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Sensitivity and feeding efficiency of the black garden ant *Lasius niger* to sugar resources

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ABSTRACT

Carbohydrate sources such as plant exudates, nectar and honeydew represent the main source of energy for many ant species and contribute towards maintaining their mutualistic relationships with plants or aphid colonies. Here we characterise the sensitivity, feeding response curve and food intake efficiency of the aphid tending ant, *Lasius niger* for major sugars found in nectar, honeydew and insect haemolymph (i.e. fructose, glucose, sucrose, melezitose and trehalose). We found that sucrose concentrations – ranging from 0.1 to 2.5 M – triggered food acceptance by *L. niger* workers with their food intake efficiency being enhanced by sugar concentrations of 1 M or higher at which points energy intake was maximised. The range of sucrose concentrations that elicit a feeding response by *L. niger* scouts thus overlaps with that of natural sugar resources. The response curves of feeding acceptance by scouts consistently increased with sugar concentration, except for trehalose which was disregarded by the ants. Ants are highly sensitive to sucrose and melezitose exhibiting low response thresholds. Sucrose, fructose and glucose share a same potential to act as phagostimulants as they had similar half feeding efficiency concentration values when expressed as the energetic content of sugar solution. Aphid-biosynthezised melezitose generated the highest sensitivity and phagostimulant potential. The feeding behavior of ants appears to be primarily regulated by the energy content of the food solution for the main sugars present in nectar and honeydew. However, feeding by scouts is also influenced by the informative value of individual sugars when it serves as a cue for the presence of aphid partners such as the aphid-biosynthesised melezitose.

1. Introduction

Sugary resources are widespread in the environment with examples including aphid honeydew, extrafloral and floral nectar, phloem and xylem sap and fruit pulp. However, the abundance, concentration, spatial distribution and degree of accessibility of these resources are highly heterogeneous. Honeydew and nectar are composed of monosaccharides and oligosaccharides (e.g. Percival, 1961; Völkl et al., 1999; Wäckers, 2001), in addition to small amounts of other chemical compounds such as amino acids, proteins and lipids (Baker and Baker, 1973; Gonzalez-Teuber and Heil, 2009; Lanza et al., 1995). Nectar tends to have a rather restricted breadth of sugars available to visitors and is primarily dominated by the disaccharide sucrose and its hexose components, fructose and glucose (Buckley, 1987; Gonzalez-Teuber and Heil, 2009; Heil, 2011; Lanza et al., 1995; Percival, 1961). In comparison, honeydew usually contains a more diverse carbohydrate profile. Indeed, the bulk of aphid excreta is mainly composed of sucrose, fructose and glucose but also contains variable amounts of trehalose and melezitose, with the latter trisaccharide being biosynthesised by the aphids (Detrain et al., 2010; Fischer et al., 2005; Fischer and Shingleton, 2001; Vantaux, 2011; Völkl et al., 1999; Wäckers, 2000; Yao and Akimoto, 2001).

Many arthropods – even carnivorous ones – are attracted to these sugar meals and have evolved physiological and neuronal mechanisms to detect and ingest carbohydrates as the main source of energy. Consequently, ants are ubiquitous and regular visitors of plant nectar and honeydew produced by aphids of which sugar content is very important for the initiation and maintenance of mutualistic relationships (Beattie, 1985; Blüthgen and Fiedler, 2004; Buckley, 1987; Engel et al., 2001; Stadler and Dixon, 2005; Way, 1963). The ecological dominance of ants is strongly linked to the flexibility of their foraging strategies. For instance, ants may adjust their feeding behaviour and the intensity of food recruitment according to the energetic and metabolic value of carbohydrate sources such as the amount and/or chemical composition of food (e.g. Detrain et al., 1999, 2010; Dussutour and Simpson, 2008;

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Hölldobler and Wilson, 1990; Jackson and Châline, 2007; Mailleux et al., 2000, 2003; Völkl et al., 1999).

A diversity of sugary resources is available to ants, thus scouts should have evolved physiological abilities to feed preferentially on the most profitable sugars. For a sugar to be a suitable meal, it must first be detected and then elicit a feeding response among ant foragers. Not all sugars are phagostimulatory. For instance, maltose, xylose, melibiose only elicit a weak feeding response (Boevé and Wäckers, 2003; Detrain et al., 2010). In contrast, four sugars (i.e. melezitose, sucrose, fructose and glucose) are regularly consumed by the majority of ants, even though species-specific sugar preferences have been demonstrated (Blüthgen and Fiedler, 2004; Völkl et al., 1999). Previous studies have established a hierarchy of sugar preferences by comparing the global foraging effort made by the whole colony based on the total amount of ingested food and/or the resulting flows of foragers (Tinti and Nofre, 2001; Völkl et al., 1999). Surprisingly, information remains limited at the level of the ant individual, even though the feeding response of scouts is the cornerstone upon which food recruitment is built. Furthermore, because ant responses were usually measured for just one sugar concentration, knowledge remains limited about how glucophagy by the ant individuals that discover the food source evolves for increasing sugar concentrations. Dose–response curves are only well-established for sucrose: previous studies have quantified the propensity of foragers to recruit nestmates (Beckers et al., 1993; Detrain et al., 1999; Dussutour and Simpson, 2008; Jackson and Châline, 2007; Wilson, 1962) along with several feeding variables, such as food acceptance, crop load, feeding time and ingestion rates (Dussutour and Simpson, 2008; Faribele and Josens, 2012; Josens et al., 1998; Josens and Roces, 2000). In contrast, the feeding response curves of ants remain unknown for the other sugars that are commonly found in nectar and honeydew. Yet, data about dose-feeding response curves are essential to assess the sensory and physiological abilities of scout individuals. Such information would contribute towards understanding how ant species have evolved a feeding behavior that is adapted to the energetic and ecological value of natural sugar resources.

Here, we investigate whether the main sugars produced by plants and aphids differ in their ability to elicit a feeding response among *Lasius niger* ants and how the feeding responses of scouts change for a wide range of sugar concentrations. We selected the black garden ant *L. niger* as the biological model to study sugar perception and feeding because this ant species is a regular visitor of both aphid colonies and plant nectar (Engel et al., 2001). Furthermore, we investigate how the ingestion rate and feeding efficiency of this aphid-tending species change in response to increasing amounts of sucrose for comparisons with existing data on other sugar-consuming ants. This research provides an interpretative physiological framework to improve our understanding about how ants forage on sugary resources and develop mutualistic relationships with aphids and plants.

2. Material and methods

2.1. Collection and rearing of colonies

Experiments were carried out on the black garden ant, *L. niger*, a common aphid-tending species in European temperate regions. Four colonies of about 1000 ants were collected in Brussels and placed in plastic containers of which edges were covered with polytetrafluoroethylene (Fluon®) to prevent ants from escaping. Test tubes covered with a red transparent foil were used as rearing nests in the laboratory. Aqueous sucrose solution (1 M) and water filled test tubes were provided *ad libitum*. Twice a week, dead insects (cockroaches or fruit flies) were added as protein sources. Colonies were kept in controlled conditions of hygrometry (65 ± 5%), luminosity (Light–Dark: 16:8 h) and temperature (20 ± 2 °C).

2.2. Experimental procedure

Behaviour of *L. niger* scouts were compared when faced with sugar solutions differing by their nature and concentration. All tested concentrations were made by dissolving sugars of high purity (at least 99% purity Fluka Analyticals Sigma–Aldrich) into pure distilled water. The following sugars were tested:

D-Glucose and D-fructose: two monosaccharides that are commonly found in fruits, nectars and aphid honeydew (Fischer and Shingleton, 2001; Percival, 1961).

Sucrose: a disaccharide made of D-glucose and D-fructose units that is widespread in nectar and aphid honeydew (Fischer and Shingleton, 2001; Percival, 1961).

Melezitose, a trisaccharide including two D-glucose units and one D-fructose unit, that is scarcely found in plant-originating sugars but frequently excreted by aphids in their honeydew (Fischer and Shingleton, 2001; Vantaux et al., 2011; Wäckers 2000, 2001).

Trehalose, a disaccharide of two D-glucose units that is known as an energy storage compound in the haemolymph of several insect species (Turunen, 1985).

Increasing concentrations were made until reaching the limit of solubility of each sugar. For each sugar, we tested the following concentrations 0.001; 0.01; 0.1; 0.5; 1 and 2.5 M. Since melezitose and trehalose were less soluble sugars, we could not test the highest 2.5 M concentration. All sugar solutions were stored at +5 °C and left at ambient temperature for 1 h before starting the experiments. Before each experimental session, ant colonies were deprived of food but allowed water for three days.

The first experiment assessed how the energetic return drawn by the ants from a sugar solution was influenced by its concentration in carbohydrates. We chose sucrose as a reference sugar to investigate how concentration influenced food intake as previously done for other ant species (in the genus *Camponotus* (Faribele and Josens, 2012; Josens et al., 1998; Josens and Roces, 2000), *Rhytidoponera* (Dussutour and Simpson, 2008), *Linepithema, Cephalotes* and *Acromyrmex* (Faribele and Josens, 2012)). We compared the feeding response of *L. niger* scouts over a range of sucrose concentrations; specifically, 0.001, 0.01, 0.1, 0.5, 1 and 2.5 M. Groups of five *L. niger* scouts were randomly taken out of the foraging arena of one colony and allowed to explore the experimental set-up during 5 min. The experimental-setup consisted in a Petri dish (9 cm in diameter) in the center of which a bowl-shaped feeder (3.8 cm in diameter) was placed. At the end of this exploration phase, a ring (4 cm diameter) was placed around the feeder in order to prevent ants from accessing the feeder while filling it up with 500 μl of the tested sugar solution. The experiment began when the ring was removed. For each concentration, we video recorded the behaviour of ants around the sucrose droplet and we measured the total time spent feeding by all of the ants. We placed all of the ants into a small vial before and after the experiment to measure the initial and final body weight of each experimental group (Mettler™ balance, nearest 0.01 mg). This measurement enabled us to estimate the average crop load after feeding on a sucrose droplet as well as the rate of sugar ingestion for each concentration. Three colonies were tested twice for each sucrose concentration (6 replicates in total per tested concentration). Each colony and each sugar concentration were tested in a random order.

The second experiment assessed the feeding response curves of *L. niger* ants faced to water or to increasing concentrations (0.001, 0.01, 0.1, 0.5, 1 and 2.5 M) of a single sugar. This experiment was done for sucrose, fructose, glucose, melezitose and trehalose.