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

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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 nongrowing 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.

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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,

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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 prepackaged 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* Fabricious (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 endoparasites. 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.
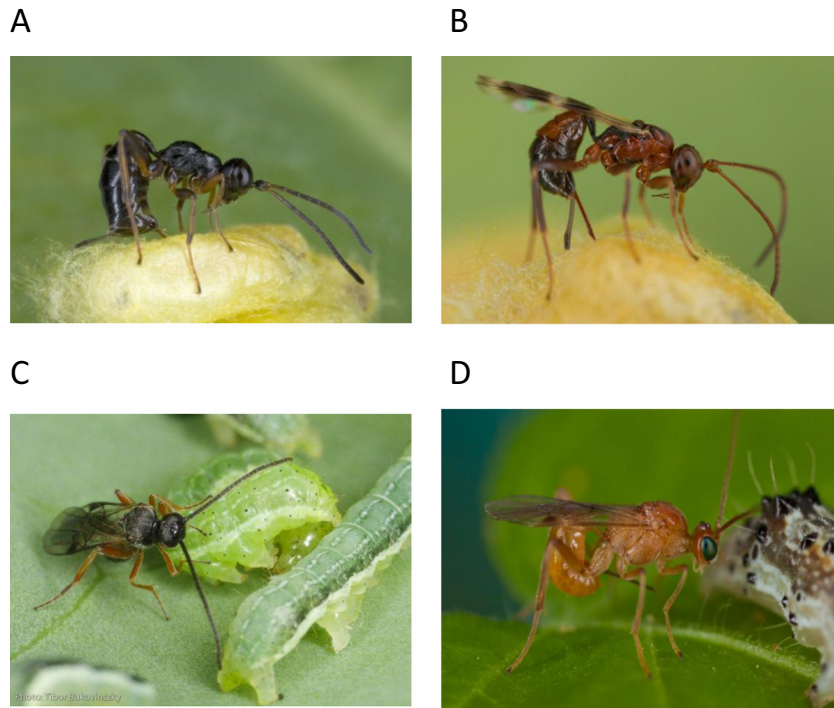
Fig. 1. The parasitoids used in this study. A. *Gelis agilis*; B. *Gelis areator*; C. *Microplitis mediator*; D. *Meteorus pulchricornis*.

Table 1
Descriptions of the four parasitoid species used in this study.

Gelis agilis Fabricius (Ichneumonidae)	*Gelis areator* Panzer (Ichneumonidae)	*Miroplitis mediator* Haliday (*Braconidae*)	*Meteorus pulchricornis* Wesmael (*Braconidae*)
Highly generalist	More specialized	More specialized	Highly generalist
Idiobiont	Idiobiont	Koinobiont	Koinobiont
Ectoparasitoid	Ectoparasitoid	Endoparasitoid	Endoparasitoid
Anhydropic eggs	Anhydropic eggs	Hydropic eggs	Hydropic eggs
0 eggs at eclosion	0 eggs at eclosion	~10 eggs at eclosion	~5 to 10 eggs at eclosion
Max. egg load ~3	Max. egg load ~5	Max. egg load ~40	Max. egg load ~30
Synovigenic	Synovigenic	Synovigenic	Synovigenic
Host-feeds	Host-feeds	Non host-feeding	Non host-feeding
Asexual reproduction	Sexual reproduction	Sexual reproduction	Asexual reproduction
Wingless adults	Winged adults	Winged adults	Winged adults

The honey-mimic was prepared as follows: fructose: 17.5 g, glucose: 17.5 g, maltose: 7 g, sucrose: 1.5 g, dissolved in 100 ml water (Harvey et al., 2012). Honey mimic contains the sugar-components comparable with the ratios found in honey and heated honey, but lacks a variety of micronutrients that are found in honey (see introduction).

2.3. Experimental protocol

All parasitoids used in the experiments were initially mated and then were immediately provided with access to hosts. For *Mi. mediator*, ten L2 *Ma. brassicae* host larvae were placed in a Petri dish (12 cm dia.), and exposed to a single female adult parasitoid for four hours. For *Me. pulchricornis*, the same method was employed using 3rd instar larvae of *M. brassicae*. After exposure, the parasitoids were removed and placed in a Petri dish provided with six 10-μl drops of either honey, heated honey or honey mimic, following the protocol of Harvey et al. (2012). This was repeated every 48 h. The exposed caterpillars were provided with fresh artificial diet every two days, and the fate of the parasitized hosts monitored daily for parasitoid egression, unsuccessful parasitism (hosts grew and developed normally) and mortality.

For *G. agilis* and *G. areator*, individual female parasitoids were provided with ten host *C. glomerata* cocoons in Petri dishes, following the protocol of Harvey (2008). They were provided with either honey, heated honey or honey mimic, depending on the group treatment. Every 48 h, the cocoons were replaced with fresh ones, and also the sugar diet was refreshed. Parasitoid cocoons were placed in plastic vials. Emerged *G. agilis* and *G. areator* were counted, as well as the number of dead *C. glomerata* cocoons.

The control group for measuring longevity (e.g. no host access) was maintained under the same experimental conditions. The experiment was repeated 12 times for each parasitoid species/ diet combination.

2.4. Statistical analysis

Initially, other analyses were included of which the data deviated from normality and homoscedasticity. Visual inspection of the residuals of both cumulative egg production and longevity were approximately normally distributed and variances were approximate similar among treatments. ANOVA was conducted to assess the overall effect of diet on daily fecundity and cumulative egg production for the four species separately. To test whether

species lifespan was dependent on diet and host accessibility, a two-way ANOVA (diet and host/no host as factors) was conducted. When models were significant Tukey multiple comparison tests were conducted to contrasts means.

3. Results

3.1. Lifetime reproductive success

The dietary regime affected lifetime reproductive success in *G. agilis* ($F_{2,33}$ = 3.34, P = 0.048) but not in *G. areator* ($F_{2,27}$ = 2.12, P = 0.14) or in the two koinobionts, *Mi. mediator* ($F_{2,38}$ = 0.04, P = 0.96) and *Me. pulchricornis*, ($F_{2,31}$ = 0.30, P = 0.74)(Fig. 2). *G. agilis* females produced significantly more offspring when provided with a honey diet than with a honey-mimic diet during its adult life; wasps also produced less offspring on heated honey but this

was not statistically significant. Cumulative fecundity curves in the four species illustrate the clear benefit of a honey diet in *G. agilis* only (Fig. 3).

3.2. Longevity

Longevity was strongly affected by host access in all four parasitoid species (*G. agilis* $F_{1,65}$ = 33.0, P < 0.001; *G. areator* $F_{1,56}$ = 27.1, P < 0.001, *Mi. mediator* $F_{1,70}$ = 45.8, P < 0.001; *Me. pulchricornis*, $F_{1,63}$ = 167, P < 0.001, Fig. 4). *Mi. mediator, Me. pulchricornis* and *G. agilis*, females had significantly shorter lifespans in the presence of hosts compared with controls, whereas in *G. areator* this pattern was reversed: wasps lived significantly longer when they had access to hosts. In the two *Gelis* species, diet also had an effect on longevity (*G. agilis* $F_{2,65}$ = 3.80, P = 0.027; *G. areator* $F_{2,56}$ = 3.46, P = 0.038) and in *G. agilis* the interaction with host availability
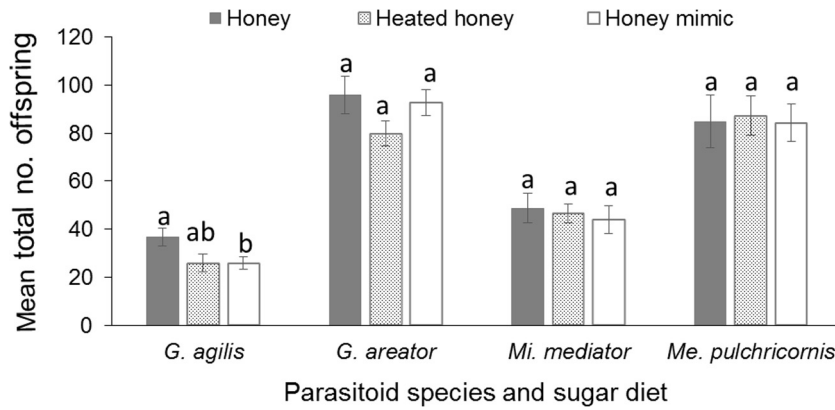
Fig. 2. Mean lifetime reproductive success in *Gelis agilis*, *G. areator*, *Microplitis mediator* and *Meteorus pulchricornis* under the different feeding treatments. Line bars represent the standard error of the mean. Bars with the same letter (at the species level) are not significantly different (Tukey-Kramer tests, P > 0.05). Sample size for all species = 12 wasps.
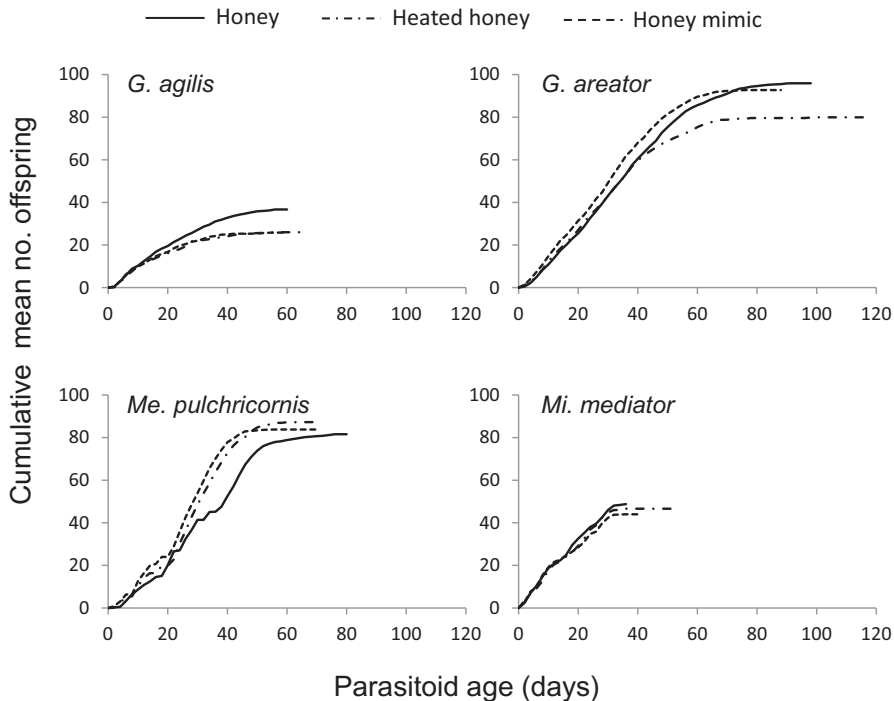
Fig. 3. Cumulative fecundity curves of (A) *Gelis agilis*, (B) *G. areator*, (C) *Microplitis mediator* and (D) *Meteorus pulchricornis* under the different feeding treatments. Sample size for all species = 12 wasps Standard error bars were omitted because they clutter the data.
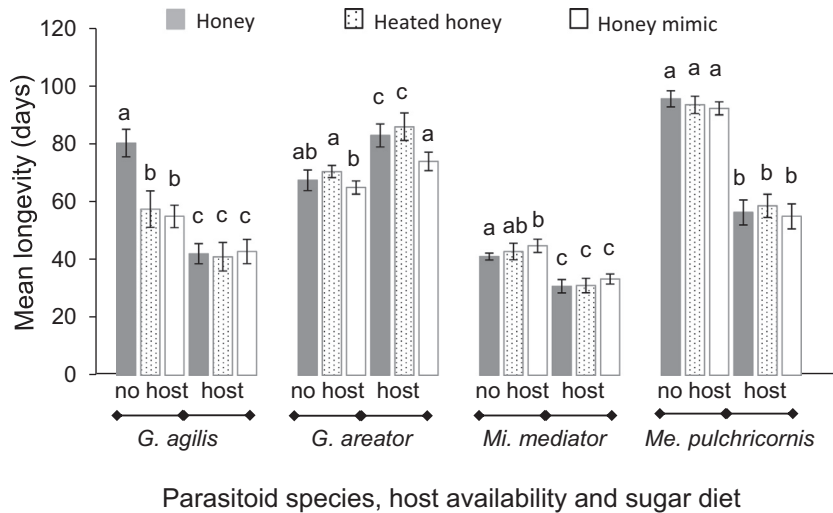
Fig. 4. Mean longevity in female *Gelis agilis, G. areator, Microplitis mediator* and *Meteorus pulchricornis* under different feeding and host access treatments. Line bars represent the standard error of the mean. Bars with the same letter (at the species level) are not significantly different (Tukey- tests, P > 0.05). Sample size for all species = 12 wasps.

was also significant $F_{2,65} = 4.36$, $P = 0.017$). Irrespective of host availability, *G. areator* had the shortest life span when reared on the honey mimic. In *G. agilis*, diet only affected longevity of the wasps when provided with hosts; in this treatment wasps provided with hosts lived longer when fed on honey than on heated honey or the honey mimic (Fig. 4). In the two koinobiont species, longevity was not affected by diet (*M. mediator* $F_{2,70} = 1.11$, $P = 0.34$; *Me. pulchricornis,* $F_{2,63} = 0.10$, $P = 0.90$) nor by the diet-host access interaction term (*Mi. mediator* $F_{2,70} = 0.07$, $P = 0.94$; *Me. pulchricornis,* $F_{2,63} = 0.45$, $P = 0.64$).

4. Discussion

The results of this investigation provide only partial support for the hypothesis that the benefits of honey feeding over sugars is dependent on the innate host exploitation strategies in the parasitoids tested. Whereas reproductive success in both koinobiont species and *G. areator* was unaffected by adult diet, the idiobiont *G. agilis* produced significantly more progeny (about 40%) when fed on honey compared with the honey-sugar mimic. Less progeny (although this was not statistically significant) were also produced by *G. agilis* wasps reared on heated honey; the cumulative fecundity curves of heated honey and honey mimic overlap almost completely (Fig. 3). Moreover, longevity in *G. agilis* with hosts was longer on honey than the other diets. A previous study (Harvey et al., 2012) also showed that *G. agilis* fed on honey produced more progeny than wasps fed on glucose or a honey-mimic, but in that study heated honey was not included in the dietary regime. It has long been known that the nutritional quality of honey can be altered and potentially decreased due to heating which breaks down various proteins it contains (White, 1957). Moreover, heating of honey has been shown to cause the antibacterial hydrogen peroxide to vaporize, while the concentration of naturally occurring toxic hydroxymethylfurfural content increases, especially in honey types with high fructose-concentrations (Tosi et al., 2002, 2004; Jachimowicz and El Sherbiny, 1975; Brodschneider and Crailheim, 2010; Johnson, 2015). However, heating of the honey had overall little effects on the survival and reproduction of all four parasitoids studied here, showing that the retained sugar contents sufficed for maintenance purposes. Honey-fed *G. agilis* in the control treatment (= no host access), however, also lived longer than controls reared on the other diets.

We had anticipated that the benefits of honey-feeding would affect reproduction in the gelines owing to phylogeny and the fact

that both species are ecto-parasitoids that produce large, yolky anhydropic eggs in very small numbers. Supplementary proteins would therefore complement those obtained via-host-feeding behavior, enabling both species to produce more progeny on honey-based diets. However, although they are congeners, *G. agilis* and *G. areator* differ in three important traits that influence egg production dynamics. First, *G. agilis* is wingless and forages for a wide range of hosts primarily in grassy habitats (Harvey et al., 2014) whereas *G. areator* is winged and more specialized, preferring to parasitize cocoons of parasitoids in the genus *Cotesia* (Harvey et al., 2015). Second, progeny production was some three times higher in *G. areator* than in *G. agilis*. The spatial area of search in the field is clearly greater for the winged species, which may account for its higher fecundity, which is similar to that shown in non-host feeding winged specialist species of hyperparasitoids of *Cotesia* including *Lysibia nana* and *Acrolyta nens* (Harvey, 2008). Third, the two *Gelis* species exhibited opposite patterns of longevity in the presence or absence of hosts. Irrespective of diet, adult lifespan was significantly reduced with host access in *G. agilis* but increased in *G. areator* (see also Visser et al., 2016). Earlier work also found that longevity in *G. agilis* was not increased when provided only with hosts and water (Harvey, 2008). This suggests that host-feeding is exclusively used for reproduction in *G. agilis*, but for both reproduction and maintenance in *G. areator*, amplifying vigor in the latter species. If this is so, then it is possible that *G. agilis* is more protein-limited than *G. areator*, explaining the benefits of a honey-based diet in this species alone. Some sugars, such as trehalose, are found in the blood of some insects (Giron et al., 2002) that may have been utilized by *G. areator*. Whatever the underlying factors are, phylogeny has not necessarily constrained the evolutionary expression of morphological and reproductive traits in different species of *Gelis* (Visser et al., 2014, 2016).

The specific properties of honey that is responsible for the beneficial effects on longevity and reproductive success in *G. agilis* are still to be determined. Honey is a remarkable food. It is known to contain over 180 substances in a highly saturated form comprised of sugars, proteins, amino acids, enzymes, minerals and the vitamins B1, B2 and C (Alvarez-Suarez et al., 2009). Furthermore, it has antimicrobial, antioxidant and hygroscopic properties (Echingo and Takenaka, 1974; Martos et al., 2000; Gheldof and Engeseth, 2002). By far the largest constituents in honey are carbohydrates, because proteins and amino acids make up only 0.5% of it (Alvaro-Suarez et al., 2009). Given the species-specificity of the benefits, it is perhaps less likely that the increase in reproduction

and lifespan is due to protection against oxidative damage, as there are no obvious aspects in the biology of *G. agilis* that would predict higher levels of oxidative damage than for the other parasitoid species. A primary protein that may be found in honey (Šimúth et al., 2004) and which is produced by two honeybee species (*Apis* spp.) is royalactin or Major Royal Jelly Protein 1 (MRJP1). One of the major functions of this protein is to enhance egg production and lifespan in honeybee queens. MRJP1 facilitates the differentiation of queens through an increase in juvenile hormone titers and a higher expression of *vitellogenin* genes, which are precursors of yolk proteins. An increase in fecundity and lifespan in the fruit fly, *Drosophila melanogaster*, was also observed when fed on a diet containing royalactin (Kamakura, 2011). Given that *D. melanogaster*, like the vast majority of insects, must invest a full complement of resources into each egg to ensure the completion of embryogenesis, the benefits of a honey diet on reproductive success are not necessarily surprising in *G. agilis*.

To exploit host proteins for the benefit of parasitic embryogenesis, endoparasitoids have evolved to produce hydropic eggs that are essentially unique in the animal kingdom (Grbic and Strand, 1998). Most koinobiont endoparasitoids invest often negligible amount of proteins into each egg, and an extra-embryonic membrane allows for the direct uptake of nutrients by the embryo from the host blood (Grbic and Strand, 1998). For parasitoids that produce anhydropic eggs, the acquisition of supplementary proteins via host-feeding and/or honey can enhance reproduction, whereas sugars and carbohydrates in nectar and/or honeydew benefit longevity. On the other hand, the production of hydropic eggs by koinobionts requires little protein investment, meaning that sugars and carbohydrates are of more importance in extending adult lifespan.

A significant trade-off between fecundity and longevity was found in *M. mediator*, *M. pulchricornis*, and *G. agilis*, supporting the argument that there are costs to reproduction in many parasitoids. Trade-offs between these parameters have been reported in other parasitoid species with contrasting life-histories (Ellers et al., 2000; Santolamazza-Carbone et al., 2009; Liu and Ueno, 2012; Zhang et al., 2014) although in some species the relationship may be neutral (Bennett et al., 2002) or even positive (Bai and Smith, 1993). However, thus far virtually all measured trade-offs between reproduction and longevity with parasitoids have been carried out in the laboratory, with the insects reared in small cages or arenas; in these situations metabolic expenditures on maintenance are probably limited since the insects have unlimited food and hosts available in very close proximity. In the field, sources of adult nutrition (e.g. nectar, honeydew) vary in both quality and availability, meaning the costs of reproduction may be significantly higher than in confined conditions, and that this trade-off will therefore be more apparent under these conditions.

In contrast with expectations, we found that both koinobionts had comparatively low fecundities (*Mi. mediator* produced only slightly more offspring than *G. agilis*). Furthermore, at least in comparison with other many other studies with koinobionts, both *Mi. mediator* and *Me. pulchricronis* had fairly long lifespans across all diets, with some females of the latter species actually living over 100 days when deprived of hosts. Many solitary koinobionts of larval stages of Lepidoptera have relatively short life spans (typically < 30 days) but are capable of producing hundreds or even thousands of offspring during their lifetimes (e.g. Cloutier et al., 2000; Harvey et al., 2001; Winkler et al., 2006; Latham and Mills, 2010; Hegazi et al., 2013). The reduced fecundity in the two species studied here suggests that suitable hosts in nature may be scarce for both koinobionts, leading to a trade-off between egg production and longevity that is more typical of that found in most idiobionts.

In summary, this study reports that the benefits of trace nutrients found in honey on egg production and reproductive success are species-specific, even amongst congeneric idiobiont parasitoids. We have also provided evidence suggesting that sugars in diets lacking a protein content are sufficient for optimizing reproduction in koinobiont parasitoids, although many more species need to be examined in order to determine if broader patterns emerge based on the variable expression of reproductive and other traits in parasitoids. In particular, more studies are needed involving parasitoids producing anhydropic eggs, including both host-feeding and non-host-feeding species across a broader taxonomic spectrum. In non-host feeding parasitoids that produce anhydropic eggs, resources necessary to initiate and perhaps maintain egg production are obtained primarily during larval feeding. Further adult dietary studies with parasitoids exhibiting different life history strategies may also help to elucidate the nature of constraints on the evolution of foraging, host-feeding and oviposition strategies of parasitoids in the field.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.jinsphys.2016.12.003.

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