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The effect of different dietary sugars and honey on longevity and fecundity in two hyperparasitoid wasps

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ABSTRACT

In nature adult insects, such as parasitic wasps or ‘parasitoids’ often depend on supplemental nutritional sources, such as sugars and other carbohydrates, to maximize their life-expectancy and reproductive potential. These food resources are commonly obtained from animal secretions or plant exudates, including honeydew, fruit juices and both floral and extra-floral nectar. In addition to exogenous sources of nutrition, adult parasitoids obtain endogenous sources from their hosts through ‘host-feeding’ behavior, whereby blood is imbibed from the host. Resources obtained from the host contain lipids, proteins and sugars that are assumed to enhance longevity and/or fecundity. Here we conducted an experiment exploring the effects of naturally occurring sugars on longevity and fecundity in the solitary hyperparasitoids, *Lysibia nana* and *Gelis agilis*. Although both species are closely related, *L. nana* does not host-feed whereas *G. agilis* does. In a separate experiment, we compared reproduction and longevity in *G. agilis* reared on either honey, a honey-sugar ‘mimic’, and glucose. Reproductive success and longevity in both hyperparasitoids varied significantly when fed on different sugars. However, only mannose- and water-fed wasps performed significantly more poorly than wasps fed on four other sugar types. *G. agilis* females fed honey produced twice as many progeny as those reared on the honey-sugar mimic or on glucose, whereas female longevity was only reduced on the mimic mixture. This result shows not only that host feeding influences reproductive success in *G. agilis*, but also that non-sugar constituents in honey do. The importance of non-sugar nutrients in honey on parasitoid reproduction is discussed.

1. Introduction

In nature, adult insects often depend on supplemental nutritional sources, such as sugars and other carbohydrates, as well as proteins, to maximize their life-expectancy and reproductive potential. These food resources are commonly obtained from animal or plant exudates, such as honeydew, fruit juices and both floral and extra-floral nectar. In parasitic wasps, or ‘parasitoids’, the benefits of sugars on fitness-related traits, such as longevity and fecundity, is well established (Jervis et al., 1993; Heimpel et al., 1997; Wäckers, 2001; Casas et al., 2003; Lee et al., 2004; Winkler et al., 2006; Wäckers et al., 2008; Desouhant et al., 2010; but see Ellers et al., 2011). It is also well known that different sugars vary in their nutritional quality for parasitoids, with some greatly extending the lifespan whilst others have little effect or may even be toxic (Jervis et al., 1993; Wäckers, 2001; Wäckers et al., 2006; Kehrli and Bacher, 2008). In the field, therefore, it may pay parasitoids to exhibit preferences for feeding on exudates from some species of plants or animals over others.

In addition to sugars obtained exogenously, some parasitoids also ‘host-feed’, imbibing blood from the host (Jervis and Kidd, 1986). Host blood is rich in proteinaceous materials, which are important in the manufacture of eggs, whereas proteins are lacking in the honeydew and nectar which are generally comprised of carbohydrates (Bernstein and Jervis, 2006). Several studies have shown that resources obtained from host-feeding may be allocated for both reproduction and/or maintenance (Heimpel and Rosenheim, 1995; Heimpel and Collier, 1996; Giron et al., 2002; Rivero and West, 2005; Kapranas and Luck, 2008; Zhang et al., 2011). Host blood is often important in the production of large, yolky ‘anhydropic’ eggs (Jervis and Kidd, 1986; Bernstein and Jervis, 2006; Harvey, 2008) that are characteristically produced by many ‘idiobiont’ ectoparasitoids, i.e. parasitoids that attack non-feeding or non-growing host stages or arrest host development prior to oviposition (Godfray, 1994; Harvey, 2005; Jervis and Ferns, 2011). In contrast, most endoparasitoids that develop inside the host are ‘koinobionts’ i.e. parasitoids that allow the host

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to continue feeding and growing during parasitism (Godfray, 1994; Harvey, 2005). In koinobionts adult female wasps do not host-feed, and invest very little protein into their tiny 'hydropic' eggs. Instead proteins are absorbed from the host blood through a specialized extra-embryonic membrane before hatching (Jervis and Kidd, 1986; Jervis et al., 2001, 2008). Host blood has also been found to contain certain sugars, such as trehalose and sucrose that are important in reducing the metabolism of lipids (Giron et al., 2002). However, this is certainly not the rule, as the longevity of some parasitoids is not extended at all by host-feeding (Rivero and West, 2005; Harvey, 2008). Host-feeding parasitoids are generally highly synovigenic, meaning that the adult female wasps emerge with few or no ripe eggs and therefore mature most of their eggs after eclosion (Ellers et al., 2000; Jervis et al., 2001, 2008).

Studies examining life-history variables such as longevity and reproduction in parasitoids have rarely integrated the nutritional value of different naturally occurring sugars and host-feeding under the umbrella of a single ecophysiological framework. Instead, most studies on the nutritional value of different sugars for parasitoids have explored one demographic character, such as longevity (Wäckers, 2001; Vattala et al., 2006), or else have used non host-feeding koinobiont parasitoid species that generally invest very low *per capita* resources into each egg (Wanner et al., 2006; Winkler et al., 2006; Faria et al., 2008; Lee and Heimpel, 2008; Wu et al., 2008). In this way it is impossible to tease apart the benefits, if any, of different sugars in concert with host feeding, on reproduction and longevity in parasitoids that require both host- and non-host resources during adult life to maximize these variables.

A previous study reported that longevity in a primary gregarious endoparasitoid, *Cotesia glomerata* L. (Hymenoptera: Braconidae), differed significantly when the wasps were fed on 14 different sugars that occur naturally (Wäckers, 2001). In this study we examine the effects of several naturally occurring sugars found in e.g. honeydew and nectar, on longevity and fecundity in two closely related species of solitary hyperparasitoids, *Lysibia nana* Gravenhorst and *Gelis agilis* Fabricius (Hymenoptera: Ichneumonidae, Cryptinae) that attack the fully cocooned pre-pupae and pupae of *C. glomerata* in the field. Both species are ectoparasitoids, are wholly synovigenic and produce anhydropic eggs (Harvey, 2008). However, they also exhibit several key differences in reproductive and morphological traits. *Lysibia nana* reproduces sexually and adults are fully winged; by contrast, *G. agilis* reproduces asexually and adult females are wingless (Harvey, 2008). Another important difference between the two species is that *G. agilis* females mutilate some host cocoons with their ovipositors and feed on the blood that leaks from the wound as a pre-requisite for egg maturation; *L. nana* females, on the other hand, do not host-feed (Harvey, 2008). Furthermore, the reproductive biology and host exploitation behavior of *L. nana* is closely correlated with brood size in *C. glomerata* whereas in *G. agilis* it is not (Harvey, 2008; Harvey et al., 2011). This suggests that *L. nana* is much more specialized in attacking *C. glomerata* than *G. agilis*.

In a second experiment, we compare longevity and fecundity in the host-feeding species *G. agilis* when the wasps are provided with glucose (a high quality sugar), honey, or a 'honey-mimic' that consists of equivalent amounts of several sugars that are found in honey. Honey has long been used in the lab as an alternate food source to sucrose solution for insects such as parasitoids, but its actual properties in influencing parasitoid reproduction and longevity have been little explored. With respect to carbohydrates, honey consists mainly of similar proportions of fructose and glucose with smaller concentrations of maltose, sucrose, and several other complex carbohydrates (Doner, 1977). As with all nutritive sweeteners, the content of honey is dominated by sugars although it also contains trace amounts of vitamins or minerals (Martos et al., 2000; Gheldof et al., 2002). Furthermore, honey also contains tiny amounts of several compounds thought to function as antioxidants, including chrysin, pinobanksin, vitamin C, catalase, and pinocembrin (Martos et al., 2000).

The aims of the study are twofold: first, to determine if longevity and fecundity in *L. nana* and *G. agilis* are affected when fed on different naturally occurring sugars; second, to determine if these demographic variables differ in *G. agilis* when different cohorts are reared on glucose, honey or a honey-mimic that lacks the trace minerals and compounds found in honey. We hypothesize (1) that longevity and fecundity in these two closely related hyperparasitoids will be similarly affected by qualitative differences in dietary sugars, and (2) honey provides a high-quality carbohydrate resource affecting longevity similarly as high-quality sugars offered singly or in a mixture, because sugars and honey are of high value for maintenance, whereas host-feeding is important for reproduction.

2. Materials and methods

2.1. Insect cultures

Lysibia nana and *G. agilis* have been reared for several years at the Netherlands Institute of Ecology (NIOO) in Heteren, the Netherlands. Both hyperparasitoids were originally obtained from cocoons of *C. glomerata* recovered from leaves of black mustard plants (*Brassica nigra*) growing adjacent to the NIOO institute. Both species were reared according to the protocol described in Harvey (2008). Cultures of *L. nana* were generated from 200 to 300 *C. glomerata* cocoons placed in rearing cages with 50 adult *L. nana* wasps for 24 h. Then, parasitized cocoons were transferred to large Petri dishes (18 cm) until adult emergence. The rearing protocol for *G. agilis* was similar, except that *G. agilis* had access to a small number of cocoons for host-feeding purposes 3–4 days before it was provided with new cocoons for oviposition The parasitoids were reared at $25 \pm 2^{\circ}C$ with a 16:8 h L:D light:dark regime. *Cotesia glomerata* was reared on *Pieris brassicae* L. (Lepidoptera: Pieridae) caterpillars and was originally collected from agricultural fields in the vicinity of Wageningen University.

2.2. Experimental protocol

2.2.1. Experiment 1: longevity and fecundity in L. nana and G. agilis reared on different sugars

The aim of this experiment was to determine if different, naturally occurring sugars affected longevity and fecundity in two hyperparasitoids of *C. glomerata*. A subset of the 14 sugars used in an earlier study by Wäckers (2001) were selected on the basis of a wide spectrum of effects on longevity in the primary parasitoid, *C. glomerata*, the host of *L. nana* and *G. agilis* in this study. Five of these sugars were selected to be offered to wasps in the present study: two monosaccharides, glucose and mannose (molar masses 180.2 g/mol), and three disaccharides, trehalose, melibiose and maltose (molar masses 342.3 g/mol). All of these sugars are found in floral nectar, whereas glucose, maltose and trehalose are also found in honeydew exudates from aphids (Wäckers, 2001). The concentration used for all sugar solutions was 1 M. This concentration represents the upper limit of sugars found in floral nectar and honeydew (Wäckers, 2001). Three droplets of 10 μL of a specific sugar solution were placed in each Petri dish using a pipette. These sugars were refreshed daily. For the control treatment, three droplets of 10 μL of water were also placed in the Petri dishes using a pipette. Cotton wool moistened with water was placed in each Petri dish to ensure that the droplets would not evaporate.