

Flowering plants serve nutritional needs of *Ascogaster quadridentata* (Hymenoptera: Braconidae), a key parasitoid of codling moth

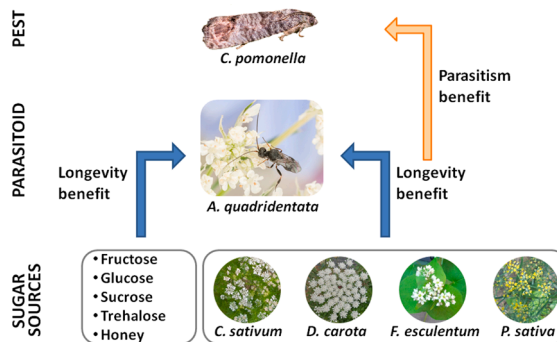
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HIGHLIGHTS

- The key parasitoid of codling moth, *Ascogaster quadridentata*, consumes various sugars and concentrations, naturally occurring in plant nectar and aphid honeydew.
- Flowers of the plants buckwheat, wild carrot, coriander and parsnip possess exposed nectaries and offer suitable nectar. The braconid wasp can survive on floral diet and reproduce successfully.
- The benefit of floral diet is greater for the parasitoid than for the host.
- Sugar limitation of this parasitoid in the field may be overcome by offering suitable plants in the orchard ground vegetation.

GRAPHICAL ABSTRACT



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ABSTRACT

The codling moth *Cydia pomonella* (Linnaeus, 1758) (Lepidoptera: Tortricidae) is the major pome fruit pest worldwide, causing direct fruit damage and significant yield losses. The egg-larval koinobiont parasitoid *Ascogaster quadridentata* (Wesmael, 1835) (Hymenoptera: Braconidae) contributes to the natural regulation of codling moth populations. Similar to many other parasitoid Hymenoptera, adult *A. quadridentata* could also benefit from high plant diversity in orchards if it fed on flowers. However, its particular nutritional requirements are rather unknown. For the first time, possible effects of sugar or flower resources on the performance of this parasitoid were studied in laboratory experiments. Wasps fed with highly concentrated sucrose or glucose solutions lived three to five times longer than starving individuals. Trehalose also supported survival, whereas mannose was not suitable. Parasitoids were able to exploit sugar solutions of low (10%) to high (64%) concentrations. Survival was more than twice as long when flowers of buckwheat, coriander, wild carrot, and parsnip were offered. Parasitism capacity was strongly linked to female longevity and thus to adequate nutrition of adults. Under the prevailing experimental conditions, performance of wasps was three times higher on flower diet compared to that of starved wasps. Suitable plants flowering during the activity period of *A. quadridentata* might therefore improve the ecosystem service provided by this important codling moth parasitoid and help increasing functional biodiversity in orchards.

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1. Introduction

Beneficial arthropods play an important role in sustainable agriculture by providing multiple ecosystem services such as pollination and natural pest control (Gurr et al., 2017). Favorable conditions for these species can be created in field or on farm scale through habitat management (Landis et al., 2000; Gurr et al., 2003). Ecological infrastructures like hedgerows and flower strips augment additional food, alternative prey as well as shelter and overwintering sites for them (Pfiffner and Wyss, 2003; Boller et al., 2004; Heimpel and Jervis, 2005; Parolin et al., 2012; van Rijn et al., 2016; Daniel et al., 2018; Hatt et al., 2019). The introduction of flowering plants in permanent crops such as apple orchards is generally recommended (Simon et al., 2010; Herz et al., 2019; Pfiffner et al., 2019). More and more farmers adopt this measure to support pollinators, but also to reduce pests and thereby fruit damage (Penvern et al., 2019). In Europe, the practice fits well with the current call for ecological intensification of agro-ecosystems in the context of the “Green Deal” (Hulot and Hiller, 2021).

In pome fruit orchards, the codling moth, *Cydia pomonella* (Linnaeus, 1758) (Lepidoptera: Tortricidae), is a major pest, causing serious fruit damages with high economic losses if untreated (Mills, 2005; Witzgall et al., 2008; Voudouris et al., 2011; Blomefield and Giliomee, 2012). The braconid wasp *Ascogaster quadridentata* (Wesmael, 1835) (Hymenoptera: Braconidae) is a widespread egg-larval parasitoid, specialized in tortricid moths (Rosenberg, 1934; Huddleston, 1984). It is the most important species in the codling moth parasitoid community (Rosenberg, 1934; Rupf, 1976; Russ and Rupf, 1976; Lacey and Unruh, 2005; Mills, 2005; Aghdam and Fathipour, 2010). Especially in cider and meadow orchards, this parasitoid can contribute to better pest control (Dib et al., 2012; Maalouly et al., 2013; Shaw and Wallis, 2014; Ismail and Albittar, 2016; Martínez-Sastre et al., 2021).

The majority of parasitoid Hymenoptera benefits from sugar-rich diet, resulting in an increased adult fitness (e.g. Jervis et al., 2008; Damien et al., 2020; Espinosa et al., 2021; Irvin and Hoddle, 2021; Xia et al., 2021) and many parasitic wasps obtain their sugar meal by visiting flowers (Russell, 2015; Zhu et al., 2020). In laboratory and field trials an extended lifespan has been confirmed for many braconid species when floral nectar was present (e.g. Winkler et al., 2009a; Nafziger and Fadamiro, 2011; Walton and Isaacs, 2011; Géneau et al., 2012; Furtado et al., 2016). Positive effects of floral resources on fecundity of wasps (Tylianakis et al., 2004; Berndt and Wratten, 2005; Irvin et al., 2006; Araj and Wratten, 2015; Jado et al., 2019), parasitism rate (Foster and Ruesink, 1984; Stephens et al., 1998; Irvin et al., 1999; Irvin et al., 2006; Araj et al., 2008; Géneau et al., 2012; Li et al., 2019) and offspring sex-ratio (Berndt and Wratten, 2005; Benelli et al., 2017) were also demonstrated.

Although some aspects on the biology and ecology of *A. quadridentata* have been studied (Rosenberg, 1934; DeLury et al., 1999a; DeLury et al., 1999b), its feeding behavior and nutritional requirements are still unknown. In laboratory rearing, wasps certainly require sugar sources such as honey to survive and parasitize hosts (e.g. Rosenberg, 1934; DeLury et al., 1999a). Thus, sugar limitation (Heimpel and Jervis, 2005) may strongly affect *A. quadridentata*, even under natural conditions. However, it is not clear whether this species visits flowering plants or consume honeydew or other sugar sources in its environment. Preliminary experiments suggest that *A. quadridentata* can use (extra-)floral nectar to maintain its longevity and parasitism performance (Herz et al., 2012; Herz and Eder, 2014; Herz and Wallach, 2015).

Consequently, the first objective of our study was to test the general suitability of different sugars and sugar concentrations for wasp survival. In a further step, we investigated the effects of specific floral diets on parasitoid's performance (survival, parasitism capacity). We chose four flower species (buckwheat, coriander, wild carrot and parsnip) that are often included in commercial seed-mixtures for creating flower strips or occur in orchards naturally (Herz et al., 2019). These plants have

open blossoms with exposed nectaries and are known to be visited by insects with less specialized and short mouthparts (Jervis et al., 1993). They are suitable for many parasitic wasps (Russell, 2015; Zhu et al., 2020 and references therein) as well as for other beneficial arthropods, such as predatory flies and pollinators (e.g. Ambrosino et al., 2006; van Rijn et al., 2016; Campbell et al., 2017; Herz et al., 2019). Next to coriander, wild carrot, and buckwheat, which is considered a ‘model plant’ for such kind of experimentation (Heimpel and Jervis, 2005), we also chose parsnip as a less-studied plant for our experiments. Parsnip is a common herbaceous native plant in our region (South-West Germany) and highly attractive for many beneficial insects. In addition, the flowers of the selected plants had been previously evaluated for potential, actually undesirable, usability by the target pest *C. pomonella* (Mátray and Herz, 2021). Such systematic screening towards ‘selective food plants’ (Baggen and Gurr, 1998; Begum et al., 2006) for *A. quadridentata* should open up the possibility of promoting this important parasitoid of codling moth by providing the most appropriate floral resources in apple orchards.

2. Material and methods

2.1. Insects and plants

Adult codling moths were kept in cylindrical plastic cages lined with cotton mesh at room temperature and 16:8 L:D h photoperiod. They were provided with water and sugar solution (5%) and allowed to oviposit on strips of plastic foil, which were collected and renewed three times a week. Part of the eggs was used for further rearing of codling moths on a semi-artificial diet according to Bathon (1981). The remaining eggs were used for parasitoid rearing and experiments.

Adult parasitoids were kept in cages at 23 ± 1 °C, 16:8 L:D h photoperiod and > 50% RH and provided with water and honey drops to allow mating and oviposition. Freshly laid *C. pomonella* eggs were also offered three times a week. After parasitization, eggs were kept in small plastic boxes until larvae emerged. These larvae were put singly into medical cups filled with semi-artificial diet. As soon as the parasitized larvae, easily recognizable due to their smaller size and white color in contrast to the pink and full-sized codling moth larvae, finished their development, they were placed in boxes with corrugated cardboard for pupation and further development until the adult wasps emerged.

The selected target plants buckwheat (*Fagopyrum esculentum* (Moench)), coriander (*Coriandrum sativum* (L.)), wild carrot (*Daucus carota* (L.)), and parsnip (*Pastinaca sativa* (L.)) were grown under standard greenhouse practices (ca. 24 ± 2 °C, 16:8 L:D h photoperiod). Seeds were obtained from ‘Appels Wilde Samen GmbH ©’, Darmstadt, Germany, and were sown in pots containing potting soil (Archut, Fruhstorfer Erde®, Typ P) in weekly intervals to ensure adequate plant supply.

2.2. Effect of different sugars and sugar concentrations on longevity of *A. quadridentata*

Several mono- and disaccharides (D (+) -Glucose, D (-) -Fructose, D (+) -Mannose, D (+) -Trehalose and D (+) -Sucrose) purchased from Carl Roth GmbH & Co KG, Karlsruhe, Germany, were used for the feeding experiments. Mixed flower honey was obtained from food retail. Solutions of various concentrations (w/w) were prepared by dissolving sugars or honey in deionized water and kept in the refrigerator until needed.

Freshly emerged (<24 h old) male and female *A. quadridentata* were placed individually into Petri dishes (diameter 10 cm). One to three droplets (volume 10 µl) of the respective sugar solution (20% (w/w)) were pipetted onto a small piece of parafilm (2 cm²), which was then placed in the Petri dish together with a cotton roll (Pluradent AG & Co KG, Chemnitz, Germany), moistened with water. For the negative control (starvation treatment), the wasps were given water only. Petri

dishes with parasitoids were placed in a climate chamber (at 22 ± 1 °C, 70% RH, 16:8 L:D). The survival of wasps was determined daily on working days. This trial was carried out twice (during spring 2017 and spring 2019), each time with 10 males and 5–10 females for each treatment. A similar test design was chosen to compare the effect of different sugar concentrations on wasp longevity. In a first test (during spring 2017), treatments consisted of water only or solutions of 10%, 20% or 40% (w/w) glucose. A second test (during spring 2019) was conducted with solutions of 10%, 20% and 55% (w/w) sucrose or water only. Experimental units were set up as described above with 10 males and 5 females of *A. quadridentata* for each treatment variant. For technical reasons, survival of wasps was considered no longer than 30 days in the trial comparing sugar types and 27 days in the trial comparing sugar concentrations.

2.3. Effect of different flowers on longevity and parasitism capacity of *A. quadridentata*

Longevity and parasitism capacity of *A. quadridentata* were examined in cage experiments, containing paired wasps (1 ♀ + 1 ♂) and various diet treatments, but without choice options. Freshly emerged wasps (<24 h old) were sexed under a stereomicroscope (Zeiss, Stemi 508) and put pairwise into cylindrical cages made out of perspex (height: 12 cm, diameter: 11 cm). Petri dishes (diameter: 12 cm) served as lids and flower-pot saucers as bottoms. A filter paper was placed on the bottom to absorb upcoming humidity. The wasps were offered: (1) water only, (2) water plus sucrose solution (20%, w/w), (3) water plus glucose solution (64%, w/w), water plus inflorescences of (4) *F. esculentum*, (5) *C. sativum*, (6) *D. carota*, or (7) *P. sativa*. The sucrose solution (20%) should correspond to previous comparable experiments, including those with codling moth (Mátray and Herz, 2021), and the glucose-solution (64%) should correspond to hexose-rich nectar of selected plants (e.g. Cawoy et al., 2006). Water and sugar solutions were provided in small plastic vials (30 ml) with a hole in the lid to insert a cotton roll, serving as a dispenser. One to three nectar-bearing inflorescences held in small water containers were offered and replaced with fresh ones every other day. Sugar solutions were renewed once per week. The cages were held in a climate chamber (Percival CLF Plant Climatics, Model: I-36VLC8) at 22 ± 1 °C with 75% RH and a photoperiod of 16:8 (L:D), including 2 h of dimmed light. Cages containing different treatments were placed in a randomized design into the chamber. Survival of males and females in these treatments was checked on each working day until death. In addition, plastic foil pieces with patches of ten codling moth eggs (<48 h old) were fixed at the lid inside the cages. These egg patches were renewed three times a week until the female in the particular cage died and further incubated at 22 ± 1 °C until all larvae had hatched. Vital neonate larvae were transferred to Eppendorf® tubes and frozen at (-) 18 °C. Subsequently, these larvae were dissected in 0.3% saline solution under a stereomicroscope for the presence of *A. quadridentata* larvae to assess parasitism and progeny production per female. The flower-comparing trial was conducted in two experimental runs during 2016/2017 and 2017/2018 with at least 20 replicates per treatment.

2.4. Data evaluation and statistical analysis

Data of each trial obtained in different experimental runs in consecutive years were pooled due to consistent laboratory conditions. Survival of *A. quadridentata* at different diet treatments was assessed using Kaplan-Meier estimates (Kaplan and Meier, 1958). In general, survival probability was modelled as a function of diet and sex, using the *surv* and *survfit* link ($\text{survfit}(\text{surv}(\text{longevity}) \sim \text{diet} + \text{sex})$) from the R-packages “*survival*” and “*survminer*”. After applying a Log-rank statistic, multiple pairwise comparison tests adjusted with Bonferroni correction revealed differences between diet treatments. The functions *survdif* and *pairwise_survdif* were used, respectively. Parasitoids surviving until the last day of the sugar-feeding experiments were censored, whereas wasps

in the flower-feeding experiments were observed until death.

Percentage parasitism in each treatment was calculated as total number of parasitized larvae related to total number of codling moth larvae, successfully hatched out of egg patches and compared for significant effects of diet, adapting a Generalized Linear Model (GLM) for binomial data. Parasitism capacity at different diets (flowers, sugars and water) was calculated as total sum of parasitized host larvae for each *A. quadridentata* female during its lifetime and was modelled using GLM for count data and negative binomial distribution to deal with overdispersion. Model residuals were inspected visually and a post-hoc multi-comparison test identified differences in parasitism performance between diet treatments. Furthermore, significance of a positive regression between longevity and parasitism capacity was explored. Back-transformed values are reported as arithmetic means (\pm standard error) throughout the manuscript. Statistical analyses were done with the software R (R Core Team 2019, version 3.6.1).

Adult food indices (AFIs), according to Wäckers et al. (2007) and Balzan and Wäckers (2013) were determined to evaluate the effects of floral and sugar diet on general fitness of *A. quadridentata*. AFIs were calculated as the ratio between average survival time in days (AFI_L = AFI of longevity) or average total sum of parasitized host larvae/female (AFI_F = AFI of fecundity) at various diets divided by the respective values at the baseline treatment with water only (negative control).

3. Results

3.1. Effect of different sugars and sugar concentrations on longevity of *A. quadridentata*

In general, the supply with different sugars significantly affected the survival of *A. quadridentata* ($\chi^2 = 184$, degrees of freedom (d.f.) = 13, p -value < 0.0001). The ranking in terms of suitability of the mono- and disaccharides tested was similar for males and females (Supplementary material, Figure A.1). Provision with mannose (20%) only slightly increased the survival of the parasitoids compared to starving ones (female: water: 4.53 ± 0.32^a days, mannose: 6.17 ± 0.64^{ab} days; male: water: 4.53 ± 0.24^a days, mannose: 7.83 ± 0.60^b days; different letters indicate significance according to Log-rank test, Bonferroni correction, $p < 0.05$ in all comparisons). In contrast, wasps lived significantly longer when fed on other sugars: males fed with trehalose (22.06 ± 2.38^c days), fructose (24.53 ± 1.86^c days), glucose (26.08 ± 2.20^c days) or sucrose (26.09 ± 2.42^c days) survived about five to six times longer than wasps supplied with water alone and also longer than those fed honey solution (15.67 ± 1.63^b days) or mannose. Also female parasitoids lived significantly longer when provided with fructose (20.16 ± 2.30^c days), glucose (25.37 ± 2.0^c days) or sucrose (30.00 ± 0.00^c days) compared to water or mannose. Feeding trehalose (16.23 ± 2.78^{bc} days) or honey solution (17.40 ± 4.53^{abc} days) had an intermediate, not always significant effect in comparison to water or mannose.

The type of sugar (sucrose, glucose) had a greater effect on the longevity of male and female *A. quadridentata* than the different concentrations of these sugars ($\chi^2 = 174$, d.f. = 13, p -value < 0.0001; Supplementary material, Figure A.2). Feeding sucrose (10%, 20%, 55%) extended lifespan six-fold compared to starving wasps (water: males: 4.36 ± 0.28^a days, females: 4.22 ± 0.49^a days, different letters indicate significance according to log-rank test, Bonferroni correction, $p < 0.05$ in all comparisons). With 10% sucrose mean survival times were: 26.67 ± 0.27^c as well as 25.60 ± 1.25^{bc} days, with 20% sucrose: 26.30 ± 0.66^c as well as 27.00 ± 0.00^{bc} days, and with 55% sucrose: 26.50 ± 0.47^c as well as 26.00 ± 0.89^{bc} days for males and females, respectively. Male wasps offered glucose lived three to four times longer than those offered water (10% glucose: 15.92 ± 1.56^b , 20% glucose: 13.75 ± 2.03^b , and 40% glucose: 18.47 ± 2.36^c days). Females also survived longer as those receiving water alone, with 16.00 ± 4.22^{abc} days (10% glucose), 23.20 ± 3.18^{bc} days (20% glucose), and 16.80 ± 3.94^{abc} days (40% glucose).

3.2. Effect of different flowers on longevity and parasitism capacity of *A. quadridentata*

Survival probability of female and male wasps was significantly influenced by diet and sex ($\chi^2 = 434$, d.f. = 13, p-value < 0.0001; Fig. 1). Starving wasps lived less than five days on average (4.0 ± 0.15^a days for females and 4.4 ± 0.16^a days for males, different letters indicate significance according to log-rank test, Bonferroni correction, $p < 0.05$ in all comparisons). In contrast, parasitoids lived almost five times longer when given the highly concentrated (64%) glucose solution (females: 19.7 ± 1.13^e days, males: 19.7 ± 0.92^{de} days). The lower (20%) concentrated sucrose solution also significantly increased the lifespan of the wasps (females: 18.7 ± 1.25^{de} days, males: 14.2 ± 1.42^{cd} days) in comparison to water. Parasitoids provided with *C. sativum* flowers on average survived 9.4 ± 0.65^b days (females) and 9.5 ± 0.67^{bc} days (males). Similar results were found for *P. sativa*-offered wasps (female: 9.9 ± 0.95^b days, male: 9.1 ± 1.05^{bc} days) as well as for *D. carota*-exposed individuals (female: 10.2 ± 1.14^b days, male: 10.3 ± 0.97^{bc} days). Thus, parasitoid life expectancy was more than doubled by providing flowers compared to the water control (Table 1, AFLI: 2.07–2.97). There were no significant differences between plant species or sexes, although males lived longest when receiving flowers of *F. esculentum* (females: 9.9 ± 1.08^b days, males: 14.9 ± 1.25^{bcd} days, Table 1: AFLI: 4.15).

Parasitism rates ranged from 30.1% up to 47.3% for *A. quadridentata*

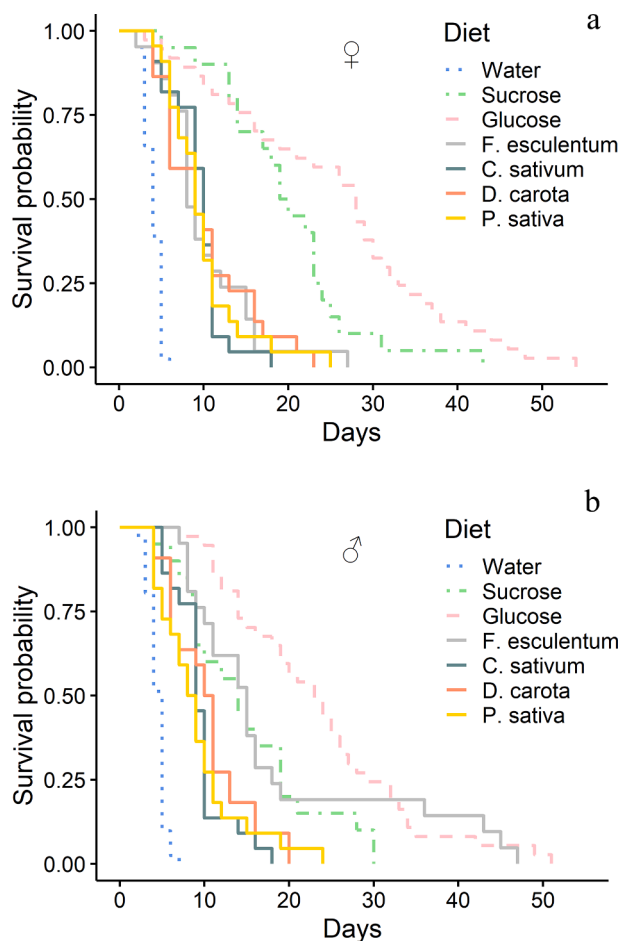


Fig. 1. Survival of *Ascogaster quadridentata* females (a) and males (b) provided with flowers of *Coriandrum sativum*, *Daucus carota*, *Fagopyrum esculentum*, *Pastinaca sativa* (solid lines), and glucose solution (64%), sucrose solution (20%) or water (broken or dotted lines). $N = 21$ –41 pairs per treatment.

females exposed to *C. sativum* and sucrose, respectively, and were quite similar for glucose (42.4%), *F. esculentum* (41.8%), *P. sativa* (41.6%) and *D. carota* (38.9%). Starving females parasitized 34% of offered hosts. Marginally significant differences occurred between coriander fed and glucose fed females (GLM, quasibinomial error distribution, $F = 2.07$, d. f. = 1.6, p-value = 0.058), but not among the other treatments.

Glucose-fed *A. quadridentata* females parasitized significantly more host larvae (31.5 ± 4.2 larvae/female compared to flower-fed or starving females (Fig. 2). Fewer - though not significantly fewer - parasitized larvae were found in the sucrose treatment (20.4 ± 3.7 larvae/female). Also in the flower treatments, less parasitized larvae were recorded with no significant differences between them (*F. esculentum*: 12.4 ± 2.3 larvae/female; *C. sativum*: 9.6 ± 1.7 larvae/female; *D. carota*: 10.8 ± 1.9 larvae/female; *P. sativa*: 12.8 ± 2.3 larvae/female). All sugar and floral diets led to a clear significant increase in parasitoid progeny in comparison to the water control with 4.3 ± 0.6 parasitized host larvae/female (Fig. 2). The calculated AFFI values (Table 1) indicated a twofold (*C. sativum*) to sevenfold (glucose) increase in the parasitism capacity of *A. quadridentata* females. In general, the total sum of parasitized host larvae/female was strongly correlated with observed lifespan ($\chi^2 = 174$, d.f. = 6, p-value < 0.0001). This positive correlation between longevity and reproduction was confirmed for all feeding treatments except water (Supplementary material, Figure A.3).

Superparasitism was frequently detected during dissection of host larvae. 40% of all dissected larvae (644 cases out of a total of 1509 host larvae) were parasitized and about half of them contained more than one *A. quadridentata* larva inside (348 = 54%). Superparasitism ranged from 7% in the water control, 10% in *F. esculentum*, 12% in *C. sativum*, 13% in *D. carota*, 15% in sucrose and glucose to 18% in the *P. sativa* treatment. In most cases, only two parasitoids were detected per host, but a few codling moth larvae contained up to 12 parasitoids.

4. Discussion

This study verifies that adults of the parasitoid *A. quadridentata* are able to meet their nutritional requirements by consuming various sugars (glucose, fructose, sucrose, trehalose), including those of different viscosities (10% to 64%). According to our results, wasps may also obtain these nutrients from flowers (presumably nectar) of plants (*C. sativum*, *D. carota*, *F. esculentum*, *P. sativa*) that grow naturally in the ground vegetation of orchards or are established there as components of flowering strips.

Table 1

Adult food indices for longevity (AFLI) and fecundity (AFFI) of *Ascogaster quadridentata* according to Wäckers et al. (2007) and Balzan and Wäckers (2013). The AFI-values are calculated by the ratio of longevity (days) or fecundity (number of parasitized host larvae/female) for female (♀) and male (♂) *A. quadridentata* exposed to nectar accessible plants compared to the control (water only, AFI = 1).

| Diet | Sex | Longevity (AFLI) | Fecundity (AFFI) |
|-----------------------------|-----|------------------|------------------|
| <i>Fagopyrum esculentum</i> | ♀ | 2.51 | 2.9 |
| | ♂ | 4.15 | – |
| <i>Coriandrum sativum</i> | ♀ | 2.35 | 2.2 |
| | ♂ | 2.15 | – |
| <i>Daucus carota</i> | ♀ | 2.53 | 2.5 |
| | ♂ | 2.34 | – |
| <i>Pastinaca sativa</i> | ♀ | 2.46 | 3.0 |
| | ♂ | 2.97 | – |
| Sucrose (20%) | ♀ | 4.68 | 4.7 |
| | ♂ | 3.55 | – |
| Glucose (64%) | ♀ | 4.92 | 7.3 |
| | ♂ | 4.47 | – |

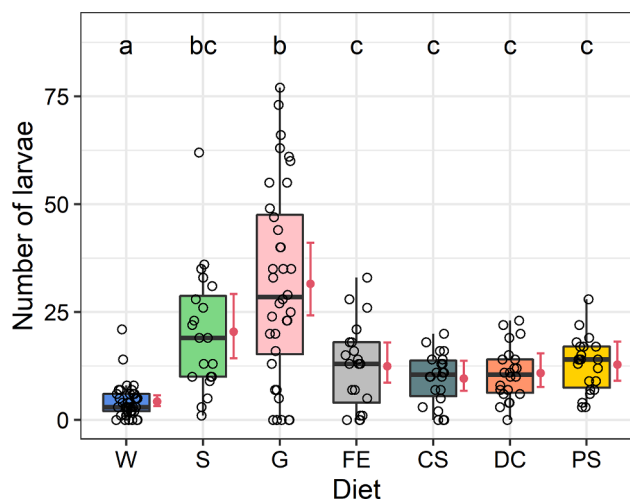


Fig. 2. Parasitism performance (number of parasitized host larvae) of *Ascogaster quadridentata* females provided with flowers of *Coriandrum sativum*, *Daucus carota*, *Fagopyrum esculentum*, *Pastinaca sativa*, and glucose solution (64%), sucrose solution (20%) or water. Treatments with the same letter in superposition do not differ at level $p < 0.05$. Points and bars next to the boxplots reflecting the models predicted mean and CI. $N = 21$ –41 pairs per treatment.

4.1. Effect of sugars and flowers on longevity of *A. quadridentata*

Sugar meals extended the lifespan of males and females more than four times compared to that of fasting wasps; similar to what has been demonstrated in other braconid species (e.g. Wäckers, 2001; Luo et al., 2010; Damien et al., 2020; Xia et al., 2021). The wasps lived longest in those experiments where kept singly in Petri dishes and exposed to droplets of sugar solutions. Mannose turned out to be quite unsuitable for *A. quadridentata*, while trehalose, known as a component of insects' honeydew, was intermediate with a strong positive effect on males. The sugars sucrose, glucose and fructose favored wasps' survival significantly, as confirmed for other hymenopteran parasitoids, for example *Diadegma semiclausum* (Hellén) (Winkler et al., 2009b) or two *Trichogramma* species (Tian et al., 2016). The type of sugar had a greater influence on wasps' survival than sugar concentration or viscosity, and glucose as well as sucrose were most suitable to prolong the lifespan of *A. quadridentata*.

When pairs of *A. quadridentata* were housed in larger cylindrical cages (volume 500 ml) in the flower feeding trial, we observed energy-consuming activities such as running, flying, courtship behavior, mating, or egg-laying. Here, the average lifespan was about 20 days in the sugar treatments and about 10 days in the flower treatments, while it was only four days in the water treatment. According to our observations under these experimental conditions and in general also in the laboratory rearing, *A. quadridentata* is a very active, 'busy' and diurnal wasp. Literature indicates that it is a strong flier and 'on the wing' to find mates or hosts (Rosenberg, 1934; DeLury et al., 1999a,b; Suckling et al., 2002). Consequently, the need for carbohydrates is likely high to provide sufficient energy for locomotion. This species certainly requires regular intake of sugar meals, which it may find on flowers with accessible nectaries. The tested plants in our study (*C. sativum*, *D. carota*, *F. esculentum*, *P. sativa*) possess disk flowers with easily accessible nectaries (Herz et al., 2019) and were confirmed to be suitable for many parasitoids and other beneficial insects with short, less specialized mouthparts in previous studies (Russell, 2015; Zhu et al., 2020 with references therein). However, survival time was higher by provision of sugar solutions than in the presence of flowers, corresponding to other feeding studies with parasitoids (for example *Cotesia glomerata* (L.) (Lee and Heimpel, 2008) or *Copidosoma aretas* (Walker) (Sigsgaard et al., 2013)). Since the sugar solutions were served *ad libitum*, unlike the flowers, the

restricted amount of floral nectar may have been insufficient to meet the wasps' demand. Determining the daily quantities of sugar or nectar required by individual wasps, as done by Furtado et al. (2016) for the braconid wasp *Psytalia concolor* (Sezpligeti), could clarify how many flowers of a given plant need to be visited by the individual wasp for adequate nutrition.

While nearly all flower species performed similar for both sexes, males lived on average five days longer when exposed to buckwheat (see also Herz et al., 2012). Prolonged survival time in males can result in higher mating opportunities as suggested by Irvin et al. (2006) for males of the braconid wasp *Dolichogenidea tasmanica* (Cameron) and access to buckwheat flowers may help to improve performance of male *A. quadridentata*. On the contrary, Xia et al. (2021) found that females of *Peristenus spretus* (Chen & van Achterberg) (Hymenoptera: Braconidae) lived longer than males with buckwheat. Furthermore, they reported that fructose was the dominant sugar in buckwheat, whereas glucose was dominant in Cawoy et al. (2006). The ratio between sucrose/hexose in buckwheat flowers also differed among various studies and were sucrose dominant in Baker and Baker (1983) and Vattala et al. (2006), but hexose (glucose, fructose) dominant in Cawoy et al. (2006), Xia et al. (2021). In general, the amount and composition of nectar depends on several factors, e.g. flower species, daytime, external growing conditions, methodology of provision, etc. (Corbet, 2003; Wade and Wratten, 2007; Morratt et al., 2009) and regarding buckwheat also on the flower morphs (pin versus thrum flowers, Cawoy et al., 2006). A simple reason for the longer survival of males on buckwheat in our experiments could be that males require smaller sugar meals than females and that the amount of nectar, which was higher in buckwheat flowers than in the other plant species (unpublished data), was sufficient to meet their demand. However, these inconsistencies suggest that plant nectar production and nutrient requirements of parasitoids need to be further investigated as a function of plant variety and growing conditions as well as insect sex, activity and other life history traits.

4.2. Effect of sugars and flowers on reproduction of *A. quadridentata*

Although carbohydrates are probably not essential for successful reproduction of *A. quadridentata*, parasitism performance was improved by floral diets. Indeed, female wasps do not depend on nectar or pollen for egg maturation, but are able to lay fertile eggs without food and/or mating (Rosenberg, 1934), similar to other braconid species (Shaw and Huddleston, 1991; Tagawa, 1992; Jarvis et al., 2001). A positive influence of floral rewards like nectar on reproduction traits is also likely, since Mohamad et al. (2015) discovered a significant increase in the number of offspring and female-biased sex-ratio of *A. quadridentata* with honey-food. This could be due to direct positive effects of nectar composition (glucose/fructose ratio, etc.) (Damien et al., 2020; Xia et al., 2021) or to occasional pollen intake by *A. quadridentata*. However, simply surviving longer with more opportunities to successfully mate or lay eggs can naturally lead to higher reproduction. According to Rosenberg (1934), females of *A. quadridentata* have a fundamentally high egg load and egg-laying capacity with 325–733 parasitized larvae, which can only be optimally realized by prolonging their lifespan. Due to the limited supply of hosts (approximately 30 eggs per week for each female), females were able to lay only a small proportion of their eggs in our experiment, and half of these hosts turned out to be superparasitized. In general, female chelonine wasps are able to differentiate between an already parasitized and a non-parasitized host (Jones, 1996), but only for a short time. Under constrained conditions, superparasitism occurs more often (Rosenberg, 1934; Ksentini and Herz, 2019), probably in contrast to conditions in nature (Quicke, 2015). However, our results show that prolonged survival by nectar or sugar leads to higher reproductive fitness, even when superparasitism occurs.

Ascogaster quadridentata is specialized in tortricid hosts that lay eggs singly (*C. pomonella*, *Cydia nigricana* (Fabricius), *Cydia splendana* (Hübner), *Lobesia botrana* (Denis & Schiffermüller), and others), thus

requiring an adequate lifespan to encounter sufficient hosts (Quicke, 1997). Furthermore, oviposition and patch residence time of *A. quadridentata* are short (unpublished data), which may help to prevent superparasitism and to promote dispersal of females under natural conditions. Beside sophisticated host finding abilities (DeLury et al., 1999a, DeLury et al., 1999b), the parasitoid females need nutrients for mobility and thus require mainly sugar-rich meals. Due to this life history, *A. quadridentata* shows time-limited, not egg-limited reproduction and could benefit greatly from flowering ecological infrastructures for nutrition as hypothesized by Tylianakis et al. (2004).

4.3. Eventual use of flowers by parasitoid and target host

We found a clear increase in survival and reproduction of *A. quadridentata* by flowers – but what is about the host? Flowering plants for field implementation have to be screened to match nutritional needs of beneficials in terms of flower attractiveness, nectar accessibility (Wäckers, 2004) as well as nectar quality and quantity (Kidd and Jervis, 1989). But a careful selection is also vital to avoid adverse effects i.e. pest proliferation (e.g. Baggen and Gurr, 1998; Irvin et al., 2006; Wäckers et al., 2007; Winkler et al., 2009a; Winkler et al., 2010; Sigsgaard et al., 2013; Jado et al., 2019). In a recent article (Mátray and Herz, 2021), we reported that codling moth lived longer when it fed on flowers or sugar solutions than when it had only water available. However, reproduction was not greatly enhanced by sugar feeding, as the majority of eggs are laid within the first week of survival, which the female moths reach even without additional food. Consequently, the impact of suitable food sources on both survival and reproduction is distinctly higher for *A. quadridentata* than for its host. Availability of food sources in the habitat is essential and of great benefit to the parasitoid, while the risk of inadvertently favoring codling moth is rather low.

All the flowering plants we tested (*C. sativum*, *D. carota*, *F. esculentum*, *P. sativa*) are promising candidates for habitat management and have the potential to improve wasps' fitness for a sustainable reduction of codling moth populations. In general, these annual or biannual plants are recommended as a component of (annual) flowering strips in apple orchards (Campbell et al., 2017; Cahenzli et al., 2019; Herz et al., 2019). Their function is primarily to support pollinators or aphidophagous natural enemies such as hoverflies or ladybirds, but, according to the results of our study, they may also act as supporters of *A. quadridentata* or other tortricid parasitoids.

Although field trials of flowering strips in orchards have shown little impact on fruit damage by codling moth (Cahenzli et al., 2019), higher parasitoid abundance and diversity of other lepidopteran pests were observed (Bostanian et al., 2004; Markó et al., 2012). In general, parasitoid promotion is important for resilient management of apple orchards, especially in organic production (Kienzle, 2010). Yet, it is still unclear, whether *A. quadridentata* wasps really forage for sugary meals outside the apple tree canopy, which is probably the main habitat structure in which they live. Dib et al. (2012) indeed did not find any codling moth parasitoids occurring in the ground vegetation of an organic orchard, but mentioned that this might have been due to the mismatch between the plants considered (no Apiaceae or buckwheat) and the parasitoids surveyed. In our experiments, the wasps also consumed trehalose, a “honeydew-indicating sugar” (Wäckers and Steppuhn, 2003), which means that they may also be attracted to aphid honeydew and like to feed on it. Even if honeydew is supposed to be less nutritious for parasitoids compared to floral nectar (Wäckers et al., 2008), it might be an important alternative in the field (Tena et al., 2013). However, the presence of honeydew-producing insects may have a positive effect not only on the parasitoid but also on the population dynamics of the pest (de Campos et al., 2020), and this needs to be addressed for codling moth as well.

The seasonal occurrence of adult *A. quadridentata* is linked to the main oviposition period of codling moth, thus in early June and – in

regions with a second generation – in late July/August (Russ and Rupf, 1976). While the appearance of a second generation would fit well with the flowering of wild carrot and parsnip, the first peak of the parasitoids probably has to rely on other plants with earlier flowering. Here, coriander and buckwheat might be more suitable, as they flower in June after sowing in spring, and the exact flowering time can even be managed by the time of sowing. In early studies, buckwheat and coriander were already successfully introduced into orchards (Herz et al., 2019), resulting for instance in higher adult fitness of the braconid wasp *D. tasmanica* (Stephens et al., 1998; Irvin et al., 1999; Irvin et al., 2006). Other field trials with buckwheat revealed reduced pest densities not only in apple orchards (Stephens et al., 1998; Irvin et al., 2000; Irvin et al., 2006) and vineyards (Nicholls et al., 2000; Berndt et al., 2002), but also in various field crops, such as cabbages (Luna et al., 2000; Pfiffner et al., 2009; Généau et al., 2012), strawberries (Sigsgaard et al., 2013), and cotton inter-planted with buckwheat. (Li et al., 2019).

4.4. Conclusion and further perspectives

In summary, our flowering plants (buckwheat, coriander, wild carrot and parsnip) are all suitable to increase the fitness of *A. quadridentata*. However, it is still necessary to verify whether these plants are actually visited by the parasitoid in the field. The next crucial step in this regard would be to determine whether *A. quadridentata* is attracted to floral traits (color, scent (Rohrig et al., 2008)) and moves from the tree layer to the ground vegetation, thus weighing the necessity to introduce tailored flowering strips for this species or other fruit pest parasitoids. In addition, *A. quadridentata* might be promoted, for example, by maintaining hedgerows in orchards (Maalouly et al., 2013), which, together with other complementary measures (Pålsson et al., 2022), contributes to sustainable codling moth reduction.

CRediT authorship contribution statement

Silvia Mátray: Experimentation, Data curation, Statistical analysis, Original draft preparation. **Annette Herz:** Conceptualization, Methodology, Funding acquisition, Supervision, Manuscript editing.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2022.104950>.

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