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Research article

The distribution of weaver ant pheromones on host trees

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Abstract. The visible anal spots deposited by *Oecophylla smaragdina* ants have been suggested to deter ant prey, affect interspecific competition and facilitate mutualists and parasites in tracking down *Oecophylla* ants. I measured the density of anal spots on host trees with and without ants and tested for correlations between spot density, ant activity and the likelihood of being detected by an ant. Spots were only found on trees with ants. On ant-trees, spots were distributed throughout the trees but with higher densities in areas with high ant activity and pheromone densities were higher on twigs compared to leaves. Also there was a positive correlation between spot density and the likelihood of being detected by ants. Anal spots may thus function as reliable cues to interacting species and be an important factor in shaping the community around *Oecophylla* colonies.

Keywords: Territorial ant pheromones, anal spots, *Oecophylla smaragdina*, chemically mediated interactions, infochemical.

Introduction

Oecophylla ants produce visible droplets from rectal sac fluids (anal spots) and deposit them on the substrate where they forage. The initial studies on anal spots by Hölldobler and Wilson showed that they serve as territorial pheromones distributed throughout the home range of the colonies (Hölldobler and Wilson, 1978; Hölldobler, 1983). It has also been shown that these pheromones are very persistent (Beugnon and Dejean, 1992). Their persistence and cover of entire ant territories may present reliable cues of ant presence and predation risk and therefore warn potential prey (Offenberg et al., 2004 a, b). Furthermore, not only prey, but all organisms with a fitness related to the presence of *Oecophylla*, may benefit from such signals, e.g. mutualists, competitors and organisms that exploit the ants (Pierce and Elgar 1985; Dicke and Grostal, 2001, Dejean et al., 2005).

A heterogenic distribution and correlation between spot density and ant activity is required before anal spots can function as reliable cues. In this study I present details on how anal spot densities differ between ant host trees and how they differ between different structures on the trees. Furthermore, I present correlations between spot densities, ant activity and predation risk.

Methods

In a mangorve forest (Ranong, Thailand) the distribution of anal spots deposited by *O. smaragdina* on host trees was assessed by counting spots on leaves (*Rhizophora mucronata*) and paper sheets attached to trees. From 9 haphazardly selected ant-trees the number of anal spots were counted on all leaves sampled on shoots with high ant activity (all shoots with ant nests or attended homopteran aggregations) and shoots with low ant activity (a shoot without nest or homopterans 2 m away from each high activity shoot). From 9 trees without ants we sampled all leaves from four shoots (N = 341 leaves). Anal spot densities (spots cm^{-2}) were calculated on the axial and the abaxial side of the leaves. Paper sheets (10.8 cm by 8.2 cm) were attached to 21 haphazardly selected ant-trees and 5 trees without ants (*R. mucronata, R. apiculata* and *Ceriops* sp.). Ant-trees were searched for shoots with high activities (as above) and for twigs with busy ant trails. For each high activity area a corresponding control was selected by choosing a shoot/twig without obvious ant activity two meter apart (same height). Paper sheets were attached to the shoots by one edge (leaf-sheets). On twigs, the sheets were wrapped around the stem (twig-sheets). After eight days the spot densities on the sheets were calculated. Twig-sheets were divided into the upper 25 percent of the twig, where the ants walk, and the 75 percent constituting the sides and lower part. Spot distributions were analysed with Wilcoxon tests or median tests if variances were unequal.

In Darwin, Northern Australia, twig-sheets (N = 21) and leaf-sheets (N = 20) were placed randomly on ant-trees and left for four days. Then a freeze killed fruit fly was glued to each sheet. The time until it was removed by an ant (detection time) was assessed together with the spot density on the sheet. Each sheet was checked every 5 minutes and the median used for analysis. On twig-sheets, ant activity was measured as the number of ants crossing the sheet min^{-1}, counted over a 10 min period. Ant activity and detection time was regressed on spot density.

Table 1. The distribution of anal spots on leaves and paper-sheets. Proportion = the proportion of leaves/papers that had at least one anal spot. *P* refers to the statistical difference in pheromone densities.

Substrate	Ant activity	Position	Proportion	Anal spots cm^{-2}	SE	*P*	N
leaves	high	–	0.38	0.0068	0.0010	<0.0001	150
	low	–	0.19	0.0016	0.00030		188
twig-sheets	high	–	1.0	0.35	0.063	0.0075	14
	low	–	0.92	0.13	0.038		12
leaf-sheets	high	–	1.0	0.087	0.014	<0.0001	31
	low	–	0.52	0.011	0.0034		27
leaves	high	lower	–	0.012	0.0018	0.007	48
		upper	–	0.0071	0.0017		48
	low	lower	–	0.0038	0.00089	0.18	36
		upper	–	0.0047	0.00072		36
twig sheets	high	lower	–	0.44	0.080	0.003	14
		upper	–	0.091	0.026		14
	low	lower	–	0.15	0.042	0.056	12
		upper	–	0.067	0.028		12

Results

The distribution of anal spots is summarized in Table 1. Anal spots were only found on ant-trees on which leaves and paper sheets were more intensively marked in high activity areas compared to low activity areas. On leaves there was a more than four-fold increase in spot density between low and high activity areas (Chi-square = 14.82, df = 1, $P < 0.0001$). Paper sheets also carried more marks in high activity areas. On the leaf-sheets there was an almost eight-fold increase in spot densities (Chi-square = 30.03, df = 1, $P < 0.0001$) and a more than two-fold increase on the twig-sheets (Chi-square = 7.16, df = 1, $P = 0.0075$).

In high activity areas, spot densities were higher on the underside of leaves (Chi-square = 7.28 df = 1, $P = 0.007$) and twigs (Chi-square = 8.81 df = 1, $P = 0.003$) compared to the upper part. In low activity areas, however, there was no difference between upper and lower densities (leaves: Chi-square = 1.92 df = 1, $P = 0.18$; twigs: Chi-square = 3.66 df = 1, $P = 0.056$). Overall, the twig-sheets were more intensively marked than the leaf-sheets (Chi-square = 13.91 df = 1, $P = 0.0002$) with averages of 0.25 ± 0.043 (SE) and 0.051 ± 0.0089 (SE) spots cm^{-2}, respectively. Also, spot densities were more than 13 times higher (Chi-square = 58.19, df = 1, $P < 0.0001$) on leaf-sheets (0.051 spots cm^{-2} ± 0.009) compared to leaves (0.0039 spots cm^{-2} ± 0.00051).

There was a positive correlation between ant activity and spot density on the twig-sheets (crossing min^{-1} = 0.84 + 15.79 spots cm^{-2}, $F_{1.17} = 52.33$, $P < 0.0001$, $R^2 = 0.75$, N = 19) and detection time was negatively correlated with anal spot density (Log[detection time] = 3.26 – 4.12 spot cm^{-2}, $F_{1.39} = 18.65$, $P < 0.0001$, $R^2 = 0.32$, N = 41). I assumed that baiting did not increase spot densities since fruit flies were carried away by single ants and thus did not elicit recruitment.

Discussion

At all three levels investigated in this study I found heterogeneity in spot densities linked to ant activity. Firstly, anal spots occurred only on trees with ants. Secondly, I observed heterogeneity in spot densities within ant-trees. In high activity areas there were higher spot densities and twigs that served as busy bottlenecks showed higher spot densities than the leaves. Also there was a positive correlation between the number of passing ants and spot densities on twig-sheets and there was an increased probability of being detected by ants on paper sheets with more anal spots. On the third level, though, there was an opposite correlation between ant activity and spot density. In high activity areas there were higher spot densities on the underside of twigs and leaves compared to the upper side where the ants walk. One reason could be that ants avoid contamination with their liquid waste products by concealing them on lower parts of structures in high activity areas where there is an increased risk of encountering spots that have not dried up yet. Higher spot densities were found on paper sheets compared to leaves probably because the spots were easier to detect on white absorbing paper compared to green leaf blades. This suggests that detectable spots on leaves underestimate the actual amount of pheromones deposited. Furthermore, almost all twig-sheets (25/26) were marked after 8 days. It therefore seems safe to conclude that *O. smaragdina* in the field deposited their anal spots heterogeneously throughout their territories and that increasing spot densities indicated an increased probability of being detected by an ant.

This heterogenic distribution and the link between pheromone density and the likelihood of encountering an ant can affect *Oecophylla* interactions in several ways. Potential prey may be deterred from high risk areas. For example the chrysomelid beetle *Rhyparida wallacei* avoid to feed on leaves contaminated with *O. smaragdina* anal spots compared to leaves without these pheromones; an effect that may cascade and translate into increased host plant fitness (Offenberg et al., 2004a,b, 2006). Also competitor species may adapt their behavior in anticipation of future encounters with *Oecophylla.* Dejean et al. (2005) showed that *Pheidole megacephala* increased soldier recruitment and changed feeding behavior at food sources surrounded by *Oecophylla* anal spots compared to sources placed in neutral surroundings. Lastly it is known that parasitic lycaenid *Euliphyra* larvae can follow up to 2 month old *Oecophylla* trails (Dejean and Beugnon, 1996) and it has been suggested that the mutualistic *Jalmenus evagoras* use the pheromones of its host ants as oviposition cues (Pierce and Elgar, 1985). Depending on the interaction, anal spots may facilitate or impede interaction strengths between *Oecophylla* colonies and the surrounding arthropod community.

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