (Braconidea), a larval parasitoid of *Drosophila*. Netherlands Journal of Zoology 31: 596–611.

Godfray, H. C. J., 1994. Parasitoids. Behavioral and Evolutionary Ecology. Princeton University Press, Princeton.

Green, R. F., 1987. Stochastic models of optimal foraging. In: A. Kamil, J. Krebs & H. Pulliam (eds), Foraging Behaviour. Plenum Press, New York, pp. 273–302.

Herting, B., 1982. A Catalogue of Parasites and Predators of Terrestrial Arthropods, Section B: Enemy/Host or Prey, Vol. II: Hymenoptera Terebrantia. Commonwealth Agricultural Bureau, Farnham Royal.

Hoffmeister, T. S. & P. Gienapp, 1999. Exploitation of the host's chemical communication in a parasitoid searching for concealed host larvae. Ethology 105: 223–232.

Hoffmeister, T. S. & S. Vidal, 1994. The diversity of fruit fly (Diptera: Tephritidae) parasitoids. In: B. A. Hawkins & W. Sheehan (eds), Parasitoid Community Ecology. Oxford University Press, Oxford, pp. 47–76.

Klomp, H., 1981. Parasitic wasps as sleuthhounds: response of an ichneumon wasp to the trail of its host. Netherlands Journal of Zoology 31: 762–772.

Lewis, W. J., R. J. Jones, H. R. Gross & A. Nordlund, 1976. The role of kairomones and other behavioral chemicals in host finding by parasitic insects. Behavioral Biology 16: 267–289.

Noldus, L. P. J. J., 1989. Chemical espionage by parasitic wasps. How *Trichogramma* species exploit moth sex pheromones. PhD thesis, Wageningen Agricultural University, Wageningen: Netherlands.

Noldus, L. P. J. J., J. H. M. Buser & L. E. M. Vet, 1988. Volatile semiochemicals in host-community location of egg parasitoids. Colloques de l'INRA 48: 19–20.

Norusis, M. J., 1994. SPSS Advanced Statistics 6.1. SPSS Inc., Chicago.

Peterson, A., 1964. Entomological Techniques. How to Work with Insects. Entomological Reprint Specialists, Los Angeles, California.

Potting, R. P. J., L. E. M. Vet & M. Dicke, 1995. Host microhabitat location by stem-borer parasitoid *Cotesia flavipes*: the role of herbivore volatiles and locally and systemically induced plant volatiles. Journal of Chemical Ecology 21: 525–539.

Prokopy, R. J., 1972. Evidence for a marking pheromone deterring repeated oviposition in apple maggot flies. Environmental Entomology 1: 326–332.

Prokopy, R. J., 1981. Epideictic pheromones that influence spacing patterns of phytophagous insects. In: D. A. Nordlund, R. L. Jones & W. J. Lewis (eds), Semiochemicals. Their Role in Pest Control. John Wiley & Sons, New York, pp. 181–213.

Prokopy, R. J. & E. F. Boller, 1970. Artificial egging system for the European cherry fruit fly. Journal of Economic Entomology 63: 1413–1417.

Prokopy, R. J. & R. P. Webster, 1978. Oviposition-deterring pheromone in *Rhagoletis pomonella*: A kairomone for its parasitoid *Opius lectus*. Journal of Chemical Ecology 4: 481–494.

Quiring, D. T. & J. N. McNeil, 1987. Foraging behavior of a dipteran leaf miner on exploited and unexploited hosts. Oecologia 73: 7–15.

Quiring, D. T., J. W. Sweeney & R. G. Bennett, 1998. Evidence for a host-marking pheromone in white spruce cone fly, *Strobilomyia neanthracina*. Journal of Chemical Ecology 24: 709–721.

Roitberg, B. D. & R. G. Lalonde, 1991. Host marking enhances parasitism risk for a fruit-infesting fly *Rhagoletis basiola*. Oikos 61: 389–393.

Roitberg, B. D. & M. Mangel, 1988. On the evolutionary ecology of marking pheromones. Evolutionary Ecology 2: 289–315.

Roitberg, B. D. & M. Mangel, 1997. Individuals on the landscape: behavior can mitigate landscape differences among habitats. Oikos 80: 234–240.

Roitberg, B. D. & R. J. Prokopy, 1987. Insects that mark host plants. An ecological, evolutionary perspective on host-marking chemicals. BioScience 37: 400–406.

Rose, U. S. R., H. T. Alborn, G. Makranczy, W. J. Lewis & J. H. Tumlinson, 1997. Host recognition by the specialist endoparasitoid *Microplitis croceipes* (Hymenoptera: Braconidae): Role of host- and plant-related volatiles. Journal of Insect Behavior 10: 313–330.

Straw, N. A., 1989. Evidence for an oviposition-deterring pheromone in *Tephritis bardanae* (Schrank) (Diptera: Tephritidae). Oecologia 78: 121–130.

Sugimoto, T., T. Ichikawa, M. Mitomi & Y. Sakuratani, 1988a. Foraging for patchily-distributed leaf-miners by the parasitoid,

*Dapsilarthra rufiventris* (Hymenoptera: Braconidae) IV. Analyses of sounds emitted by a feeding host. Applied Entomology and Zoology 23: 209–211.

Sugimoto, T., K. Kawado & K. Tadera, 1988b. Responses to the host mine of two parasitic wasps, *Dapsilarthra rufiventris* (Hymenoptera: Braconidae) and *Chrysocharis pentheus* (Hymenoptera: Eulophidae). Journal of Ethology 6: 55–58.

Suiter, D. R., D. A. Carlson, R. S. Patterson & P. G. Koehler, 1996. Host-location kairomone from *Periplaneta americana* (L.) for parasitoid *Aprostocetus hagenowii* (Ratzeburg). Journal of Chemical Ecology 22: 637–651.

Vet, L. E. M. & M. Dicke, 1992. Ecology of infochemical use by natural enemies in a tritrophic context. Annual Review of Entomology 37: 141–172.

Vinson, S. B., 1976. Host selection by insect parasitoids. Annual Review of Entomology 21: 109–133.

Vinson, S. B., 1984. How parasitoids locate their hosts: A case of insect espionage. In: T. Lewis (ed.), Insect Communication. Acadamic Press, London, pp. 325–348.

Vinson, S. B. & W. J. Lewis, 1965. A method of host selection by *Cardiochiles nigriceps*. Journal of Economic Entomology 58: 869–871.

Waage, J. K., 1978. Arrestment responses of the parasitoid, *Nemeritis canescens*, to a contact chemical produced by its host, *Plodia interpunctella*. Physiological Entomology 3: 135–146.

Weseloh, R. M., 1981. Host location by parasitoids. In: D. A. Nordlund, R. L. Jones & W. J. Lewis (eds), Semiochemicals. Their Role in Pest Control. John Wiley & Sons, New York, pp. 79–95.

Westcott, R. L., M. T. Aliniazee & R. L. Penrose, 1985. *Rhagoletis basiola* in apple: A new host record. Pan-Pacific Entomologist 61: 262.

Wiskerke, J. S. C., M. Dicke & L. E. M. Vet, 1993. Larval parasitoid uses aggregation pheromone of adult hosts in foraging behaviour: a solution to the reliability-detectability problem. Oecologia 93: 145–148.