



# Do floral resources affect fitness of adult *Cydia pomonella* (Linnaeus 1758) (Lepidoptera: Tortricidae)?

Silvia Mátray  and Annette Herz 

Julius Kühn Institute (JKI) – Federal Research Centre for Cultivated Plants, Institute for Biological Control, Heinrichstr. 243, Darmstadt, D-64287, Germany

## Research Paper

**Cite this article:** Mátray S, Herz A (2021). Do floral resources affect fitness of adult *Cydia pomonella* (Linnaeus 1758) (Lepidoptera: Tortricidae)? *Bulletin of Entomological Research* **111**, 726–732. <https://doi.org/10.1017/S0007485321000468>

Received: 21 December 2020  
Revised: 11 May 2021  
Accepted: 23 May 2021  
First published online: 22 June 2021

### Keywords:

Apple cultivation; codling moth; ecosystem services; floral nectar; flower strips; functional biodiversity

### Author for correspondence:

Annette Herz,  
E-mail: [annette.herz@julius-kuehn.de](mailto:annette.herz@julius-kuehn.de)

### Abstract

The introduction of flowering plants into orchards can increase functional biodiversity in pome fruit cultivation. Plants provide nectar, pollen and prey resources supporting pollinators and natural enemies. However, pests may also benefit from floral diets and a careful selection of plants is necessary to reduce any risk of pest proliferation. The codling moth *Cydia pomonella* is a major pest in apple growing worldwide and adults are known to consume sugars. The impact of floral diets (parsnip, wild carrot, coriander, red clover) on longevity, fecundity and fertility of adult codling moth was examined under laboratory conditions. In general, male moths lived longer than females, regardless of dietary treatments. Moths survived longest when supplied with parsnip flowers as a floral diet. Contrary to carrot, coriander resulted in higher longevity of adult *C. pomonella* compared to moths provided with red clover as a negative control. Adult nutrition on floral diets did not affect fecundity substantially. As expected, the majority of eggs were laid within the first week. Prolongation of moths' lifespan by floral diets did not significantly increase the total number of eggs laid in contrast to a diet with 25% sucrose solution. According to these results, the risk of inadvertently promoting codling moth when growing selected flowering plants in the orchard will be rather low, because the fitness of the moths and especially the reproduction of the females will not be substantially enhanced.

## Introduction

Habitat manipulation is a common strategy for enhancing multiple ecosystem services in agro-ecosystems, such as pollination and biological pest control (Gurr *et al.*, 2017). The targeted introduction of flowering plants into agro-ecosystems is usually recommended to boost functional biodiversity in the field (Uyttenbroeck *et al.*, 2016; Campbell *et al.*, 2017), e.g. by providing nectar and pollen resources, shelter, overwintering sites and alternative prey for beneficial arthropods (Wyss, 1995; Pfiffner and Wyss, 2004; van Rijn and Wäckers, 2016; Daniel *et al.*, 2018). Enriching the ground vegetation in farmlands with flowering plants can contribute to higher abundances of beneficial arthropods, resulting in reduced pest infestation and less crop damage (e.g. Tschumi *et al.*, 2015). This strategy is highly relevant for perennial crop systems such as apple orchards (Simon *et al.*, 2010; Herz *et al.*, 2019), where permanent flower strips or structures can be implemented rather easily in the management practice (Cahenzli *et al.*, 2019; Pfiffner *et al.*, 2019). In general, farmers favour supporting natural enemies for better aphid regulation in apple orchards (Pevern *et al.*, 2019).

The design of an insect-friendly herb layer in a particular crop system mainly depends on key pests and their targeted antagonists as well as their complex interactions in the arthropod community present (Simon *et al.*, 2010). Insectary plants must be attractive and exploitable for natural enemies without promoting pests ('tailored flower strips') (Campbell *et al.*, 2017; Gurr *et al.*, 2017). Thus, a 'multitrophic approach' in flower selection prior to habitat introduction is necessary to enhance functional biodiversity (Baggen and Gurr, 1998; Lavandero *et al.*, 2006; Winkler *et al.*, 2009a, 2009b, 2010; Géneau *et al.*, 2012). The screening process for suitable plants for the nutrition of beneficial arthropods is based on floral architecture, pollen and nectar accessibility and exploitability, including nectar composition and concentration as well as insects' mouthpart morphology (Baker and Baker, 1983; Boggs, 1987; Wäckers *et al.*, 1996; Winkler *et al.*, 2009a). Floral nectar mainly consists of three sugar components, i.e. sucrose, glucose and fructose and is secreted in various concentrations from exposed or more concealed nectaries. It serves as an energy resource essential for the fitness of most beneficial insects and thus for their body maintenance, mobility, reproduction and egg maturation (e.g. Wäckers, 2004; Wäckers and van Rijn, 2005; Irvin *et al.*, 2006; Lavandero *et al.*, 2006; Winkler *et al.*, 2009a). On the other hand, adult lepidopteran pests may also benefit from nectar (e.g. Baggen and Gurr, 1998; Irvin *et al.*, 2006; Wäckers *et al.*, 2007; Winkler *et al.*, 2010; Sigsgaard *et al.*, 2013). Several laboratory studies on nutritional requirements of lepidopteran

pests confirmed an enhanced adult fitness by the provision of sugars (Wäckers *et al.*, 2007). Moths showed elongated lifespans, when offered carbohydrate-rich food (Savopoulou-Soultani *et al.*, 1998; Stevens *et al.*, 2002; Balzan and Wäckers, 2013). Savopoulou-Soultani *et al.* (1998), Stevens *et al.* (2002) and Atanassov and Shearer (2005) also recorded higher fecundity of tortricid moths, provided with sugar solution, honey solution or extrafloral nectar.

The codling moth *Cydia pomonella* L. (Lepidoptera, Tortricidae) is a major pest in apple, pear and walnut orchards all over the world (Barnes, 1991; Beers and Brunner, 1992; Mills, 2005; Witzgall *et al.*, 2008; Voudouris *et al.*, 2011; Blomefield and Giliomee, 2012), causing serious economic loss, especially in organic apple production. While the biology of codling moth is generally well understood, it has so far not been investigated, whether adult codling moth may benefit from nectariferous plants in the orchard. Howell (1981) and Wenninger and Landolt (2011) reported that provision of sucrose solution resulted in longer lifespan, but remarkably without affecting moths' fecundity and fertility. Since there had been little research on flower feeding by adult *C. pomonella* and the resulting effect on their fitness, we examined the impact of various floral diets on longevity, fecundity and fertility of this pest insect in laboratory trials. We chose flowering plants (*Coriandrum sativum* L., *Daucus carota* L., *Pastinaca sativa* L. and *Trifolium pratense* L.) that had been shown to be beneficial for natural enemies and pollinators (e.g. Stephens *et al.*, 1998; Ambrosino *et al.*, 2006; Vattala *et al.*, 2006; Winkler *et al.*, 2009a; Campbell *et al.*, 2017; Foti *et al.*, 2019; Herz *et al.*, 2019; Jado *et al.*, 2019). This kind of screening and resulting exclusion of plants with undesirable positive effects on codling moth from seed mixtures can help to tailor flower strips for conservation biological control in apple orchard management.

## Materials and methods

### Insects and plants

Codling moths for experiments were taken from a non-diapausing laboratory strain, reared on a semi-artificial diet according to Bathon (1981). Five males and five females were killed with ethyl acetate to examine proboscis length. After storing the insects in 90% lactic acid solution for approximately 60 h to soften tissues, the proboscis was carefully pulled out of the caput and embedded in Hoyer's Medium (D. Henshaw, Entomological Equipment, UK), using needles to fix the unrolled proboscis. Afterwards, microphotographs were taken under the stereomicroscope (Zeiss, Stemi 508) and measurement of the whole proboscis length was made from these pictures by using the software Zen-Lite (blue edition) (Zeiss Deutschland). Plants were selected based on flower morphology as well as on their proven suitability for beneficial insects. Except for *T. pratense*, all plant species used are categorized as 'open-nectar plants' (Klotz *et al.*, 2002; Campbell *et al.*, 2017) with exposed nectaries, hence probably accessible for *C. pomonella*. The Fabaceae plant *T. pratense* served as a negative control, since the concealed nectar glands in its flowers are not within reach of the moth proboscis (table 1). Seeds supplied by 'Appels Wilde Samen GmbH ©', Darmstadt, Germany, were sown in potting soil (Archut, Fruhstorfer Erde®, Typ P) and grown in the greenhouse under standard conditions. In addition, parsnip was cultivated on an adjacent experimental field and flower heads were collected from there.

We measured the sucrose equivalent of floral nectar by use of a handheld refractometer (Bellingham & Stanley Eclipse 45-82, Bellingham + Stanley Ltd., Kent, UK). Four samples with 15 single flowers each were processed at 20 °C for each plant species. Nectar was taken via microcapillaries (Ringcaps® Hirschmann) directly from the prepared nectar glands from flowers freshly taken from the greenhouse or field. In case of *D. carota*, it was necessary to transfer a sample of flowers into a 2 ml Eppendorf tube followed by centrifugation at 14,000 rpm for 60 s to obtain a minimum nectar volume (3 µl) for measurement.

### Experimental design

We conducted cage experiments in a climate chamber (Percival CLF Plant Climatics, Model: I-36VLC8) at 23 °C, with 75% RH and a photoperiod of 16:8 (L:D) to determine lifespan, realized fecundity and fertility of adult codling moth under different floral diet treatments. Pupae were taken from the rearing strain, sexed under the stereomicroscope (Zeiss, Stemi 508) and weighed on a precision balance (Ohaus, Pioneer, PA214C). Each pupa was held separately in an individual medical cup up to the date of emergence. After emergence, a pair of moths (<24 h old) were transferred into white plastic cups (Polarcup®, with 500 ml volume and height of 9.5 cm) covered with cotton gauze and fixed with an elastic, according to Wenninger and Landolt (2011) and Winkler *et al.* (2009a). Each cup contained a water dispenser and one to three nectariferous inflorescences of *D. carota*, *P. sativa*, *C. sativum* or *T. pratense*, maintained in water vessels. *Trifolium pratense* was considered as a negative control because its nectar is probably not accessible for the codling moth's proboscis according to our measurements. Sucrose solution (25%, w/w) served as a positive control. A small piece of filter paper in each cup absorbed excess moisture released by the plant parts. New flowers were provided at least every 2 days to refresh nectar supply. Survival of moths was checked daily or occasionally every second day and dead individuals were removed and weighed. Once a week, moths were transferred into new cups and deposited eggs in the old vial were counted. These egg-bearing cups were incubated for further 7 days at 23 °C to enable larval hatching. During this period, cups were checked regularly; all hatched larvae were counted and subsequently removed. The experiments were conducted with at least 20 replicates per treatment for two consecutive years.

### Data analysis

All statistical analyses were performed with the software R (R Core Team, 2018, version 3.5.1). Moths that escaped or died accidentally during the experiment were excluded from the analysis. Survival probabilities of codling moth in various treatments were determined by Kaplan–Meier estimates and survival curves were drawn for each treatment (Kaplan and Meier, 1958), using the R packages 'survival' and 'survminer'. Results obtained in the two experimental periods were pooled for further analysis, because laboratory conditions and insect/plant material were similar. The number of days survived was fitted as a function of diet and sex, using the *surv* and *survfit* link (*survfit(surv(longevity) ~ diet + sex)*). A Log-Rank statistic was calculated and pairwise post-hoc comparison tests, adjusted with Bonferroni correction, were performed, using the functions *survdiff* and *pairwise\_survdiff*, respectively. Generalized Linear Models (GLMs) for count data were applied to assess the effects of different diets on

**Table 1.** Plant species used in the experiments, characterized by flower morphology and nectar production according to Klotz *et al.* (2002)

Species	Family	Flower type	Floral reward/amount	Sugar concentration of nectar (%)
<i>Coriandrum sativum</i> L.	Apiaceae	Disc flowers with exposed nectaries	Nectar/present	71 ( $\pm 2.5$ )
<i>Daucus carota</i> L.	Apiaceae	Disc flowers with exposed nectaries	Nectar/present	67 ( $\pm 2.2$ )
<i>Pastinaca sativa</i> L.	Apiaceae	Disc flowers with exposed nectaries	Nectar/present	70 ( $\pm 2.9$ )
<i>Trifolium pratense</i> L.	Fabaceae	Flag blossom with concealed nectaries	Nectar/present	61 ( $\pm 0.8$ )

The reported sugar concentration of nectar was determined in the present study.

realized lifetime fecundity and egg fertility. The total number of eggs or larvae per female (= fecundity or fertility) was modelled as a function of diet and, in case of fecundity, also of pupal weight. Negative binomial distributions were adapted due to overdispersion of data. The Akaike information criterion was considered as reference for model selection and residuals were inspected visually. Likelihood-Ratio-Tests (LRT) following model simplification tested the significance of explanatory variables. Post-hoc multicomparison tests (Tukey method) were applied to detect differences between the diet treatments. In addition, a series of GLMs with Poisson or  $\gamma$  distribution analysed the influence of pupae weight on moth longevity and fecundity under different diet regimes, as well as the impact of adult nutrition on moth body weight, following the procedure of model selection as described above. Adult food indices (AFIs), according to Wäckers *et al.* (2007) and Balzan and Wäckers (2013), were determined to evaluate the effects of diet on general fitness of codling moth. AFIs were calculated as the ratio between average survival time in days or average total sum of eggs per individual at various diets divided by the respective values at the baseline treatment with *T. pratense* (negative control).

## Results

### Accessibility of flowers for codling moth

All included plants produced highly viscous nectar with sugar concentrations from 61 to 71% (table 1) in comparison to the 25% sucrose solution (positive control). Except for *T. pratense*, all other plants offered nectar in open disk flowers (table 1). Male moths had a significant longer proboscis than females (male: mean ( $\pm$ standard error (SE)): 978  $\mu$ m ( $\pm 12.6$  SE), female: 938  $\mu$ m ( $\pm 12.1$  SE),  $t = 2.314$  with 8 degrees of freedom (df),  $P = 0.0494$ ). The nectar-bearing region of the 12–15 mm long tubular-shaped Fabacean flower of *T. pratense* was therefore out of reach for codling moth males and females, while the exposed nectaries of the three Apiaceae (*C. sativum*, *D. carota*, *P. sativa*) were well accessible.

### Impact of floral diet on lifespan of codling moth

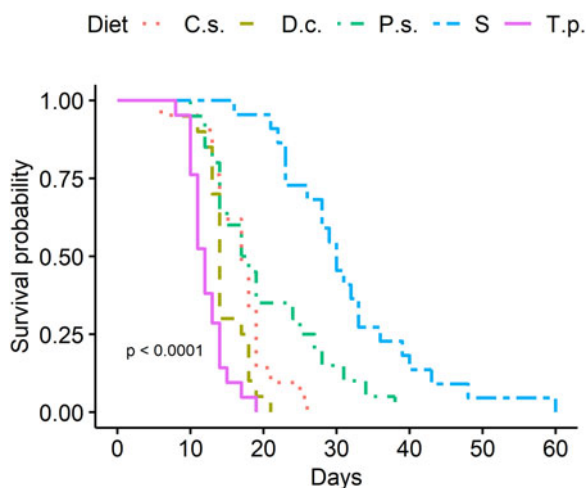
Survival probability of females and males was significantly influenced by diet and sex ( $\chi^2 = 228$ , df = 9,  $P \leq 2 \times 10^{-16}$ ) (figs 1 and 2). In general, male moths lived longer than female *C. pomonella*, regardless of the dietary treatment. Both sexes lived longest under the sucrose treatment with a mean of 29.00 ( $\pm 1.17$  SE) days for female and 31.36 ( $\pm 0.92$  SE) days for male moths. In addition, the provision of *P. sativa* flowers resulted in an extended lifespan for both sexes (female: 19.90 days ( $\pm 1.68$  SE), male: 28.35 days ( $\pm 1.56$  SE)) in comparison to the other tested plant species.

Moths offered flowers of *C. sativum* showed a slightly prolonged survival time (female: 16.71 days ( $\pm 0.96$  SE), male: 25.29 days ( $\pm 1.03$  SE)). Floral nectar of *D. carota* had little effect on moth longevity (female: 14.70 days ( $\pm 0.64$  SE), male: 22.75 days ( $\pm 0.97$  SE)) and did not differ statistically from the *T. pratense* (control) treatment (female: 12.29 days ( $\pm 0.55$  SE), male: 19.57 days ( $\pm 1.17$  SE)). The pupal weight of moth was highly influenced by sex: male pupae (42.25 mg ( $\pm 0.48$  SE)) weighed less than female pupae (54.11 mg ( $\pm 0.67$  SE),  $t = 14.55$ ,  $P < 2 \times 10^{-16}$ ). Survival time of males increased with pupal weight and was also influenced by diet (pupal weight: LRT = 10.370, df = 1,  $P = 0.001281$ , diet: LRT = 85.090, df = 4,  $P < 2 \times 10^{-16}$ ), but the interaction was not significant. Longevity of female moths was independent of pupal weight (LRT = 0.06, df = 1,  $P = 0.8065$ ) and only affected by dietary treatments (LRT = 133.79, df = 4,  $P < 2 \times 10^{-16}$ ). Adult moths' body weight was mainly linked to sex, since male moths were significantly lighter than females ( $t = 7.431$ ,  $P < 3.06 \times 10^{-12}$ ), regardless of the dietary treatment. Moth body weight at the time of death decreased with increasing age except for individuals treated with sucrose solution.

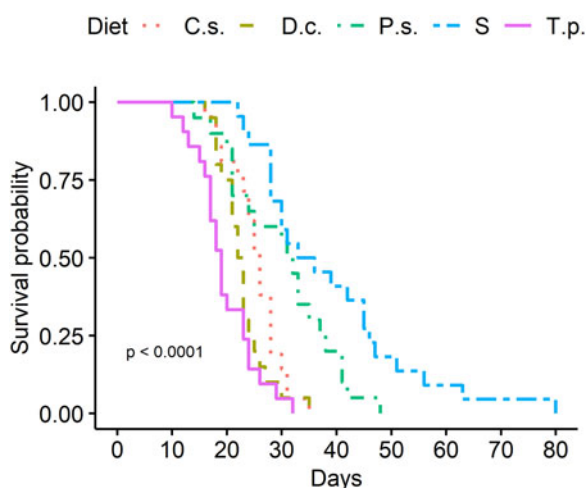
### Impact of floral diet on reproduction of codling moth

Lifetime fecundity of female *C. pomonella* increased with pupal weight (LRT = 18.269, df = 1,  $P = 1.918 \times 10^{-5}$ ) and was also affected by diet to some extent (LRT = 13.849,  $P \leq 0.0077$ ), though the interaction between diet and pupal weight was not significant (LRT = 7.4068, df = 4,  $P = 0.1159$ ). Although females treated with *T. pratense* laid on average the lowest number of eggs (142.86 ( $\pm 13.71$  SE)) in comparison to females provided with the nectar of *C. sativum* (161.62 ( $\pm 20.27$  SE)), *D. carota* (163.55 ( $\pm 13.07$  SE)) and *P. sativa* (170.95 ( $\pm 17.24$  SE)), these differences were not significant due to high variation between individuals (fig. 3). Adults fed with sucrose laid significantly more eggs on average (215.05 ( $\pm 18.53$  SE)) in comparison to *T. pratense* ( $z$ -value = 3.316,  $P = 0.0081$ ) and *C. sativum* ( $z$ -value = 2.791,  $P = 0.0420$ ), but not with respect to the other floral diets. In general, more than half of the total egg load was laid within the first week after emergence in all treatments. Females supplied with *T. pratense* laid 89% of all their eggs within the first week, followed by *D. carota* (81%) and *C. sativum*-fed (72%) moths. Adults provided with *P. sativa* and sucrose solution laid 62 or 57% of the total amount within the first week, respectively.

Lifetime fertility of *C. pomonella* was highly correlated to the number of eggs laid per female ( $r = 0.89$ ). The total number of hatched larvae per female was not significantly affected by adult diet treatments (LRT = 5.2484, df = 4,  $P = 0.2627$ ) (fig. 3). Hatching rate ranged from 51% in the *D. carota*-treatment up to 61% in the sucrose-treatment. Hatching rate was nearly



**Figure 1.** Survival of *C. pomonella* females treated with flowers of C.s. = *Coriandrum sativum*, D.c. = *Daucus carota*, P.s. = *Pastinaca sativa*, T.p. = *Trifolium pratense* or S = sucrose solution, *N* = 20–21 per treatment.

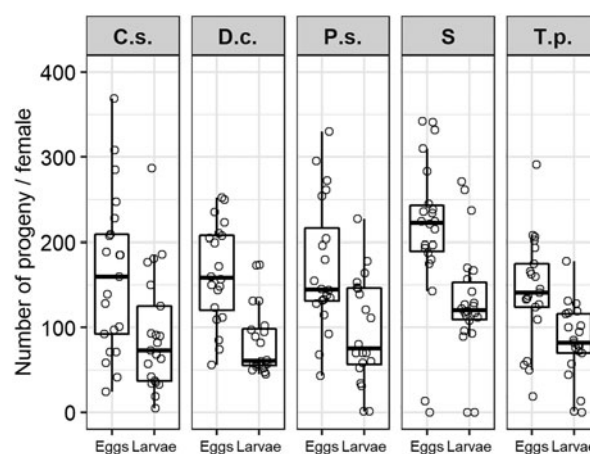


**Figure 2.** Survival of *C. pomonella* males treated with flowers of C.s. = *Coriandrum sativum*, D.c. = *Daucus carota*, P.s. = *Pastinaca sativa*, T.p. = *Trifolium pratense* or S = sucrose solution, *N* = 20–21 per treatment.

identical in *P. sativa* (56%) and *C. sativum*-treatments (57%) and quite similar to both negative and positive control (*T. pratense*: 58% vs. sucrose solution: 61%).

**Impact of adult diet on fitness of codling moth**

Codling moth males and females are not able to feed nectar from *T. pratense* flowers and their longevity and fecundity at this treatment served as a baseline indicator for their fitness (AFI = 1, table 2). Although having access to exposed nectaries of *C. sativum* and *D. carota*, fecundity of *C. pomonella* increased only slightly by less than 15% (AFFI 1.13–1.14, table 2). In contrast, fecundity increased by 50% (table 2) when having access *ad libitum* to sucrose solution (25%) and survival time of both sexes doubled. *Pastinaca sativa* enhanced lifespan (like *C. sativum*), but affected the number of laid eggs less notably (AFFI 1.20).



**Figure 3.** Realized lifetime fecundity and fertility of *C. pomonella* treated with flowers of C.s. = *Coriandrum sativum*, D.c. = *Daucus carota*, P.s. = *Pastinaca sativa*, T.p. = *Trifolium pratense* or S = sucrose solution. There is no statistical difference between diet treatments regarding the number of larvae hatched.

**Discussion**

We examined the impact of floral diet on the adult fitness of *C. pomonella* as a key pest in apple production. The short proboscis of *C. pomonella* did not reach the hidden nectar in zygomorphic flowers of *T. pratense*, but the moths were able to feed from open disk flowers. Nectar intake from the umbellifers *C. sativum* and especially *P. sativa* significantly increased the survival of male and female *C. pomonella*, but affected reproduction (lifetime fecundity or fertility) much less. These plants produce a nectar rich in sugar (60–70%) with high viscosity, which makes it difficult for moths to absorb (May, 1985). Therefore, the ingestible amount of nectar may have been limited, whereas the fluid 25% sucrose solution was easily consumed, even providing *ad libitum* as diet surplus for the insects. In general, nectar viscosity is a function of sugar concentration and also humidity (van Rijn and Wäckers, 2016), especially when secreted from exposed nectaries. Winkler *et al.* (2009a) reported that *Pieris rapae* L. was able to imbibe nectar from several plants at 90% rel. humidity, but not when plants were provided at 45% rel. humidity. The conditions in our experiment ensured a rel. humidity of 75%, which prevented rapid water loss in the nectar. However, we cannot rule out the possibility that the use of cut inflorescences or the renewal of flower heads every 2 days may have restricted the nectar supply of these plants (in particular *D. carota* and *C. sativum*) more than under natural conditions. For example, in a study by Wade and Wratten (2007), the life expectancy of a parasitoid was shorter when cut rather than intact coriander flowers were used. We also observed that individual nectar droplets in single florets of *P. sativa* were larger than those in flowers of *C. sativum* or *D. carota*. Thus, the volume of nectar droplets secreted can also determine whether certain flowers are more profitable to moths than others. In addition, nectar volume and quality will be influenced by plant growing conditions, microclimate, daily secretion rate, and other external and internal factors (Corbet, 2003) that were not considered in our study. Moth survival time was highest by provision of the sugar solution and individuals even tended to gain body weight. Howell (1981) and Wenninger and Landolt (2011) described similar results and assumed that *C. pomonella* is generally attracted by sweet food sources. Male moths in particular benefited from sugar sources (Cisneros and Barnes,

**Table 2.** Adult food indices (AFI) according to Wäckers *et al.* (2007) and Balzan and Wäckers (2013)

Diet	Sex	Longevity (AFLI)	Fecundity (AFFI)
<i>C. sativum</i>	F	1.36	1.13
	M	1.29	–
<i>D. carota</i>	F	1.20	1.14
	M	1.16	–
<i>P. sativa</i>	F	1.63	1.20
	M	1.54	–
Sucrose	F	2.57	1.51
	M	1.99	–

The AFI-value is calculated by the ratio of longevity (days) or fecundity (number of eggs/female) of *C. pomonella* females (F) and males (M) exposed to nectar accessible plants or sucrose solution (25%) compared to the control based on *T. pratense* (AFI = 1).

1974; Schumacher *et al.*, 1997; Wenninger and Landolt, 2011). An increased energy level favours further mobility and dispersal (Irvin *et al.*, 2006; Wenninger and Landolt, 2011), which results in more mating opportunities for the males, increasing populations and benefits for upcoming generations (Howell, 1981; Wenninger and Landolt, 2011). In female moths, access to 25% sucrose solution led to the longest lifespan (double AFLI) and also the highest number of offspring (50% more eggs, indicated by AFFI), while floral nectar had no distinctive effect on lifetime fecundity and fertility. Due to highly variable egg load (fig. 3), which is obviously typical for this species (Geier and Briese, 1978) and which may more depend on nutrients acquired during larval development, no statistical differences occurred between floral treatments. In an early study, Howell (1981) reported that, when codling moth fed on various carbohydrate solutions in the laboratory, diet did not affect fecundity or hatching rate of eggs, but increased longevity. Howell (1981) and other researchers (e.g. Geier, 1963; Deseö, 1971; Hagley, 1972; Savopoulou-Soultani *et al.*, 1998) also found that the main oviposition of *C. pomonella* and other tortricid pests occurred in the early stage of moth life. An analogous oviposition pattern was observed in our study and the absolute number of eggs laid in the first week was quite similar in all treatments (coriander: 2431, carrot: 2649, parsnip: 2115, sucrose: 2700, red clover: 2672 eggs in total). Consequently, a prolonged lifespan does not necessarily result in a significant higher lifetime fecundity of codling moth, supporting the assumption that adult *C. pomonella* do not need additional food to reproduce adequately, as stated by Geier (1963), Howell (1981) and Benz (1991). Nevertheless, the rate of egg deposition within the first week differed between the various dietary treatments and the oviposition period was longer than 3 weeks when parsnip flowers or sucrose were offered. Atanassov and Shearer (2005) also observed an extended egg deposition period of *Grapholita molesta* Busck supplied with accessible extrafloral nectar and Boggs (1997) and Cahenzli and Erhardt (2012) found a similar pattern in some butterfly species as well. Perhaps the moths perceive suitable food sources and are able to adapt their oviposition pattern to the availability of food sources in the surroundings. An adequate or even over supply of carbohydrates could also prevent the exploitation of other body reserves and allow their use for further egg maturation. However, adequate nutrition may be more relevant to other life history traits than reproduction or longevity: under natural conditions, mobility and dispersal are also

important for females to find suitable host plants (Gu *et al.*, 2006), and regular sugar intake may be even more important for maintaining these functions.

Instead, lifetime fecundity of female codling moth was clearly influenced by pupal weight, since the amount of deposited eggs was higher for moths emerging from heavier pupae. Geier (1963), Deseö (1971) and Cisneros and Barnes (1974) have already described a positive correlation between pupal weight and fecundity. Pupal weight is caused by a combination of intrinsic and extrinsic factors, such as genetic disposition, sex, climate conditions, diapausing and larval diet (Geier, 1963; Cisneros and Barnes, 1974; Boggs, 1997). Since the quality and quantity of larval food certainly has a major influence on pupal weight and thus on the fecundity of the moths, we cannot rule out the possibility that artificially reared moths show different nutritional requirements or physiological characteristics than natural populations.

The number of hatched larvae in this study depended strongly on the number of deposited eggs, but not on diet, confirming the results of Wenninger and Landolt (2011), who found no differences in total egg fertility in their feeding experiments with *C. pomonella*. We observed no decreasing fertility of eggs with increasing female age in contrast to results from Deseö (1971) and Hagley (1972), and hatching rate was not different between diet treatments.

The increase of pest fitness due to the presence of suitable floral resources in the field depends on a complex of biotic and abiotic factors, as e.g. the occurring plant species and composition, orchard management, climate conditions, abundance of antagonists, as well as feeding behaviour of the key pest (Simon *et al.*, 2010). Although adult *C. pomonella* successfully consumed nectar from all open disk flowers in our study, it has to be clarified if moths actively forage and benefit from floral nectar in nature. Codling moths generally mate and oviposit at night. Whether they disperse from tree to tree or also occur in ground vegetation to visit flowers during the day for nectar consumption is not known. Other potential food sources may be more important and may come from aphid honeydew, extrafloral nectaries on host plants, tree sap or even fruit debris available in the canopy.

According to calculated AFFI and AFLI in our trials, *T. pratense*, *D. carota*, *C. sativum* and somewhat less so, *P. sativa*, seemed to be appropriate 'low-risk' candidates for field use. However, further studies involving single and mixed flowering plants in apple orchards will be necessary to investigate the feeding behaviour of codling moth and its main natural enemies such as parasitoids. Various field studies on the effects of flower strips for biocontrol in apple orchards did not yield consistent results (Herz *et al.*, 2019). For instance, less fruit damage caused by codling moth was observed in plots with flowering plants by Altieri and Schmidt (1985), as well as recently by Cahenzli *et al.* (2019), contrary to the findings of Brown (2001), who reported an increase of damaged apples. In addition to testing further nectariferous plant species, other sugar sources occurring in the orchard, such as honeydew or apple flesh, may be taken into account, since Wiesmann (1935) observed that adult *C. pomonella* fed on aphid honeydew in the field. It is likely that moths are able to utilize sugar components of honeydew (Baker and Baker, 1983). Perhaps codling moth benefits even more from honeydew available in the apple tree canopy than from floral nectar, similar to the olive moth *Prays oleae* Bernard, which showed highest longevity and reproduction by provision of insects' honeydew (Villa *et al.*, 2017).

In this study, we found that survival, but not reproduction of adult codling moth increased when having the opportunity to feed on the nectar of several umbellifers. These findings underline the need for a careful selection of plant species in seed mixtures to obtain 'tailored' flower strips, favourable only for beneficials and not for pests. Our results may help to improve the concept and success of conservation biological control in apple orchards by cautious management of functional biodiversity.

**Acknowledgements.** The authors gratefully acknowledge the financial support from the project 'Innovative design and management to boost functional biodiversity of organic orchards – ECOORCHARD', CORE Organic Plus (28698), cofinanced by the European Commission as well as by the Federal Ministry of Food and Agriculture with the Federal Programme for Ecological Farming and Other Forms of Sustainable Agriculture (BÖLN) – FKZ: 2814OE005 (Germany). We are indebted to Nils Drexler, who conducted laboratory experiments in 2017, as part of his BSc-Thesis. Also, we would like to express our gratitude to Milena Runge, Stefanie Hemmerling and Simon Feiertag for their help in conducting the experiments and providing plant and insect material. We would like to thank Dr Doreen Gabriel, Julius Kühn Institute, Institute for Crop and Soil Science, Braunschweig for helpful support in statistics.

## References

- Altieri MA and Schmidt LL** (1985) Cover crop manipulation in northern California orchards and vineyards: effects on arthropod communities. *Biological Agriculture & Horticulture* **3**, 1–24.
- Ambrosino MD, Luna JM, Jepson PC and Wratten SD** (2006) Relative frequencies of visits to selected insectary plants by predatory hoverflies (Diptera: Syrphidae), other beneficial insects, and herbivores. *Environmental Entomology* **35**, 394–400.
- Atanassov A and Shearer PW** (2005) Peach extrafloral nectar impacts life span and reproduction of adult *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae). *Journal of Agricultural and Urban Entomology* **22**, 41–47.
- Baggen LR and Gurr GM** (1998) The influence of food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). *Biological Control* **11**, 9–17.
- Baker HG and Baker I** (1983) Floral nectar sugar constituents in relation to pollinator type. In Jones CE and Little RJ (eds), *Handbook of Experimental Pollination Biology*. New York: Van Nostrand Reinhold, pp. 117–141.
- Balzan MV and Wäckers FL** (2013) Flowers to selectively enhance the fitness of a host-feeding parasitoid: adult feeding by *Tuta absoluta* and its parasitoid *Necremnus artynes*. *Biological Control* **67**, 21–31.
- Barnes MM** (1991) Codling moth occurrence, host race formation, and damage. In van der Geest LPS and Evenhuis HH (eds), *World Crop Pests – Tortricid Pests: Their Biology, Natural Enemies and Control*, vol. 5. Amsterdam: Elsevier Science Publishers, pp. 313–327.
- Bathon H** (1981) Zur Zucht des Apfelwicklers, *Laspeyresia pomonella* (L.) (Lep., Tortricidae), auf einem künstlichen Nährmedium. *Mitteilungen der deutschen Gesellschaft für allgemeine und angewandte Entomologie* **2**, 136–140.
- Beers EH and Brunner JF** (1992) Implementation of the codling moth phenology model on apples in Washington State. *Acta Phytopathologica et Entomologica Hungarica* **27**, 97–102.
- Benz G** (1991) Physiology, reproduction and ecology. In van der Geest LPS and Evenhuis HH (eds), *World Crop Pests – Tortricid Pests: Their Biology, Natural Enemies and Control*, vol. 5. Amsterdam: Elsevier Science Publishers, pp. 89–147.
- Blomefield TL and Giliomee JH** (2012) Fecundity and mortality of codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), under field conditions in South Africa. *African Entomology* **20**, 316–324.
- Boggs CL** (1987) Ecology of nectar and pollen feeding in Lepidoptera. In Slansky F and Rodriguez JG (eds), *Nutritional Ecology of Insects, Mites, and Spiders*. New York: Wiley and Sons, pp. 369–391.
- Boggs CL** (1997) Reproductive allocation from reserves and income in butterfly species with differing adult diets. *Ecology* **78**, 181–191.
- Brown MW** (2001) Flowering ground cover plants for pest management in peach and apple orchards. *IOBC wprs Bulletin* **24**, 379–382.
- Cahenzli F and Erhardt A** (2012) Enhancing offspring quality or quantity? Different ways for using nectar amino acids in female butterflies. *Oecologia* **169**, 1005–1014.
- Cahenzli F, Sigsgaard L, Daniel C, Herz A, Jamar L, Kelderer M, Kramer Jacobsen S, Kruczyńska D, Matray S, Porcel M, Sekrecka M, Świergiel W, Tasin M, Telfser J and Pfiffner L** (2019) Perennial flower strips for pest control in organic apple orchards—A pan-European study. *Agriculture, Ecosystems & Environment* **278**, 43–53.
- Campbell A, Wilby A, Sutton P and Wäckers F** (2017) Getting more power from your flowers: multi-functional flower strips enhance pollinators and pest control agents in apple orchards. *Insects* **8**, 101.
- Cisneros FH and Barnes MM** (1974) Contribution to the biological and ecological characterization of apple and walnut host races of codling moth, *Laspeyresia pomonella* (L.): moth longevity and oviposition capacity. *Environmental Entomology* **3**, 402–406.
- Corbet SA** (2003) Nectar sugar content: estimating standing crop and secretion rate in the field. *Apidologie* **34**, 1–10.
- Daniel C, Matray S, Stoeckli S and Niggli U** (2018) Pest management in organic apple, pear and stone fruit. In Vacante V and Kreiter S (eds), *Handbook of Pest Management in Organic Farming*. Wallingford: CAB International, pp. 130–150.
- Deseö KV** (1971) Study of factors influencing the fecundity and fertility of codling moth (*Laspeyresia pomonella* L., Lepidoptera, Tortricidae). *Acta Phytopathologica* **6**, 243–252.
- Foti MC, Peri E, Wajnberg E, Colazza S and Rostás M** (2019) Contrasting olfactory responses of two egg parasitoids to buckwheat floral scent are reflected in field parasitism rates. *Journal of Pest Science* **92**, 747–756.
- Geier PW** (1963) The life history of codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), in the Australian Capital Territory. *Australian Journal of Zoology* **11**, 323–367.
- Geier PW and Briese DT** (1978) The demographic performance of a laboratory strain of codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae). *Journal of Applied Ecology* **15**, 679–696.
- Géneau CE, Wäckers FL, Luka H, Daniel C and Balmer O** (2012) Selective flowers to enhance biological control of cabbage pests by parasitoids. *Basic and Applied Ecology* **13**, 85–93.
- Gu H, Hughes J and Dorn S** (2006) Trade-off between mobility and fitness in *Cydia pomonella* L. (Lepidoptera: Tortricidae). *Ecological Entomology* **31**, 68–74.
- Gurr GM, Wratten SD, Landis DA and You M** (2017) Habitat management to suppress pest populations: progress and prospects. *Annual Review of Entomology* **62**, 91–109.
- Hagley EA** (1972) Observations on codling moth longevity and egg hatchability. *Environmental Entomology* **1**, 123–125.
- Herz A, Cahenzli F, Penvern S, Pfiffner L, Tasin M and Sigsgaard L** (2019) Managing floral resources in apple orchards for pest control: ideas, experiences and future directions. *Insects* **10**, 247.
- Howell JF** (1981) Codling moth: the effect of adult diet on longevity, fecundity, fertility, and mating. *Journal of Economic Entomology* **74**, 13–18.
- Irvin NA, Scarratt SL, Wratten SD, Frampton CM, Chapman RB and Tylianakis JM** (2006) The effects of floral understoreys on parasitism of leafrollers (Lepidoptera: Tortricidae) on apples in New Zealand. *Agricultural and Forest Entomology* **8**, 25–34.
- Jado RH, Araj SE, Abu-Irmaileh B, Shields MW and Wratten SD** (2019) Floral resources to enhance the potential of the parasitoid *Aphidius colemani* for biological control of the aphid *Myzus persicae*. *Journal of Applied Entomology* **143**, 34–42.
- Kaplan EL and Meier P** (1958) Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* **53**, 457–481.
- Klotz S, Kühn I, Durka W and Briemle G** (2002) BIOLFLOR—Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. *Schriftenreihe für Vegetationskunde* **38**, 334pp. Retrieved 14 April 2020, from <http://www.ufz.de/biolflor/index.jsp>.

- Lavandero B, Wratten SD, Didham RK and Gurr G** (2006) Increasing floral diversity for selective enhancement of biological control agents: a double-edged sword? *Basic and Applied Ecology* **7**, 236–243.
- May PG** (1985) Nectar uptake rates and optimal nectar concentrations of two butterfly species. *Oecologia* **66**, 381–386.
- Mills N** (2005) Selecting effective parasitoids for biological control introductions: codling moth as a case study. *Biological Control* **34**, 274–282.
- Penvern S, Fernique S, Cardona A, Herz A, Ahrenfeldt E, Dufils A, Jamar L, Korsgaard M, Kruczyńska D, Matray S, Ozolina-Pole L, Porcel M, Ralle B, Steinemann B, Świergiel W, Tasin M, Telfser J, Warlop F and Sigsgaard L** (2019) Farmers' management of functional biodiversity goes beyond pest management in organic European apple orchards. *Agriculture, Ecosystems & Environment* **284**, 1–11.
- Pfiffner L and Wyss E** (2004) Use of sown wildflower strips to enhance natural enemies of agricultural pests. In Gurr GM, Wratten SD and Altieri MA (eds), *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods*. Wallingford: CABI-Publishing, pp. 167–188.
- Pfiffner L, Cahenzli F, Steinemann B, Jamar L, Chor Bjørnc M, Porcel M, Tasin M, Telfser J, Kelderer M, Lisek J and Sigsgaard L** (2019) Design, implementation and management of perennial flower strips to promote functional agrobiodiversity in organic apple orchards: a pan-European study. *Agriculture, Ecosystems & Environment* **278**, 61–71.
- R Core Team** (2018) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at <https://www.R-project.org/>.
- Savopoulou-Soultani M, Milonas PG and Stavridis DG** (1998) Role of availability of food to the adult *Lobesia botrana* (Lepidoptera: Tortricidae) in its reproductive performance. *Journal of Economic Entomology* **91**, 1341–1348.
- Schumacher P, Weyeneth A, Weber DC and Dorn S** (1997) Long flights in *Cydia pomonella* L. (Lepidoptera: Tortricidae) measured by a flight mill: influence of sex, mated status and age. *Physiological Entomology* **22**, 149–160.
- Sigsgaard L, Betzer C, Naulin C, Eilenberg J, Enkegaard A, Kristensen K and Michaud JP** (2013) The effect of floral resources on parasitoid and host longevity: prospects for conservation biological control in strawberries. *Journal of Insect Science* **13**, 104.
- Simon S, Bouvier JC, Debras JF and Sauphanor B** (2010) Biodiversity and pest management in orchard systems: a review. *Agronomy for Sustainable Development* **30**, 139–152.
- Stephens MJ, France CM, Wratten SD and Frampton C** (1998) Enhancing biological control of leafrollers (Lepidoptera: Tortricidae) by sowing buckwheat (*Fagopyrum esculentum*) in an orchard. *Biocontrol Science and Technology* **8**, 547–558.
- Stevens P, Froud K and Jamieson L** (2002) Effects of adult feeding on longevity and fecundity of *Ctenopseustis obliquana* (Lepidoptera: Tortricidae). *New Zealand Journal of Crop and Horticultural Science* **30**, 229–234.
- Tschumi M, Albrecht M, Entling MH and Jacot K** (2015) High effectiveness of tailored flower strips in reducing pests and crop plant damage. *Proceedings of the Royal Society B: Biological Sciences* **282**, 1–8.
- Uyttenbroeck R, Hatt S, Paul A, Boeraeve F, Piqueray J, Francis F, Danthine S, Frederich M, Dufrene M, Bodson B and Monty A** (2016) Pros and cons of flowers strips for farmers. A review. *Biotechnologie Agronomie Societe et Environnement* **20**, 225–235.
- van Rijn PC and Wäckers FL** (2016) Nectar accessibility determines fitness, flower choice and abundance of hoverflies that provide natural pest control. *Journal of Applied Ecology* **53**, 925–933.
- Vattala HD, Wratten SD, Phillips CB and Wäckers FL** (2006) The influence of flower morphology and nectar quality on the longevity of a parasitoid biological control agent. *Biological Control* **39**, 179–185.
- Villa M, Marrão R, Mexia A, Bento A and Pereira JA** (2017) Are wild flowers and insect honeydews potential food resources for adults of the olive moth, *Prays oleae*? *Journal of Pest Science* **90**, 185–194.
- Voudouris CC, Sauphanor B, Franck P, Reyes M, Mamuris Z, Tsitsipis JA, Vontas J and Margaritopoulos JT** (2011) Insecticide resistance status of the codling moth *Cydia pomonella* (Lepidoptera: Tortricidae) from Greece. *Pesticide Biochemistry and Physiology* **100**, 229–238.
- Wäckers FL** (2004) Assessing the suitability of flowering herbs as parasitoid food sources: flower attractiveness and nectar accessibility. *Biological Control* **29**, 307–314.
- Wäckers FL and van Rijn PCJ** (2005) Food for protection: an introduction. In Wäckers FL, van Rijn PCJ and Bruin J (eds), *Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*. Cambridge: Cambridge University Press, pp. 1–14.
- Wäckers FL, Bjørnsen A and Dorn S** (1996) A comparison of flowering herbs with respect to their nectar accessibility for the parasitoid *Pimpla turionellae*. *Proceedings of the Section Experimental and Applied Entomology of The Netherlands Entomological Society* **7**, 177–182.
- Wäckers FL, Romeis J and van Rijn P** (2007) Nectar and pollen feeding by insect herbivores and implications for multitrophic interactions. *Annual Review of Entomology* **52**, 301–323.
- Wade MR and Wratten SD** (2007) Excised or intact inflorescences? Methodological effects on parasitoid wasp longevity. *Biological Control* **40**, 347–354.
- Wenninger EJ and Landolt PJ** (2011) Apple and sugar feeding in adult codling moths, *Cydia pomonella*: effects on longevity, fecundity, and egg fertility. *Journal of Insect Science* **11**, 161.
- Wiesmann R** (1935) Untersuchungen über den weiblichen Genitalapparat, das Ei und die Embryonalentwicklung des Apfelwicklers *Carpocapsa* (*Cydia*) *pomonella*. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **16**, 370–377.
- Winkler K, Wäckers FL, Kaufman LV, Larraz V and van Lenteren JC** (2009a) Nectar exploitation by herbivores and their parasitoids is a function of flower species and relative humidity. *Biological Control* **50**, 299–306.
- Winkler K, Wäckers F and Pinto DM** (2009b) Nectar-providing plants enhance the energetic state of herbivores as well as their parasitoids under field conditions. *Ecological Entomology* **34**, 221–227.
- Winkler K, Wäckers FL, Termorshuizen AJ and van Lenteren JC** (2010) Assessing risks and benefits of floral supplements in conservation biological control. *BioControl* **55**, 719–727.
- Witzgall P, Stelinski L, Gut L and Thomson D** (2008) Codling moth management and chemical ecology. *Annual Review of Entomology* **53**, 503–522.
- Wyss E** (1995) The effects of weed strips on aphids and aphidophagous predators in an apple orchard. *Entomologia Experimentalis et Applicata* **75**, 43–49.