

INTRODUCTION

Edaphopausus favieri (Fairmaire) is a highly specialized myrmecophile having astonishing behavioral interactions with its host, *Pheidole pallidula*. It is licked by the workers but is never fed by trophallaxis. Instead, it eats eggs (Escherich, 1899), larvae and living workers of its host (Le Masne, 1961a, b).

Although this beetle behaves as a predator, it has been found only in nests of *Ph. pallidula*. However, it is fully winged and has well developed compound eyes. It may thus be suspected to live also outside the nests of *Ph. pallidula*. As this beetle must assure its outbreeding, it can be presumed that it moves from one nest to another by going up trails of its host.

We briefly investigate here the possibility of trail following by *E. favieri*. This behavior will be studied in detail in another paper (Cammaerts R., Detrain C. and Cammaerts M.-C., *in prep.*). Furthermore, we report the trail-following response of another guest of *Ph. pallidula*, the Tenebrionid beetle *Dichillus minutus* (Solier). A comparison of the response of the two beetles to the trail of their common host, *Pheidole pallidula*, may contribute to the knowledge of the reasons governing the use or not of host trails by myrmecophiles.

MATERIAL and METHODS

Edaphopausus favieri

Six individuals of *E. favieri* were found in nests of *Ph. pallidula*, in the region of Banyuls (France, Pyrénées-Orientales), in April 1988. They were isolated from ants until experimented on.

The beetles were tested during 10 minutes on circular trails (ø: 10 cm) traced with appropriate trail pheromone solutions. These solutions were deposited on pencil-drawn circumferences, divided into 10° arcs, on extra strong paper, with a metallic normograph pen. Up to 6 beetles were deposited at one time in the center of such trails.

Dichillus minutus

A dozen of *Dichillus minutus* were found in the same region as *Ph. pallidula* (Banyuls and Lavall, April 1988) and at Ampus, in the vicinity of Draguignan (France, Provence, 01/06/1988).

These beetles were tested under red light on similar trails (1 gland/trail), but only 6.4 cm in diameter to take into account their slow locomotion.

Pheidole pallidula

Trail-following results for minor and major workers of *Ph. pallidula* are taken from the original data of Detrain *et al.* (1988). These authors showed that the trail pheromone of this dimorphic species is issued from the poison gland of the minor workers. The optimal concentration is about 1 poison gland for an artificial circular trail of 10 cm in diameter. Their results, expressed in mean numbers of 5° arcs followed by the ants, are here converted into median numbers of

10' arcs, in order to standardize them with the present experimental data.

A stock solution in hexane of 20 minor workers' poison glands was made, and from this, diluted solutions were prepared for testing the beetles.

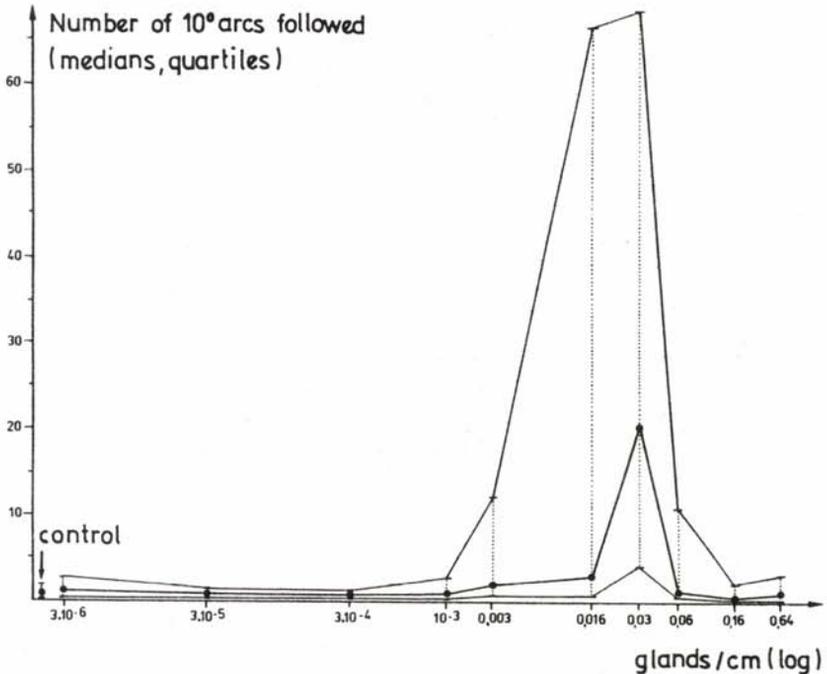


Figure 1. Trail-following response of *Edaphopausus favieri* to different *Pheidole pallidula* minor workers' poison gland concentrations. Logarithmic scale for trail concentration.

Figure 1. Suivi de la piste de *Pheidole pallidula* par *Edaphopausus favieri*, en réponse à différentes concentrations de glandes à poison d'ouvrières minor. Les concentrations sont portées en abscisse, selon une échelle logarithmique.

RESULTS

Response of *E. favieri* to different pheromone concentrations

E. favieri begins to follow the trail at a concentration of 0.003 glands/cm and shows an optimal response at 0.03 glands/cm. From a concentration of 0.06 glands/cm onwards, an increasing number of beetles appears to avoid the trail, refusing to cross it (Figure 1).

Trail pheromone, glands/cm	Median number of arcs followed by		
	<i>E. favieri</i>	minor ♀	major ♀
3.10 ⁻⁶	1.1	0.6	0.6
3.10 ⁻⁵	0.9	0.7	0.6
3.10 ⁻⁴	0.6	0.8	0.8
1,6.10 ⁻⁴	0.9	-	-
0.003	2.0	2.8	2.5
0.008	-	2.1	6.3
0.016	3.0	-	-
0.03	20.1	2.0	3.7
0.06	0.7	-	-
0.13	-	2.0	2.7
0.16	0.1	-	-
0.3	0.8	2.3	2.7
0.6	-	2.0	3.0

Table 1. Comparison of the trail-following response of *Edaphopausus favieri*, of minor and of major *Pheidole pallidula* workers to different minors' poison gland concentrations. Bold numbers indicate optima for concentrations and maxima for scores. Median values of 2.0 and more are significant at $\alpha = 0.01$ (Median test).

Tableau 1. Comparaison du suivi de la piste par *Edaphopausus favieri* et par des ouvrières minor et major de *Pheidole pallidula*, pour diverses concentrations d'extraits de glandes à poison de minor. Les chiffres gras indiquent, pour les concentrations, les valeurs optimales et, pour le suivi de la piste, les valeurs maximales. Les médianes égales ou supérieures à 2.0 diffèrent significativement du contrôle, pour $\alpha = 0.01$ (test de la médiane).

To what degree is the response of the beetle equal to that of the workers ?

Table 1 shows that both minor and major workers begin to follow the trail at a concentration of 0.003 glands/cm. At this concentration, trail following by the myrmecophilous beetle is still weak. The beetle's optimal concentration (0.03 glands/cm) is 10 and 4 times higher than that of the minor and major workers (0.003 glands/cm and 0.008 glands/cm).

Furthermore, *E. favieri* presents significant trail-following behavior only for a small range of concentrations, because for concentrations equal to or higher than 0.06 glands/cm, the beetle no longer follows the trail (see above and Figure 1). This is not the case for workers (Table 1). Non-parametric median tests indicate that at these high concentrations their score remains significant at $\alpha = 0.01$.

Moreover, the beetle walks 3 to 7 times further on the trail at its optimal pheromone concentration than the workers do on theirs (Table 1). In another paper (Cammaerts R., Detrain C. and Cammaerts M.-C., *in prep.*), we show that the greatest distances covered by *E. favieri* are further than those expected for trail leaving with a constant probability.

Specificity of trail following by *E. favieri*

E. favieri only follows the trail of its host, *Ph. pallidula*. It does not at all follow the trail of two species of *Tetramorium* and of two species of *Crematogaster* that may live in the same environment (Figure 2).

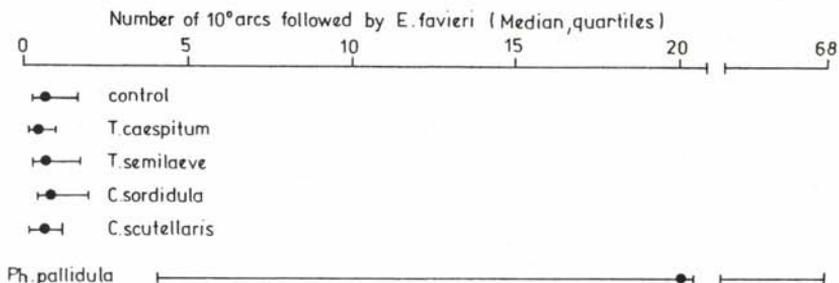


Figure 2. Trail-following response of *Edaphopaussus favieri* to artificial circular trails traced with hexanic extracts of poison or tibial (for the genus *Crematogaster*) glands of 1 ant.

Figure 2. Suivi, par *Edaphopaussus favieri*, de pistes circulaires artificielles tracées au moyen d'extraits hexaniques de la glande à poison ou des glandes tibiales (pour le genre *Crematogaster*) d'une fourmi.

Trail-following ability of *Dichillus minutus*

We found that this beetle normally does not move in daylight. Thus we had to test its trail-following ability in the dark (in fact, under red light).

At a concentration of 0.05 glands/cm, *D. minutus* does not follow the *Ph. pallidula* trail, the number of arcs followed not differing from the control (N = 16). Moreover, the beetle does not appear to be repelled. Placing it for some time with workers or testing it on a less concentrated trail (0.025 glands/cm) had no effect.

DISCUSSION

Possible adaptive value of *E. favieri*'s trail-following characteristics

The trail following of this myrmecophilous beetle is optimal for a pheromone concentration 4 to 10 times higher than that for major and minor workers. In nature, we may expect that such trails sustain a high traffic of minor workers. So, *E. favieri* responds best to trails more likely to lead it to nest entrances.

It is noteworthy that *E. favieri* follows the trail a greater distance than the ants. In a paper in preparation (Cammaerts R., Detrain C., Cammaerts M.-C.), we show that the beetle's probability of leaving the trail is low and constant for distances up to about 50 cm and becomes even lower for distances above 50 cm. The resulting beetle's small probability of losing the trail reduces its risk of desiccation and of encounters with predators. In comparison, minor workers' probability of losing the trail is higher and constant (Detrain *et al.*, 1988). In ants, this could be linked to exploratory behavior and may contribute to the discovery of new food sources (Deneubourg *et al.*, 1986).

Another adaptive reaction of the beetle could be its avoidance of trails twenty times or more concentrated than the optimal concentration for minor workers. We show elsewhere (Cammaerts R., Detrain C. and Cammaerts M.-C., *in prep.*) that such concentrations also have a repellent effect when they are punctually presented to the beetle. Under natural circumstances, high concentrations of poison gland contents may perhaps be discharged during agonistic behavior. The modalities of these emissions and their possible consequences for *E. favieri* will be discussed in the above-mentioned paper (*op. cit.*).

Specificity of *E. favieri*'s trail following

It is not surprising to learn that a host-specific beetle can only follow the trail of its host ant.

We may hypothesize that *E. favieri* uses *Ph. pallidula*'s trail pheromone for locating new nests. This has been suggested for other social insects' guests in order to assure them their resources (army ants' guests: Akre and Rettenmeyer, 1968; *Reticulitermes* termitophilous Staphylinids: Howard, 1980) or to locate small numbers of their conspecifics (Howard, 1980).

Trail following or not

Many social insects' guests may be found on the trails of their hosts (see Kistner's 1982 review) but so far there has been very little experimental evidence that they follow the trail pheromone. Such proof has been provided for termitophilous Collembola (*Cyphoderus bidenticulatus*: Ritter et al., 1977) and Staphylinids (*Xenistusa hexagonalis* and *Trichopsenius depressus*: Howard, 1980) and for myrmecophiles: the Nitidulid *Amphotis marginata* (Hölldobler, 1978), the roach *Attaphila fungicola* (Moser, 1964; see above) and some army ant guests (Akre and Rettenmeyer, 1968). On the other hand, not all guests follow their host's trail. Akre and Rettenmeyer (1968) have shown that guests of army ants that follow trails in nature, also follow natural trails laid down by these ants on filter paper, while others, mainly phoretics, are poor followers of these chemical trails. However, the correlation they found should not lead us to form a general opinion too rapidly about a link between the trail-following ability of myrmecophiles and the rest of their social interactions.

For example, trail following has never been recorded for the most documented of the myrmecophiles, the well integrated Staphylinids of the genera *Atemeles* and *Lomechusa*. Like *E. favieri*, these rove beetles are able to fly. *Atemeles* even has to move in spring from a *Myrmica* nest to a *Formica* one, and the reverse in late summer or autumn (Hölldobler, 1970). Experimental work has failed to show trail-following ability in *Atemeles* (Hölldobler, 1969). This strongly contrasts with *E. favieri*'s behavior.

In this respect, the absence of trail following by *D. minutus* is an important finding. This Tenebrionid beetle is tolerated by *Ph. pallidula*, although only slightly licked by them and sometimes bitten (as *E. favieri* may be). It lives on the refuse of the nest (Le Masne, 1970 and personal observations) and this accounts for the fact that it is mainly found in the outlying parts of the nest, where refuse deposits exist.

We wish to put forward a hypothesis about the absence of trail-following behavior in *D. minutus*. This lies in the supposition that *D. minutus* better resists desiccation than *E. favieri*. Indeed, it has a dark and hard cuticle and can be found just inside the rim of the nest (our observations at Banyuls and Lavall), in the immediate vicinity of nests of the free-living spider *Uroctea durandi* Latr., where food debris exists (Le Masne, 1970) or away from any nest, under stones (we observed 6 individuals aggregated together at Ampus). Therefore, it is possible that *D. minutus* searches nest entrances without being in as critical a situation as *E. favieri*.

Another possible explanation for the absence of trail following by *D. minutus* is that this beetle is perhaps not host specific. Bernard (1968) states that this beetle can be found in *Tapinoma* and *Crematogaster* nests, but gives no details. This has to be confirmed. Another *Dichillus* species, *D. tenebrosus* Reit., has been found both in nests of *Ph. pallidula* and of *Monomorium gracillimum* (Karawajew, 1909).

The present interpretations show the need for further observations before establishing adaptive links between the host trail following, the physiology and the ecology of myrmecophiles.

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