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SHORT COMMUNICATION

Nectar feeding increases exploratory behaviour in the aphid parasitoid *Diaeretiella rapae* (McIntosh)Y.-D. Varennes¹, M. Gonzalez Chang¹, S. Boyer^{1,2} & S. D. Wratten¹¹ Bio-Protection Research Centre, Lincoln University, Lincoln, Canterbury, New Zealand² Unitec Institute of Technology, Auckland, New Zealand**Keywords**Biological control, *Brevicoryne brassicae*, *Fagopyrum esculentum*, floral subsidies, *Myzus persicae***Correspondence**

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Abstract

Feeding on floral nectar has multiple positive effects on parasitic wasps, including increased longevity and fecundity, and in addition, nectar feeding can also alter parasitoid behaviour. To advance understanding of the effects of nectar feeding on *Diaeretiella rapae* (McIntosh) [Hymenoptera: Braconidae], the activities of 1-day-old female *D. rapae* with or without a prior buckwheat (*Fagopyrum esculentum*) nectar meal were quantified. Nectar increased searching time of *D. rapae* by a factor of 40 compared with individuals provided with water only and reduced the time spent stationary. The number of attacks to aphids by nectar-fed parasitoids was not significantly ($P = 0.06$) higher than that of unfed *D. rapae*, suggesting that the conditions of the experiment facilitated host finding by 'quiet' parasitoids. Nevertheless, nectar feeding modified the behaviour of *D. rapae* in a way that parasitoids were more explorative and less inactive. This represents one additional mechanism through which nectar feeding impacts parasitoid biology and suggests that a synergy between increased host searching, increased longevity and increased fecundity should lead to an enhancement of biocontrol when *D. rapae* females have access to nectar in the field.

Introduction

In their adult stage, parasitoid wasps feed on carbohydrate-rich liquids, for example floral nectar or honeydew (Jervis et al. 1993; Jervis 1998). This feeding strongly increases parasitoid longevity, and in the case of synovigenic parasitoids (i.e. able to mature eggs during their adult stage), it also increases egg maturation rate (Berndt and Wratten 2005; Vattala et al. 2006; Winkler et al. 2006; Lee and Heimpel 2008; Araj et al. 2009). In the field, the addition of flowering vegetation nearby or within crops generally, but not always, enhances pest parasitism rate (Tylianakis et al. 2004; Heimpel and Jervis 2005; Lavandero et al. 2006; Jonsson et al. 2008; Gurr et al. 2012; Wäckers and van Rijn 2012; Balmer et al. 2014). In addition to increasing longevity and fecundity, nectar feeding can also affect other biological functions of parasitoids, such as host searching, host perception and flying

abilities. For example, the aphid parasitoid *Aphidius ervi* (Haliday) [Hymenoptera: Braconidae] allocated more time to walking (exploratory behaviour) and attacking hosts when it had fed on nectar than when starved, in which case it remained stationary for most of the time (Araj et al. 2011). Other studies have used diluted honey solutions instead of nectar and have shown that the parasitoids *Microplitis croceipes* (Cresson) [Hymenoptera: Braconidae] and *Cotesia rubecula* Marshall [Hymenoptera: Braconidae] had longer flying bouts when fed than when starved (Takasu and Lewis 1995; Siekmann et al. 2004). However, fed and unfed *C. rubecula* allocated equal times to walking and being stationary, suggesting that feeding did not increase exploration by walking and did not reduce times of apparent inactivity (Siekmann et al. 2004). Such contrasting results suggest that there may be specific differences in nectar metabolism and behavioural responses to feeding.

The present study focussed on *Diaeretiella rapae* (McIntosh)[Hymenoptera: Braconidae], a solitary koinobiont endoparasitoid of about 60 aphid species, including several major agricultural pests (Pike et al. 1999; Kavallieratos et al. 2004, 2013; Desneux et al. 2006). Longevity, egg load and number of offspring of *D. rapae* can be increased by nectar feeding (Tylianakis et al. 2004; Jamont et al. 2013). The effect of feeding on *D. rapae* behaviour has not been studied but could be expected to be similar to that on *A. ervi*, because they are phylogenetically and morphologically close to each other. To contribute to advancing the understanding of how nectar feeding affects *D. rapae*'s biological functions, the behaviours of nectar-fed and starved *D. rapae* were observed.

Materials and Methods

Buckwheat (*Fagopyrum esculentum* Moench, cultivar Katowase) was used as a nectar source. This plant is commonly used in this way in studies of parasitoid nutrition and habitat management for conservation biological control (Zehnder et al. 2007; Fiedler et al. 2008). Plants were sown continually to ensure a full provision of flowers during the experiment, and they grown in a glasshouse at Lincoln University, New Zealand, from January to March 2014, with natural lighting.

D. rapae parasitoids were reared on the green peach-potato aphid *M. persicae* at $24 \pm 2^\circ\text{C}$, 16 : 8 h photoperiod, on oilseed rape (OSR) plantlets. Mummified aphids were detached from leaves with the tip of a paintbrush and isolated in individual 1.5-ml microcentrifuge tubes with a cotton-wool stopper (ensuring ventilation) until parasitoids emergence. Two to three hours after emergence, parasitoids were sexed visually (the ovipositor appears clearly as a black peak at the tip of female's abdomen) and groups comprising two female and three male parasitoids were directly placed in transparent plastic containers ($6 \times 6 \times 12$ cm) with a 3×5 cm mesh opening on one side for ventilation. Parasitoids in containers were given access to either (i) water only (starved parasitoids) or (ii) water and buckwheat flowers from a potted plant (nectar-fed parasitoids). Visual checks ensured flowers had nectar on the day they were used. After 24 h, one female was randomly selected and placed in an observation arena, which consisted of a Petri dish containing an OSR leaf bearing ca. 40 *M. persicae* (all instars). The leaf originated from a parasitoid-free culture and was cut from the plant few minutes before starting the experiment. To minimize the disturbance made to aphids, no aphid was

removed from the leaf. In consequence, the number of aphids on the leaf was not constant and varied between 30 and 50. The transfer of the parasitoid female to the observation arena was performed by enclosing the targeted insect in a 1.5-ml microcentrifuge tube and shaking the tube above the Petri dish; then, the lid of the Petri dish was put back on. This method was not always successful, but it was preferred to others (paintbrush, buccal aspirator) because it did not involve touching the insect and avoided mechanical damage to wings or legs. Occasionally, parasitoids escaped during transfer from the container to the observation arena, and in this case, the second female was used. If the first selected female was successfully transferred to the observation arena, the second one was discarded. Males ensured female fertilization, but their behaviour was not observed. Five minutes after its transfer in the observation arena, wasp's behaviour was observed for c. 30 min and recorded using The Observer software (Noldus Information Technology, Wageningen, The Netherlands). One female parasitoid in each treatment was observed on a same day. This was repeated on ten successive days, leading to twenty observations in total. A new Petri dish and a new OSR leaf were used in each observation, all of which were performed by the same observer (YDV).

Parasitoid behaviours were described in a catalogue of behaviours developed following Araj et al. (2011) and Ayal (1987), as follows: 'Stinging' corresponded to the parasitoid touching an aphid with its ovipositor, while 'Attacking' represented the parasitoid holding its attack position, that is the abdomen was placed below the thorax and pointed forward. After preliminary observations, and based on Ayal (1987), two categories of locomotion were distinguished: 'Checking' and 'Searching'. 'Checking' consisted of the parasitoid walking while touching the substrate with antennal tips, whereas 'Searching' consisted of walking while holding antennae forward. Based on visual observation, wasps walked more slowly when 'Checking' than when 'Searching'. 'Checking, motionless' was the same as 'Checking', but the parasitoid was motionless, that is it completely stopped walking. 'Grooming' corresponded to the parasitoid rubbing its body with its legs. 'Stationary' described the periods of total immobility. The time in each behaviour was divided by the total observation time, and relative times spent in each behaviour were then analysed. The number of 'Stinging' events was divided by total observation time before analysis and expressed as the number of occurrences per minute. The effect of treatment (fed vs. starved) on time spent (or number of

occurrences, in the case of ‘Stinging’) was analysed with ANOVA for each behaviour separately. The date of each observation was also included in the analyses to account for potential biases linked with environmental conditions (laboratory temperature and light intensity, although stable, might have varied slightly). Data were either non-transformed, square-root transformed, or log-transformed to comply with the ANOVA normality and homogeneity assumptions. All analyses were performed with R 3.1.1 (R Core Team 2014).

Results

‘Grooming’ was the main activity of all wasps (on average, 43% of the observation time). Flying was not analysed as only four individuals had very brief flights. Date had no effect on any behaviour except in the case of the ‘Checking motionless’ ($F_{9,9} = 3.57$, $P = 0.04$). Feeding altered the pattern of behaviour displayed by *D. rapae* females (fig. 1): fed ones spent significantly more time ‘Searching’ than unfed ones ($F_{1,9} = 7.13$, $P = 0.03$). Unfed parasitoids rarely adopted the ‘Searching’ behaviour; thus, the relatively low period that fed parasitoids spent searching (c. 4% of the observation period) was still about 40 times greater than that shown by unfed parasitoids. Fed females spent less time stationary ($F_{1,9} = 12.7$, $P = 0.006$) or ‘Checking, motionless’ ($F_{1,9} = 8.26$, $P = 0.02$) than unfed ones. The length of time spent in attack position (‘Attacking’ behaviour) was not significantly different between fed and unfed females ($F_{1,9} = 2.19$, $P = 0.17$). The number of stings/minute

was only marginally higher for fed females compared to that of unfed females (fed: 1.32/min, unfed: 0.63/min, $F_{1,9} = 4.81$, $P = 0.06$). Fed and unfed insects spent similar lengths of time ‘Checking’ or ‘Grooming’ (respectively, $F_{1,9} = 0.55$, $P = 0.48$; $F_{1,9} = 0.38$, $P = 0.55$).

Discussion

Feeding increased the time allocated to searching and greatly decreased the time spent in being immobile. Our results suggest that, in 30 min, fed parasitoids could explore an area 40 times larger than unfed parasitoids, and according to model studies, a 40-fold increase in search rate over a parasitoids’ lifetime would reduce the pest population by the same amount, which would represent a very significant improvement in biocontrol efficacy (Kean et al. 2003). However, ingested sugars are consumed via metabolic activity (Jervis et al. 2008); therefore, one feeding event would increase search rate for a limited time only. Frequent nectar feeding may intensify searching behaviour throughout parasitoid’s lifetime, and because feeding also increases the longevity of *D. rapae* (Tylianakis et al. 2004; Jamont et al. 2013), nectar consumption may substantially increase the area searched by a parasitoid over its lifetime.

The number of ‘Stinging’ events was not significantly different between fed and unfed *D. rapae*, in contrast with observations on *A. ervi* (Araj et al. 2011). Given that fed *D. rapae* performed in average twice more stings than unfed conspecifics, the lack of significance could indicate a high variability in the number of stinging events. This was somehow unexpected, as ten replicates were used here compared to six in Araj et al. Stinging by unfed parasitoids might have been facilitated in the present experiment, because hosts were close to each other (c. 2 mm), and as a consequence, they could be reached easily by unfed parasitoids, despite the periods of immobility of these parasitoids.

The results presented here indicate that as early as 24 h after emergence, feeding on nectar increases the searching intensity of *D. rapae* compared with starved wasps and decreases the time spent immobile, suggesting that, in 24 h, *D. rapae* females burn a significant part of the metabolic reserves accumulated during larval stage. Alongside with other benefits of nectar feeding – namely increased longevity and fecundity – the enhancement of searching activity is another mechanism that favours the reproductive success of *D. rapae*. This strengthens the hypothesis that planting nectar-providing vegetation in the

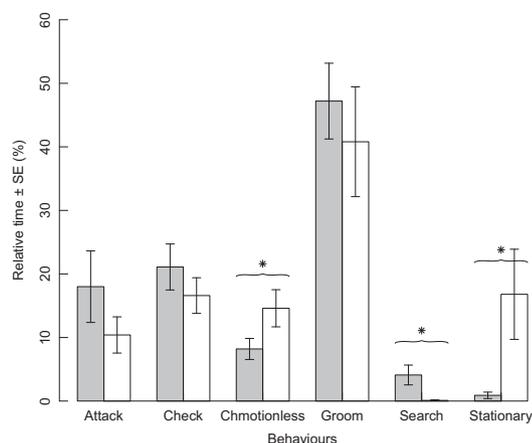


Fig. 1 Portion of time (relative times) spent performing different behaviours by nectar-fed (grey bars) and unfed (white bars) *D. rapae* females. $N = 10$ wasps of each condition were observed for 30 min. Asterisks above bars indicate a significant difference between fed and unfed insects ($P < 0.05$).

habitat of *D. rapae* should enhance its biological control efficacy. In semi-field conditions (potted *Brassica napus* plants sparsely distributed on a 120 m² short-grass plot), the presence of nectar-providing plants next to aphid-infested plants increased the number of mummies of *D. rapae* by 60% (Jamont et al. 2014). This should motivate further research towards the use of nectar-providing plants in the field to enhance biological control by *D. rapae*.

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