

## Host trail following by the guest ant *Formicoxenus provancheri*

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*Abstract.* *Formicoxenus provancheri*, a guest ant of *Myrmica incompleta*, is able to follow artificial trails made with the poison gland secretion of its host. The trail-following response is elicited at the same range of concentrations as for the host species. The performance of *Formicoxenus* is enhanced by the presence of the host. The adaptive value of these phenomena is discussed.

*Key words.* Artificial trails; trail-following; guest ants; parasite dissemination; *Myrmica*; *Formicoxenus*.

Guest ants, or xenobiotic ants, are social parasites<sup>1</sup>. They live in small colonies in the periphery of the larger nests of their host species. The brood is normally kept apart from the host chambers. The nearctic guest ant, *Formicoxenus provancheri*, has been studied recently<sup>2-4</sup>. It is known that each colony contains only one egg-laying female<sup>2</sup>. The other inseminated females do not lay unless the active queen disappears or unless they leave the parental chamber to found their own colony, either in the same host nest or in another one. The problem of parasite dissemination has been examined: Staeger<sup>5</sup> observed that *Formicoxenus nitidulus*, a palearctic species, follows the natural foraging trails of its host, the red wood ant *Formica pratensis* (a Formicinae species). This was confirmed recently, in the laboratory, by Elgert and Rosen-gren<sup>6</sup>, who showed in addition that the host foraging trails are followed by *F. nitidulus*, but less accurately than trails established during migration. It was interesting to investigate this phenomenon of host trail-following in the couple *F. provancheri*/*M. incompleta*, two species of the same subfamily (Myrmicinae), where foraging trails are mainly subterranean.

#### Materials and methods

Specimens of *Formicoxenus provancheri* and of their host, *Myrmica incompleta*, were collected from various parts of Québec, Canada, in June 1989, and reared in either mixed or homospecific colonies, according to the techniques previously published<sup>3,4</sup>.

The trail pheromone of *Myrmica rubra* is produced by the poison gland and its main compound is ethyl dimethyl pyrazine (EDMP)<sup>7,8</sup>. It was checked that *M. incompleta* ergates use the same pheromonal source and that EDMP is also the trail pheromone of this species<sup>9</sup>. The study of host trail following by *F. provancheri* compared several dilutions of poison gland extracts of *M. incompleta* prepared in hexane solutions. 100 µl of the solution were deposited on a circular trail. When testing several dilutions of pheromone we operated in order of increasing concentration.

Trails 10 cm in diameter were made by siphoning the trail pheromone solution from a calibrated vial through a Teflon tube onto an extra-strong Bristol paper disc. The trail pheromone solution was continuously delivered, using a peristaltic pump, and the tube tip was connected to a fine needle which contacted the paper disc placed on a rotating plate (45 R/min). This made a continuous flow of pheromone extract for multiple revolutions (roughly 20) until the correct volume was applied. This technique, already used by Gerardy and Verhaeghe<sup>10</sup>, gave trails which were uniform in concentration and had a narrow solvent line (1 mm width). The paper disc was then deposited in the foraging arena (plastic box 31 × 20 cm) of the tested society, the food being removed before the test. When an ant walked on the paper disc, it was observed, and if it went to the circumference the number of 10° arcs followed by the ant on the circumference was recorded.

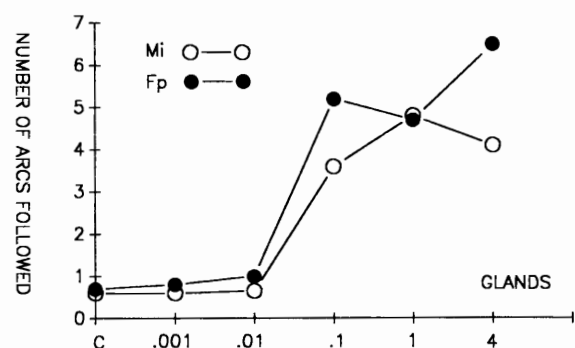
10-min observations were made for each trail. It was verified that *M. incompleta* workers do not reinforce the trail under these conditions: no gaster contact with the paper was observed. It is not known whether the *Formicoxenus* lay their own trails.

Distributions of numbers of 10° arcs run over by individual ants are presented by their medians and their quartiles. Comparisons with control (pure hexane) were made with the Chi-square test for the whole distribution, and the median test for the medians (the former being more sensitive).

#### Results

In a first set of experiments, artificial trails from extracts of *M. incompleta* were deposited into foraging areas of two pure homospecific *M. incompleta* societies, with increasing concentrations from 0.001 gland to 4 glands/trail (fig.). A rest of half an hour was left to the societies between two tests. The *Myrmica* workers begin to follow the trails at a concentration of 0.1 gland/trail, and with higher concentrations the results are similar. From 0.1 gland/trail the results are significantly different from those for the pure hexane control (Chi-square for the whole distribution and median test).

In a second set of experiments, the artificial trails of *M. incompleta* and control were deposited into foraging areas of two pure homospecific *Formicoxenus* societies, separated from the host for at least 15 days. The same concentrations increasing from 0.001 gland to 4 glands/trail were used (table). The ants were very responsive to the host trail pheromone: the distribution is significantly different even with 0.001 poison gland, although the median value is not significantly different from the control at this concentration, indicating that a few ants are more responsive (5% of the ants follow more than 4 arcs in controls versus 23.3% with 0.001 and 23.6% with 0.01 gland). The trail-following response becomes more marked with 0.1 gland: in this case the median increases from 0.7–0.8 to 5.2 arcs and then stabilizes at higher concentrations of 1 to 4 glands/trail. By plotting the medians of the guest and host ants' responses as a function of the trail concentrations, it appears that both spe-



Comparison of trail-following response (median number of arcs followed) of *M. incompleta* (*Mi*) and *F. provancheri* (*Fp*) workers for different concentrations of poison glands of *M. incompleta*.

Number of 10° arcs followed by individual *F. provancheri* on artificial trails with poison glands of the host *M. incompleta*.

Number of arcs followed	Number of host glands			A: <i>Fp</i> only			B: <i>Fp</i> + <i>Mi</i>
	Control	0.001	0.01	0.1	1	4	1
0	5	4	3	1	1	0	0
1	68	40	45	11	13	14	7
2–3	20	12	24	18	12	6	9
4–5	4	7	7	6	8	5	3
6–8	1	6	8	10	14	5	4
9–12		1	4	6	5	4	4
13–20		2	2	10	3	6	8
21–30		1	1	8	8	3	3
31–50				3	4	4	1
51–80				2	1	2	2
> 81					1	6	4
N	98	73	94	75	70	55	45
X <sup>2</sup>		*	*	***	***	***	***
							(1)
Median	0.7	0.8	1	5.2	4.7	6.5	7.5(2)
Median test		NS	NS	**	**	**	**
Quart	0.35–1.1	0.4–2.8	0.5–2.8	1.8–15.5	1.6–6.7	0.9–23.3	1.0–18.2

A: *Fp* only: *F. provancheri* pure homospecific societies.

B: *Fp* + *Mi*: one host gland tested with *F. provancheri* living in *Fp-Mi* mixed colony as compared to one host gland tested with *Fp* living in a homospecific colony. (1): distribution  $0.05 < p < 0.10$  NS; (2): median  $p < 0.01$ .

N: Number of ants followed. Significant with  $p < 0.05$ :\*,  $p < 0.01$ :\*\*,  $p < 0.001$ :\*\*\*.

X<sup>2</sup> and median compared to control.

cies begin to follow the trail at the same concentration of 0.1 gland/trail with slightly higher (but not significant) performances of the guest ant at the optimal concentrations (fig.).

In a third experiment, a paper with a one-gland host extract was introduced into the foraging arena of a mixed society (*F. provancheri* with their host *M. incompleta*). The results show that the performance of *Formicoxenus* is enhanced by the presence of the host: the Chi-square is not significant ( $0.05 < p < 0.10$ ) but the median is significantly higher, indicating a slight augmentation of the response of the ants (table).

#### Conclusions and discussion

Our experiments show that *F. provancheri* are able to follow the trails of their host *M. incompleta*. The trail-following response is elicited by the same range of concentrations as for the host species (from 0.1 gland to four glands/trail). We did not use more concentrated trails, which could have had repellent effects on the parasite, as reported for the myrmecophilous beetle *Edaphopausus favieri* facing high concentrations of *Pheidole pallidula* ants<sup>11</sup>. The host trail-following pattern is similar to the one observed with *F. nitidulus*<sup>6</sup> and in previous observations on myrmecophiles and termitophiles: myrmecophilous beetles<sup>11</sup>, cockroaches<sup>12</sup>, army ants' guests<sup>13</sup>, and termitophilous staphilinids<sup>14</sup>. The adaptive value of host-trail following is generally related to the dispersal strategy of the guest. In *F. provancheri* the biology of dispersion is not well known. The newly inseminated females are supposed to reenter the nest, and dissemination could occur by 'budding', with a few ergates, or by isolated foundation in the vicinity of the host nest<sup>13</sup>. *M. incompleta* form very large unicolonial populations in dispersed habitats. As mating takes place outside the

nest, the fecundated females could simply use the host trails in the very numerous foraging subterranean galleries of the host. Host-trail-following experiments with newly inseminated foundresses are to be performed to elucidate this point.

Host-trail following is not a general strategy in myrmecophilous arthropods: the larvae of *Maculinea* (Lepidoptera) are not able to follow the trails of their *Myrmica* ant hosts. The larvae are simply carried by the host workers into the ant nest<sup>15</sup>.

It is interesting to note that the response of the parasite increases in the presence of the host compared to the response of isolated parasites. This phenomenon also exists in the beetle *E. favieri* in the presence of its host *Pheidole pallidula*<sup>11</sup>. The mechanism is unknown, although it could simply be the arousal of the parasite by the host's presence. The adaptive value of this phenomenon is definitely to increase the probability of finding the host nest entrances (for a myrmecophile), or to avoid being lost in the numerous abandoned host galleries (for a parasite ant).

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