



Honey and honey-based sugars partially affect reproductive trade-offs in parasitoids exhibiting different life-history and reproductive strategies



Jeffrey A. Harvey^{a,b,*}, Tijl A. Essens^a, Rutger A. Las^c, Cindy van Veen^c, Bertanne Visser^d, Jacintha Ellers^b, Robin Heinen^a, Rieta Gols^c

^a Department of Terrestrial Ecology, Netherlands Institute of Ecology, Droevendalsesteeg 10, 6708 PB Wageningen, The Netherlands

^b VU University Amsterdam, Department of Ecological Sciences, Section Animal Ecology, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

^c Laboratory of Entomology, Wageningen University, Droevendaalsesteeg 1, 6700 EH Wageningen, The Netherlands

^d Evolutionary Ecology and Genetics Group, Biodiversity Research Centre, Earth and Life Institute Université Catholique de Louvain, Croix du Sud 4, 1348 Louvain-la-Neuve, Belgium

ARTICLE INFO

Article history:

Received 24 June 2016

Received in revised form 12 December 2016

Accepted 18 December 2016

Available online 23 December 2016

Keywords:

Development

Fecundity

Gelis

Longevity

Meteorus pulchricornis

Microplitis mediator

ABSTRACT

Adult dietary regimes in insects may affect egg production, fecundity and ultimately fitness. This is especially relevant in parasitoid wasps where many species serve as important biological control agents of agricultural pests. Here, we tested the effect of honey and sugar diets on daily fecundity schedules, lifetime reproductive success and longevity in four species of parasitoid wasps when reared on their respective hosts. The parasitoid species were selected based on dichotomies in host usage strategies and reproductive traits. *Gelis agilis* and *G. areator* are idiobiont ecto-parasitoids that develop in non-growing hosts, feed on protein-rich host fluids to maximize reproduction as adults and produce small numbers of large eggs. *Meteorus pulchricornis* and *Microplitis mediator* are koinobiont endoparasitoids that develop inside the bodies of growing hosts, do not host-feed, and produce greater numbers of small eggs. Parasitoids were reared on diets of either pure honey (containing trace amounts of proteins), heated honey (with denatured proteins) and a honey-mimic containing sugars only. We hypothesized that the benefits of proteins in honey would enhance reproduction in the ectoparasitoids due to their high metabolic investment per egg, but not in the koinobionts. Pure honey diet resulted in higher lifetime fecundity in *G. agilis* compared with the honey-mimic, whereas in both koinobionts, reproductive success did not vary significantly with diet. Longevity was less affected by diet in all of the parasitoids, although there were variable trade-offs between host access and longevity in the four species. We argue that there are both trait-based and association-specific effects of supplementary nutrients in honey on reproductive investment and success in parasitoid wasps.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

Trait variation among species is generally considered as a result of long-term selection driven by a wide range of environmental conditions but which is often constrained by phylogeny (Houle, 1992). Parasitoid wasps (Hymenoptera) are frequently used to study various aspects of life-history strategies in insects. Importantly, trade-offs among fitness functions often play a crucial role in determining trait expression in parasitoids (Ellers et al., 1998; West and Rivero, 2000; Heping et al., 2008; Harvey, 2008; Harvey et al., 2012). Because their development is dependent upon the (often) limited resources contained in a single resource (the host),

parasitoids are under intense selection to optimize the allocation of these resources to different metabolic functions, such as maintenance and reproduction (Godfray, 1994; Mayhew and Blackburn, 1999; Jervis et al., 2008). Furthermore, trade-offs may influence the evolution of life-history strategies, as suggested by the inverse relationship between longevity and egg production across a wide variety of parasitoid Hymenoptera species (Blackburn, 1991a,b). However, how the nutritional value of food resources influences fitness-related traits in parasitoids with varying life-history strategies and phylogenetic affiliation, remains poorly examined.

A number of major divisions in life history strategies of parasitoid Hymenoptera have been proposed (Godfray, 1994), but an extensive meta-analysis by Mayhew and Blackburn (1999) found strong support for two dominant life-history strategies in parasitoid Hymenoptera, i.e., idiobionts and koinobionts, each characterized by a different set of associated life history traits (Askew and Shaw,

* Corresponding author at: Department of Terrestrial Ecology, Netherlands Institute of Ecology, Droevendalsesteeg 10, 6708 PB Wageningen, The Netherlands.

E-mail address: j.harvey@nioo.knaw.nl (J.A. Harvey).

1986). Idiobionts are parasitoids that attack non-growing or paralyzed hosts where resources for offspring are ostensibly fixed at oviposition (Harvey, 2005). By contrast, koinobionts attack hosts that continue feeding and growing after being parasitized (Harvey, 2005). The amount of host resources available for the development of idiobionts is therefore mostly static, whereas for koinobionts there may be a profound size differential of the host between parasitism and host death (Mackauer and Sequeira, 1993; Godfray, 1994; Harvey, 2005). Furthermore, idiobionts are generally ectoparasitoids and lay very large, yolky 'anhydropic' eggs onto the cuticle of the host; these eggs necessarily contain all pre-packaged resources for the successful completion of embryonic development (Jervis and Kidd, 1986). In many idiobionts the resources necessary to initiate and/or maximize egg production are obtained via 'host-feeding' behavior, whereby the adult female parasitoid, using her ovipositor, inflicts a wound in the host cuticle and drinks protein-rich fluids that emerge from the wound (Jervis and Kidd, 1986; Rivero and West, 2005). Most koinobionts, on the other hand, are endoparasitoids that lay tiny, yolk-deficient eggs inside of the host body, where the developing embryo absorbs proteins in the host hemolymph through a porous membrane in the egg chorion (Jervis and Kidd, 1986). Very few (if any) species of koinobiont parasitoids are known to host-feed. Instead, they effectively 'cheat' by investing low amounts of *per capita* resources into each egg, and produce huge numbers of eggs that may be laid rapidly inside the host. In contrast, idiobionts often compensate for low egg production with an extended life-span, as resources necessary for egg production may be instead utilized for maintenance (Price, 1972).

As adults, many parasitoid species obtain supplementary sugars from nectar during their lifetime, though these sugars vary in quality and composition (e.g., (extra)-floral nectar, honeydew from aphids etc.). Three of the main sugars in floral nectar are sucrose, glucose and fructose (Stahl et al., 2012). Carbohydrates derived from nectar moderate the metabolic use of stored lipids (Ellers, 1996; Ellers et al., 1998, 2000; Ellers and Jervis, 2004), and potentially increase fitness in parasitoid wasps by increasing their lifespan or else switching the allocation of stored metabolic resources towards egg production (e.g., Heimpel et al., 1997; Wäckers, 2001; Lee et al., 2004; Winkler et al., 2006; Wäckers et al., 2008; but see Ellers et al., 2011). In the laboratory, honey is often used for the rearing of parasitoids and other insects, and is considered an excellent substitute for nectar, being highly nutritious for insects. Honey mainly consists of the carbohydrates fructose and glucose, but additionally contains approximately other 200 substances (da Silva et al., 2016), including vitamins and about 0.5% of proteins, mainly functioning as enzymes and a source of amino acids (Bogdanov et al., 2008). Several of these enzymes are related to the antimicrobial properties of honey, such as glucose oxidase and bee defensin-1 (Kwakman et al., 2010). Other enzymes present in honey are invertase and diastase, which are involved in the breakdown of sugars, as well as catalase, which protects the cell from oxidative damage (Ball, 2007).

A previous study showed that a honey diet significantly enhanced reproductive success in a facultative hyperparasitoid wasp, *Gelis agilis* (Harvey et al., 2012). Adult female wasps fed on honey produced twice as many progeny as those fed on glucose or a mixture of sugars naturally contained in honey. *Gelis agilis* is an ecto-parasitoid with typical traits associated with idiobiosis e.g. large eggs, low fecundity, host-feeding behavior, extended lifespan (Harvey, 2008). However, it is not known if the benefit of honey on reproductive success in parasitoids is restricted to idiobionts or even to *Gelis agilis* alone.

In the present study, we compare the effect of honey/sugar diets on longevity and reproduction in two idiobiont species and two koinobiont species. *Gelis areator* Panzer and *G. agilis* Fabricius

(Hymenoptera: Ichneumonidae) (Fig. 1A, B) are solitary idiobiont ecto-parasitoids (and facultative hyperparasitoids) that are known to attack a broad range of hosts (Harvey, 2008; Harvey et al., 2015; Visser et al., 2016). Both species exhibit typical idiobiont traits, although *G. areator* reproduces sexually and is fully winged, whereas *G. agilis* is asexual and wingless. *Microplitis mediator* Haliday and *Meteorus pulchricornis* Wesmael (Hymenoptera: Braconidae) (Fig. 1C, D) are solitary koinobiont endoparasitoids that in turn exhibit traits typically associated with species in this group. Here, we measured reproductive success and longevity of the four parasitoids from eclosion in female wasps fed either on honey, heated honey (heating denatures proteins) and a honey mimic containing sugars in the same proportions as they occur in honey. We hypothesized first, that (1) the idiobionts have lower fecundity but longer life-spans compared to koinobiont endoparasitoids. To assess trade-offs, we then hypothesized that (2) honey would increase the reproductive capacity in the idiobionts but not in the koinobionts. This is based on the assumption that proteins and amino acids in honey supplement those obtained from host-feeding behavior in the production of anhydropic eggs, but not in the production of small, hydropic eggs in the two koinobionts that do not host-feed. We also hypothesized (3) that there would be a trade-off between reproduction and longevity in all four parasitoids due to the costs of egg production and foraging, and lastly (4) that, within each treatment (e.g. host access or control), longevity would not differ due to the uptake of sugars contained in all diets for maintenance.

2. Materials and methods

2.1. Insects

A summary of traits for the parasitoids used in this study can be found in Table 1. Individuals of Lepidoptera and Hymenoptera were kept at 22 ± 2 °C under a 16:8 h L:D regime. *P. brassicae*, *Ma. brassicae*, *Mi. mediator* and *C. glomerata* were obtained from cultures in Wageningen University (WU), the Netherlands, and were originally collected from agricultural fields in the vicinity of the University in the 1990s and which are regularly replenished with fresh field-collected specimens. *P. brassicae* larvae were fed with *Brassica oleracea* var. *Cyrus* (Brussels sprouts) maintained at WU. *C. glomerata* were reared on 1st instars of *P. brassicae* (see also Harvey, 2008). The two *Gelis* species were obtained from cocoons of *C. glomerata* that were placed in grass adjacent to the Netherlands Institute of Ecology Buildings (NIOO) in Wageningen. *Me. pulchricornis* was originally obtained from fields close to Nagoya University, Japan and which was originally reared on *Mythimna separata* caterpillars. In the Netherlands it was reared for two years on larvae of *Ma brassicae* prior to the experiment.

2.2. Diet treatments

Wasps were fed on different diets, i.e., honey, heated honey and honey mimic. We used Langnese™ wildflower honey, derived from various locations and botanical origin. Heating was undertaken by placing honey in the microwave until boiling point and reheating twice for 10 s. According to Skinner (2009) heating honey up to 37 °C destroys nearly 200 components, some of which are known to have antibacterial properties. Heating up to 40 °C destroys invertase, an important enzyme. Heating of honey to 50 °C for more than 48 h turns the honey into caramel (the most valuable honey sugars become analogous to sugar). Heating honey higher than 60 °C for more than 2 h will cause rapid degradation, and heating honey higher than 70 °C for any time period will cause rapid degradation and caramelization.

Download English Version:

<https://daneshyari.com/en/article/5593169>

Download Persian Version:

<https://daneshyari.com/article/5593169>

[Daneshyari.com](https://daneshyari.com)