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Bumble bees (Hymenoptera: Apidae: *Bombus terrestris*) collecting honeydew from the giant willow aphid (Hemiptera: Aphididae)

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Abstract

Only rarely have bumble bees (*Bombus*) been observed collecting honeydew from aphids (Aphididae) feeding on phloem sap. This behavior may be rare because the percentage of sugar in honeydew egested from aphids is generally well below the sugar concentration in floral nectars preferred by bumble bees. Nonetheless, in August 2018, near St. Buryan, Penzance, Cornwall, UK (56.0602°N; -5.6034°W) we observed large numbers of wild *Bombus terrestris* (Linnaeus) collecting honeydew from a colony of the giant willow aphid *Tuberolachnus salignus* Gmelin feeding on the stems of the willow *Salix alba*. Unlike aphid-tending ants, who glean fresh honeydew directly from the aphid anal opening, the bumble bees were collecting honeydew from leaf litter below the aphid colony. We hypothesized that honeydew collected from exposed ground surfaces was more concentrated due to evaporation under ambient conditions than that released directly from the anus (fresh honeydew). We thus monitored sugar concentrations of fresh honeydew and compared them with the concentrations of the crop contents of worker bumble bees foraging from the leaf litter. Our data show that the concentration of sugar in fresh honeydew was as much as 10% w/w lower than that collected from leaf surfaces, as measured from the crop contents of foragers. The unusually hot, dry weather in Cornwall may have enhanced evaporative concentration of honeydew while restricting floral nectar sources, thus favoring honeydew collection by *B. terrestris*, a generalist bumble bee forager.

Keywords

Tuberolachnus salignus, *Salix alba*, solute concentrations, foraging behavior

Introduction

Most bee species depend on carbohydrates, primarily sucrose, glucose and fructose (Baker and Baker 1983), and diverse amino acids (Baker and Baker 1986) collected from floral nectar to fuel foraging flights and to feed larval offspring. On occasion bumble bees (*Bombus*) have been observed collecting honeydew exudates of aphids (Aphididae) (Brian 1957; Morse 1982; Wagner and Cameron 1985; Batra 1993; Bishop 1994). Honeydew foraging is well known in ants, many of which have evolved mutualistic interactions with aphids (Way 1963; Letourneau and Choe 1987; Völkl et al. 1999; Offenberg 2001), and honey bees (Crane and Walker 1985), and has been recorded recently in diverse solitary bees (Meiners et al. 2017) collecting from scale insects (Coccidae), but has rarely been reported in bumble bees (Batra, 1993). This could be because some honeydews are well below the sugar concentrations preferred by nectar-foraging bumble bees, which is 40-65% w/w (Harder 1986; Bailes et al. 2018). Honeydew egested from the giant willow aphid *Tuberolachnus salignus* Gmelin, for instance, ranges from only 0-20% solutes w/w (Mittler 1958).

Nonetheless, in Aug 2018 we observed large numbers of *Bombus terrestris* gleaning honeydew from surfaces below an aphid colony feeding on willow (*Salix*) in Southwest Cornwall, UK. The rarity of this behavior in bumble bees suggested that abnormal environmental conditions might be involved as a result of an unusually dry summer. Drought and relatively high temperature conditions are known to reduce total sugar content in nectar – three times less in some flower species – leading to decreased flower visitation rates by bumble bees (Descamps et al. 2018). Increased ambient temperature and water stress could thus cause bumble bees to become opportunistic foragers, taking advantage of non-floral sugar sources.

Honeydew can be collected either directly from the anus of aphids (common in ants) or after falling onto surfaces below an aphid colony (Douglas 2006). When fallen droplets of honeydew are exposed to dry air, their solute concentration is expected to increase by evaporation (Douglas 2006; Corbet et al. 1979). Given the unusually dry conditions in Cornwall during the summer of 2018, we examined whether dehydrated honeydew, relative to the freshly egested product, provided a sugar-rich food source for bumble bees.

Methods

In early August 2018, during an extended period of unusually hot, dry weather, we heard loud buzzing in the vicinity of a willow shrub growing in a cultivated flower garden at Boskenna Farm, St. Buryan, Penzance, Cornwall, UK (56.0602° N; -5.6034° W). On Aug 6, from dawn to dusk (0500-2130 BST), we observed *B. terrestris* (Linnaeus) females and males collecting honeydew that rained down approximately 1.2 m onto leaf litter directly beneath a colony of the cosmopolitan (Blackman and Eastop 2006) giant willow aphid *T. salignus* Gmelin feeding on the stems of *Salix alba* Linnaeus (Fig. 1A). The flowers in the garden included *Verbena bonariensis* Linnaeus

Figure 1. A Giant willow aphids (*Tuberolachnus salignus*) on a branch of *Salix alba*; larger aphids range from 5.1–5.7 mm **B** *Bombus terrestris* collecting honeydew from leaf litter beneath several branches bearing the aphids **C** holding a plastic plate beneath the aphid colonies to collect honeydew droplets **D** collecting honeydew droplets from the plate using a 5 µl glass capillary tube **E** compressing a worker bumble bee to force regurgitation of crop contents onto the plate **F** using a refractometer to measure solute concentration of honeydew.

and other flowering species in low abundance. The area surrounding the garden was predominantly arable farmland with hedgerows. A second *S. alba* shrub in the garden was also infested with *T. salignus*. To determine whether bumble bees were gleaning honeydew that was more concentrated than the fresh exudate released by the aphids, we monitored solute concentrations of fresh T. *salignus* honeydew over the course of the day and compared them with the concentrations in the crops of worker bumble bees collecting honeydew from the leaf litter below the aphid colony.

At 4-hr intervals during the day (5:45 am, 9:45 am, 1:55 pm, 5:45 pm and 9:15 pm British Summer Time) we made spot counts of all bumble bees on the ground within a ~1.2 m^2 area underneath the aphid colony (Fig. 1B). During each of the 5 sampling periods, we collected fresh aphid honeydew onto a 12 cm x 15 cm unwettable plastic tray held 10-15 cm beneath the highest density patches of aphids (Fig. 1C). Droplets of honeydew falling onto the tray were quickly collected into 5 μl glass capillary tubes (Fig. 1D). We measured total solute concentration (%w/w) in the honeydew with a hand refractometer (Fig. 1F) modified for low volumes (Bellingham and Stanley, Tunbridge Wells, UK). The results are expressed as the equivalent percent sucrose, g solute per 100 g solution (Corbet 2003; Descamps et al. 2018). We were unable to get a clear concentration reading of the fresh honeydew for the first time interval (5:45 am) but obtained a reading 8 am, between the first and second recording intervals.

During each of the five time intervals (when bees were foraging), we collected a random sample of 5-6 live bees foraging on the honeydew using 15-cm long forceps. They were kept cool on ice and taken indoors for measurement of solute concentration in the crop. To measure crop solute concentration, we placed each worker bee onto a clean unwettable 12 x 15 cm plastic plate, holding the bee in place with a foam plunger (Fig. 1E). We applied light pressure to the abdomen, causing regurgitation of the crop contents, which we collected immediately into a 5 μl capillary tube. We used the same hand refractometer to measure solute concentration as that used to measure the fresh honeydew. We excluded any collected males from measurement because they do not regurgitate crop contents. Bees were taken back to the field site and released after sampling. For some time periods all the bees randomly collected were males and thus no crop content data are recorded.

Aphids were identified using Dixon and Thieme (2007), the bumble bees using Prys-Jones and Corbet (2011), and the willow using Meikle (1984). Latitude and longitude coordinates were obtained using the GPS map coordinates function in Google Maps on an iphone.

Results

The total number of *B. terrestris* (workers and males) gleaning honeydew from the surfaces of leaf litter changed through the day, with the largest number of bees arriving early, and numbers declining through the day (Fig. 2A); by 2115 h, when it was dark, no bees were seen. Of 54 bumble bees recorded, only one was collecting honeydew along a willow stem; the others collected from the leaf litter.

Solute concentrations in honeydew egested freshly by the aphids were consistently low, ranging from 12% in early morning to 18% in the afternoon and 16% by sunset (Fig. 2B). The solute concentrations in bumble bee crops were nearly always higher than the fresh honeydew solute concentrations, ranging from 16% to 28% (Fig. 2B).

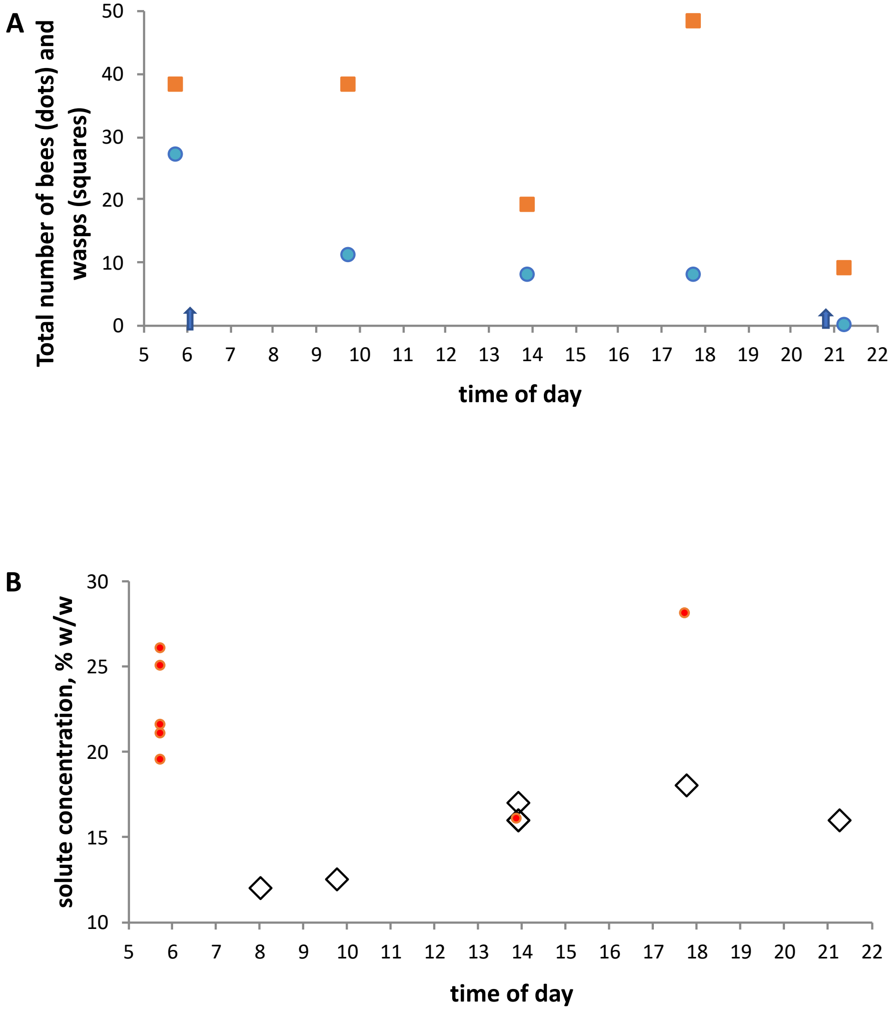

Figure 2. A Diurnal changes in total numbers of bees (blue dots) and wasps (red squares) **B** solute concentration in fresh honeydew (diamonds) and bumble bee crop contents (red dots). Arrows show times of sunrise and sunset.

Discussion

Why were so many *B. terrestris* workers collecting aphid honeydew on this occasion? Our finding that bumble bee crop contents were more concentrated than fresh honeydew indicates that bumble bees were not solely collecting the very dilute fresh honeydew. The abnormal environmental conditions at the time likely played a part in this rarely observed behavior. The summer of 2018 was the hottest in England since records began, and Cornwall was under significant drought stress, with no significant rainfall from June to August. It is therefore likely that food and water resources from flowers were much reduced, affecting pollinator attractiveness. Bumble bees could enhance their food reward by collecting the more concentrated honeydew. The high temperatures and low relative humidity would cause rapid evaporative concentration of fallen honeydew droplets, perhaps raising the solute concentration to a level acceptable to bumble bees. Their crops may also have contained sugar solutions from other sources. It is notable that Batra's (1993) observations of bumble bees collecting honeydew were made in unusually hot, dry weather, and the egested honeydew had evaporated to dryness.

While we did not quantify the amount of honeydew falling onto the leaf litter, it was audible as it rained down onto the dry leaves in the early morning when fewer bees were buzzing. The honeydew droplets were between 3 and 5 μl, as estimated when drawing droplets into 5 μl capillary tubes. Multiple droplets per second fell from the aphids onto the plastic tray held beneath the colony. As the aphids continued to feed and release honeydew from dawn to dusk, they provided a reward bonanza for the bumble bees at this time.

Global climate change leading to drought and temperature stress has led to multiple reports that wildflowers important to bees experience reduced nectar production with lower sugar quantity (Waser and Price 2016; Descamps et al. 2018; Phillips et al. 2018); heat- and water-stressed flowers are visited less frequently as food rewards are negatively impacted (Descamps et al 2018; Phillips et al. 2018). Under such environmental conditions, bumble bees can modify their foraging behavior to search for alternative sugar sources (Cartar 2004; Dreisig 2012; Fowler et al. 2016). Increased temperature and water stress could, therefore, cause bumble bees to become opportunistic foragers, taking advantage of non-floral sources of sugar, such as concentrated honeydew deposits. This may be a more general phenomenon in bees, as Meiners et al. (2018) found that 42 species of native bees in California become opportunistic foragers on scale insect secretions at times of low floral availability.

Bombus terrestris, a short tongued bumble bee, was the sole bumble bee species seen collecting honeydew at our site, even though several other species are common in the area, including the long-tongued *B. pascuorum* (Scopoli). This might be explained by the fact that *B. terrestris* (subgenus *Bombus*) is a generalist bumble bee, similar to other members of the subgenus *Bombus sensu stricto*, and preadapted to foraging on a wide array of food sources. In fact, two of only three published observations of bumble bees collecting aphid honeydew in North America (Morse 1982; Batra 1993; Wagner and Cameron 1985) pertain to *B. terricola* Kirby (subgenus *Bombus*). Species of this subgenus appear predisposed to search widely for diverse food sources (Walther-Hellwig and Frankl 2000), which may explain their ecological success across much of western Europe. Another possible reason for the concentration of *B. terrestris* at the site is that a *B. terrestris* colony was nesting in a stone retaining wall several m from the aphid infestation. The aphid colony could therefore be reached with little effort in terms of flight energy. We do not know the nesting origins of the individuals observed in our study.

No other bees, such as honey bees or solitary bees, collected honeydew at the site, nor did we see any ants, although it has been reported that *T. salignus* colonies in the UK are often tended by ants (Paul 1974; Sopow et al 2017). The wasp *Vespula germanica* (Fabricius) was, however, collecting honeydew in relatively large numbers at the site. They were 2-6 times more abundant than the bees (Fig. 2A) and tended to collect honeydew from the willow stems in the vicinity of the aphids, although some collected from the leaf litter. Wasps were actively foraging throughout the day, as well as at dawn and dusk, earlier and later than the bumble bees, suggesting they may perform better under low light conditions.

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