



Lasius niger ants discriminate aphids based on their cuticular hydrocarbons

Corsin Lang^{a,1}, Florian Menzel^{a,b,*}

^aInstitute of Ecology and Evolution, University of Bern

^bInstitute of Zoology, University of Mainz

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Mutualistic interactions between organisms depend on the ability of each partner to recognize the other. In ant–aphid mutualisms, ants have to recognize whether an aphid colony is worth tending. Many aphid species can live in mutualistic associations with ants (trophobiosis), whereas others are never tended and are frequently preyed upon by ants. Since aphids often produce low amounts of honeydew when not tended by ants, the ants should be able to recognize potential trophobionts based on signals other than honeydew. Conversely, aphids should signal if they are potential trophobionts. We investigated whether ants recognize potential trophobiont aphids based on their behaviour, morphological or chemical properties. We studied the behaviour of *Lasius niger* ants towards four myrmecophilous and four nonmyrmecophilous aphid species, and presented live individuals, dead aphids and aphid cuticular hydrocarbons. *Lasius niger* invariably attacked nonmyrmecophilous species, but antennated myrmecophilous aphids. This differentiated reaction was shown towards living and dead aphids, but could also be elicited using dummies covered with aphid cuticular hydrocarbons. Neutral control objects were antennated, but the ants quickly lost interest. Thus, *L. niger* uses aphid cuticular hydrocarbons to discriminate between different aphid species. Aphid cuticular hydrocarbons consisted mainly of *n*-alkanes, with low amounts of branched alkanes and *n*-alkenes. A detrended correspondence analysis showed that myrmecophilous and nonmyrmecophilous species could be differentiated based on their cuticular hydrocarbons, in particular their *n*-alkane composition. Hence, myrmecophilous aphid species might use a common cuticular hydrocarbon signal, which *L. niger* uses to classify aphids into potential trophobionts and potential prey.

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For many ant species, honeydew, a sugar-rich excretion of aphids and other plant-sucking Hemiptera, constitutes an important part of their diet (Blüthgen & Feldhaar 2010). This relationship is called trophobiosis, and it is often mutualistic. The ants obtain carbohydrates and, to a lesser degree, amino acids from the honeydew. The trophobionts originally produce honeydew as a waste product; since they feed on sugar-rich, but nitrogen-poor phloem sap, they have to excrete excess sugar (Stadler & Dixon 2008). They may benefit from the ants by being protected against predation and parasitism and by reduced fungal infection rates (Stadler & Dixon 2005, 2008; Nielsen et al. 2010). However, depending on aphid species and environmental circumstances, ant attendance can also have negative effects on aphid fitness (Stadler & Dixon 1999, 2005). Depending on the ants' current diet options (Offenberg 2001), the trophobiotic relationship can even tilt over into predation. For

example, *Lasius flavus* frequently preys on its trophobiont partners (Pontin 1978; Fischer et al. 2001). In temperate regions, the most important trophobionts are aphids (Dixon 1998). While many aphid species are facultatively or obligatorily tended by ants (myrmecophilous), other species are never tended (nonmyrmecophilous; Stadler & Dixon 2008). Nonmyrmecophilous species are often preyed upon by ants (F. Menzel, personal observation). Surprisingly, even individuals of myrmecophilous species are often untended (Stadler 2004). This can be partly because of poor host plant quality, which results in poor honeydew quality (Fischer & Shingleton 2001; Fischer et al. 2005) or to aphid competition for ant attendance (Fischer et al. 2001). Myrmecophily in aphids is an evolutionarily labile trait, which has evolved in multiple aphid subfamilies and has frequently been lost (Stadler et al. 2003). Even within the same genus, myrmecophily can have evolved or disappeared multiple times (Shingleton & Stern 2003).

From the ant's point of view, whether or not an aphid species is an attractive trophobiont mainly depends on its honeydew composition and quantity (Cushman & Addicott 1989; Cushman 1991; Völkl et al. 1999). In general, ants prefer to tend species that produce large quantities of honeydew that contains high

* Correspondence: F. Menzel, Institute of Zoology, Department of Evolutionary Biology, Joh.-von-Müller-Weg 6, 55128 Mainz, Germany.

E-mail address: menzef@uni-mainz.de (F. Menzel).

¹ C. Lang is at the Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland.

amounts of amino acids and/or di- and trisaccharides (Völkl et al. 1999). The trisaccharide melezitose is especially attractive to ants, and those aphids that produce it are usually tended while those lacking it are not (Woodring et al. 2004; Detrain et al. 2010).

Being tended can be highly beneficial for certain myrmecophilous aphid species, but can also lower the fitness in others (Stadler & Dixon 1999). However, since being tended is better than being preyed upon by the ants, aphids can increase honeydew output or quality in response to ant attendance. For example, they can increase overall honeydew production (Stadler & Dixon 2005). They can also increase the concentration of melezitose or amino acids when tended by ants to make the honeydew more attractive and maintain ant attendance (Fischer & Shingleton 2001; Yao & Akimoto 2001, 2002). However, this exacts physiological costs on the aphids since, for example, increasing amino acid content of the honeydew leaves less nitrogen for the aphids themselves (Yao & Akimoto 2002). Furthermore, aphids can change their honeydew excretion pattern from slower excretion of larger droplets to more frequent excretion of smaller ones (Yao & Akimoto 2002).

Honeydew production and composition vary both between and within aphid species. They depend on the species and the quality of the host plant (Fischer & Shingleton 2001; Fischer et al. 2005), and on whether or not they are ant-tended. As a consequence, currently untended myrmecophilous aphids may produce honeydew of low quality or quantity. However, since ants often prey on aphids (Pontin 1978; Fischer et al. 2001), it should be adaptive for aphids to signal their quality as a potential trophobiont to prevent the ants from preying on them. Such a signal should then be independent of honeydew quality. Ants, on the other hand, should also profit from using such a signal if they profit more from tending a good trophobiont for a longer time instead of preying on it. Besides behavioural or morphological characteristics, a candidate channel for this signal is the cuticular hydrocarbon profile. Aphids, like other insects, possess species-specific cuticular hydrocarbon profiles (Howard & Blomquist 2005; Raboudi et al. 2005). Cuticular hydrocarbons (CHC) occur in essentially all species and primarily function as a waterproofing agent (Gibbs & Rajpurohit 2010). In many solitary and especially social insects, however, they are also used as recognition cues. Various insects use hydrocarbon profiles to recognize other individuals of their own species, their sex, or, in social insects, their colony membership (Howard & Blomquist 2005). While intraspecific recognition based on CHC has been extensively studied in various insects, little is known about the importance of CHC in interspecific recognition (Menzel et al. 2008). In particular, recognition based on cues other than honeydew has been little studied in ant–aphid interactions.

We studied ant behaviour towards myrmecophilous and nonmyrmecophilous species, and tested which cues are sufficient to elicit tending behaviour. We presented eight of the most common myrmecophilous and nonmyrmecophilous aphid species to colonies of *Lasius niger*. For each species, we offered (1) live aphids, (2) dead aphids and (3) their CHC (presented on washed dead aphids). These three treatments contained increasingly fewer cues by which the ants could recognize the aphids: Dead aphids (but not live ones) lack behavioural cues, and CHC (but not dead aphids) lack morphological cues of the aphids, as well as potential traces of honeydew on the aphid's body surface. We predicted that (1) in our experimental setting, ants would show less aggressive, but more tending behaviour towards individuals of myrmecophilous species than nonmyrmecophilous ones, and (2) the discrimination between these species is mediated by CHC, that is, aphids can signal trophobiont quality with cues other than honeydew quality or quantity. To facilitate easy recognition, myrmecophilous aphids should converge towards similar CHC patterns. Therefore, we tested the hypothesis that (3) the CHC composition of

myrmecophilous aphid species differs consistently from that of nonmyrmecophilous ones.

METHODS

Experimental Animals

Six colonies of *L. niger* and eight aphid species (adult stage) were used for the test procedure. The ant colonies were collected in June and July 2010 from a fallow field near Uettligen, BE, Switzerland (46°58'37"N; 7°22'46"E). They were brought into the laboratory and kept in open plastic boxes (63 × 35 cm and 15 cm high), with fluron-coated walls to prevent the ants from escaping. We used four myrmecophilous aphid species, which are often tended by *L. niger* (Lampel & Meier 2007; F. Menzel, personal observation), and four nonmyrmecophilous species (Table 1). Whether or not each species was myrmecophilous was extracted from Lampel & Meier (2007) and Stadler (2004). We chose the species based on their frequent occurrence in the same habitat as *L. niger*. Seven of the species were among the most common ones around Bern and occurred syntopically in or near the same fallow field as *L. niger*, where they were collected for this study in July 2010. Since there were too few nonmyrmecophilous aphid species available, a further species, *Sitobion avenae*, which is also native to Switzerland, was obtained from Andermatt Biocontrol (Biobest Biological Systems, Westerlo, Belgium). A ninth species, *Stomaphis quercus* (Lachnidae; collected in Wabern, BE, Switzerland), was further included in the chemical analysis since it is taxonomically distant from the other aphid species. This species is obligatorily attended by *Lasius fuliginosus* (Dixon 1998; Hopkins & Thacker 1999).

Behavioural Assays: Experimental Set-up

The eight aphid species were presented to the six *L. niger* laboratory colonies in haphazard order. We tested whether the ants reacted differently towards myrmecophilous and nonmyrmecophilous aphid species. Each of the eight aphid species was presented in three treatments: (1) living aphids, (2) dead aphids (killed by freezing) and (3) their CHC, applied to dummies. Thus, the three treatments contained increasingly fewer potential recognition cues that the ants could use to differentiate between aphid species.

We prepared CHC for the third treatment by immersing aphids in hexane for 10 min (Blomquist 2010). Nonpolar fractions of these extracts were obtained via fractionation over SiOH columns (Chromabond, Macherey-Nagel, Düren, Germany) using hexane as solvent. These fractions contained only hydrocarbons in gas chromatography–mass spectrometry (GC–MS) analyses. The hydrocarbons (dissolved in hexane) were then concentrated, carefully

Table 1
Aphid species studied (except for *S. quercus*, all in subfamily Aphidinae (Aphididae)) and the host plants from which they were collected

Aphid species	Tribe	Host plant
Myrmecophilous		
<i>Aphis fabae</i>	Aphidini	<i>Cirsium arvense</i>
<i>Aphis sambuci</i>	Aphidini	<i>Sambucus nigra</i>
<i>Aphis urticae</i>	Aphidini	<i>Urtica dioica</i>
<i>Metopeurum fuscoviride</i>	Macrosiphini	<i>Tanacetum vulgare</i>
<i>Stomaphis quercus</i>	Lachnidae: Lachnini	<i>Betula pendula</i>
Nonmyrmecophilous		
<i>Macrosiphoniella tanacetaria</i>	Macrosiphini	<i>Tanacetum vulgare</i>
<i>Macrosiphum cholodkovskyi</i>	Macrosiphini	<i>Filipendula ulmaria</i>
<i>Sitobion avenae</i>	Macrosiphini	<i>Hordeum vulgare</i>
<i>Uroleucon jaceae</i>	Macrosiphini	<i>Centaurea jacea</i>

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