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Attract and distract: Manipulation of a food-mediated protective mutualism enhances natural pest control

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ABSTRACT

Ants can act simultaneously as predators and as protectors of honeydew producing pests. As a result, their impact on plants can be both positive and negative. By guarding honeydew producers against their natural enemies, ants can severely disrupt biological control programs and are often seen as important indirect pests. Chemical control, as well as physical ant-exclusion is employed to disrupt the mutualistic relationship between ants and honeydew producers. However, the exclusion or killing of ants also eliminates their services as biocontrol agents. Herein, we tested whether it is possible to use artificial sugar supplements to shift the balance in ant-pest interaction from pest guarding to pest control. Sugar feeders were supplied either on the ground near the tree trunk, or on the tree branches of citrus trees. Subsequently we assessed whether the provisioning of artificial sugar sources i) alters ant activity ii) disrupts the association between the ant *Lasius grandis* and the aphid *Aphis spiraecola* and iii) reduces the aphid populations over time. Compared to control trees (no sugars), ant activity within the tree was significantly reduced when the sugar feeders were placed on the ground and significantly increased when the feeders were placed on the tree branches. Ant tending of aphid colonies was reduced in all trees featuring sugar feeders. Similarly, aphid colony size was significantly reduced relative to control trees, both for trees with sugars on the ground or on the branches. However, the reduction was more pronounced when the sugars were offered on the tree branches. Finally, the abundance of natural enemies being associated with the aphid colony was significantly increased on trees with sugars on the branches. This shows that the provisioning of artificial sugar sources has practical potential as a sustainable strategy for ant management in programs aiming at the biological control of honeydew producing pests.

1. Introduction

Ants are generalist predators that can be highly effective in protecting plants by attacking and removing herbivores (Rosumek et al., 2009). In addition, most ant species have a substantial need for sugars as a main source of energy. This combination of traits has been at the basis of a range of defensive mutualisms in which various organisms employ sugar rewards to recruit ants and their protected services (Wäckers, 2002). This includes extrafloral nectaries, which are produced by many plant species to attract ants and other pest natural enemies (Heil, 2015; Wäckers, 2005). However, ant protection also extends to honeydew excreting herbivores, such as aphids and mealybugs. In exchange for their honeydew, ants often effectively guard these herbivores against natural enemies, improve colony hygiene, and transport them to new plants (Stadler and Dixon, 2005; Way, 1963). As a (net) result, ants frequently act as indirect pests in agricultural ecosystems. Often, measures are needed to disrupt the mutualistic relationship between ants and honeydew producers and thereby reduce pest infestations and plant damage. The most commonly employed methods involve the use of insecticides to kill the ants (Juan-Blasco et al., 2011; Moreno et al., 1987), or the use of sticky barriers to exclude ants from the crop (James and Stevens, 1997; Oliveira, 1997; Shorey et al., 1996). There are numerous studies demonstrating reduced populations of honeydew producers, and in some cases reduced plant damage, following ant-exclusion (Calabuig et al., 2014; Pekas et al., 2010; Styrsky and Eubanks, 2007). However, excluding ants also eliminates their services as biocontrol agents. Therefore, a method that distracts the ants from tending the honeydew producers while retaining ant predation could be optimal in terms of pest control.

Ants require both carbohydrates and protein. Protein is obtained from prey and scavenging whereas, carbohydrates are primarily obtained from (extra)floral nectar and honeydew produced by Hemiptera (Carroll and Janzen, 1973; Wäckers, 2005). The

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proportion of each food source to the ant's diet depends on various factors such as the ant species, the (reproductive) state of the ant colony and food source availability. Ants will forage more for protein under conditions of high carbohydrate availability (Offenberg, 2001) and when larvae are present in the nest (Oliver et al., 2012). When guarding honeydew producing Hemiptera, ants can balance their nutritional requirements by using the honeydew producers either as a source of sugar or as protein source (predation). Availability of alternative sugar sources can shift the balance towards protein exploitation (Engel et al., 2001). In cases where ants can chose between sugar alternatives, they discriminate on the basis of sugar quantity, concentration and composition (Detrain et al., 2010, 1999). When multiple honeydew producers co-occur on the same plants, ants tend to prey on the species representing the least attractive honeydew sources while guarding the preferred source (Engel et al., 2001). Also, a plant´s production of extrafloral nectar may yield the same result. By providing copious amounts of sugar supplements, plants can (partly) satiate the sugar requirements of ants and thus weaken the protective mutualisms between ants and honeydew producing herbivores (Becerra and Venable, 1989). This sugar supplementation strategy could be mimicked by using sugar feeders to distract ants from guarding honeydew producing pests. Nagy et al. (2013) used a honey solution to distract the common black ant *Lasius niger* (L.) from tending aphids and thus reduced aphid populations in apple orchards. Similarly, sucrose feeders were effective in reducing ant-tending of the pineapple mealybug, *Dysmicoccus brevipes* (Cockerell) (Hemiptera: Pseudococcidae) by the predaceous fire ant *Solenopsis geminata* (Fabricius) (Carabalí-Banguero et al., 2013). In other cases however, attempts to employ artificial sugar sources failed to disrupt protective interactions with the honeydew producers and were not successful in reducing herbivore populations (Del-Claro and Oliveira, 1993; Rico-Gray and Morais, 2006).

Here we compare different sugar application strategies to test if it is possible to distract ants from tending aphids, while maintaining ants as pest predators in the crop. For this study we used the system of *Lasius grandis* tending the aphid *Aphis spiraecola* Patch (Hemiptera: Aphididae) in commercial citrus orchards.

Lasius grandis is one of the most abundant ant species in Mediterranean citrus (Alvis and Garcia-Marí, 2006). It is behaviorally dominant and its activity has been associated with population increases of honeydew and non-honeydew producing herbivores (Calabuig et al., 2014; Pekas et al., 2010). It starts foraging on the citrus canopy in April and its activity peaks at the end of May (Pekas et al., 2011). *Aphis spiraecola* is one of the most important aphid species attacking citrus and in the Mediterranean is commonly tended by *L. grandis* (Garcia-Mar & , 2012; Pekas et al., 2011). It is native to eastern Asia, from where it expanded to South Africa and the American continent. It invaded the Mediterranean in 1960. This aphid remains on citrus trees throughout the year, but is most abundant in May coinciding with the presence of young citrus shoots (Garcia-Marí, 2012). *Aphis spiraecola* is attacked by a broad range of natural enemies including predatory larvae of Diptera (belonging to the families Syrphidae and Cecidomyiidae), larvae of Neuroptera, larvae and adults of Coleoptera (Coccinellidae), immature and adults of spiders (Araneae) and parasitoid wasps (Garcia-Mar & , 2012; Gómez-Marco et al., 2015).

Using this model system, we tested whether we could shift the balance between ant tending and ant predation through the provisioning of sugar feeders with a high quality sugar supplement and through the choice of sugar feeder position. Concretely, we compared two distinct sugar feeder locations, either placed at the base or inside the citrus tree. We tested the impact of these distinct feeder locations on 1) ant numbers visiting the citrus trees; 2) aphid-tending activity; 3) aphid colony growth; and 4) the abundance of aphid natural enemies.

2. Material and methods

2.1. Study site and experimental design

The study was conducted in 2012 in a citrus orchard with clementine mandarin (*Citrus reticulata* Blanco (vars. clemenules and Marisol)) of approximately 0.5 ha. The field site was located 23 km south of Valencia, in the middle of the main citrus growing region of Spain (latitude 39° 17′ 52,47″ N; longitude 0° 23′ 52,38″ W; H 30; DATUM WGS84). The climatic conditions are Mediterranean, with dry summers and mild winters. The trees were drip irrigated and weeds were mowed mechanically from March to October. Pests were managed according to methods compatible with organic farming. One treatment with mineral oil was applied in June against the first generation of *Aonidella aurantii* (Mask.) (Hemiptera: Diaspididae). However, this application did not coincide with the period in which our experiments were conducted.

The experiment was replicated three times, each time with a different set of five trees per treatment. The experimental design was a randomized complete block, with three treatments and three replicate blocks. It included the following three treatments: i) feeders with sugar solution placed on the tree branches, ii) feeders with sugar solution placed on the ground near the tree trunk and iii) control trees that received no sugar feeders. For each treatment, a total of 15 trees were selected on the basis of having workers of the ant *L. grandis* moving up/down the trunk and for harboring colonies of *A. spiraecola*. Out of these 15 trees, five trees were randomly allocated to each of the three replicates. Per tree, four *A. spiraecola* colonies (between 10 and 15 individuals) were selected and labeled at the start of the experiment, adding up to a total of 60 colonies being tested per treatment.

Sugar feeders consisted of 250 ml plastic bottles sealed with a perforated lid 28 mm in diameter. A round piece of filter paper was adjusted in the interior side of the lid to slow down the dripping of the sugar. The sugar used was Biogluc®, a ready to use sugar solution diluted 1:1 with water. This resulted in a 35.7% (w/w) sugar solution containing fructose (37.5%), glucose (34.5%), sucrose (25%), maltose (2%) and oligosaccharides (1%). For treatment (i) five sugar bottles per tree were placed upside down on the main tree branches downwards from the aphid colonies. Sugar bottles were attached with an adjustable plastic cable. For treatment (ii) the sugar bottles were fixed upside down to a wooden stick (15 cm) inserted in the soil using adhesive tape. In this treatment, the five bottles were placed in a circle around the tree trunk keeping approximately 10 cm between bottles and 5 cm distance between bottles and tree trunk. From preliminary observations we saw that bees and wasps were attracted to the sugar bottles and replaced the ants from feeding on the sugar solution. To avoid this, the sugar bottles were covered with a plastic mesh (openings size 25 × 28 mm), effectively excluding the larger sugar-feeding arthropods, yet allowing ants to feed on the sugar.

2.2. Sampling

To assess the effect of sugar provisioning on either the branches or on the ground we evaluated the following parameters:

Ant activity, defined as the number of ants ascending and descending the tree trunk (crossing an horizontal line at approximately 50 cm from the soil) during one minute.

Ant attendance, defined as the percentage of *A. spiraecola* colonies with at least one ant present during an observation period of 30 s. Aside from the four marked colonies (see below), we examined ant presence at an additional ten *A. spiraecola* colonies randomly selected per tree.

Aphid colony size, assessed as the number of aphids in each of the four marked colonies on each experimental tree.

Natural enemy abundance, assessed as the sum of aphid predators and parasitoids observed on the four marked and the ten randomly sampled *A. spiraecola* colonies during a 30 s observation period per