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# Plant feeding by an omnivorous predator affects plant phenology and omnivore performance

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## ABSTRACT

Plant feeding by omnivorous predators can induce plant defences, which decreases the performance of herbivores and influence behaviour of other predators. However, it is not known what are the consequences of this feeding for the plant and how this, in turn, affects the omnivore. We therefore investigated the effects of plant feeding by the omnivorous predator *Macrolophus pygmaeus* on plant development and reproduction. We also assessed the effects of these plant changes on survival and reproduction of the omnivore. Sweet pepper plants exposed to *M. pygmaeus* had significantly lower numbers of leaves and open flowers than clean plants, but numbers of fruits were similar. Moreover, the presence of the omnivore significantly shortened the period for flowers to become fruits. The dry weights of leaves plus stems and fruits were similar on clean plants and plants with the omnivore. Significantly higher numbers of seeds were found in fruits from plants with the omnivore than from clean plants. The survival rates of *M. pygmaeus* females and nymphs increased with numbers of flowers. Our results show that the presence of this omnivorous predator can benefit plants by increasing seed production, but the changes in plant phenology do not seem to benefit the omnivore.

## 1. Introduction

Plants face many biotic and abiotic challenges, of which herbivory is one of the most severe. Herbivory of flowers and other reproductive tissues can directly affect plant reproduction by decreasing the number of flowers, fruits and seeds (Bertness et al., 1987; Cunningham, 1995; Krupnick et al., 1999; McCall and Irwin, 2006). Removal of leaf tissue by herbivores can cause reduction in photosynthesis, suppression of plant growth and reduced biomass (Lemoine et al., 2017; Poveda et al., 2003). Herbivory on leaves can also alter flower phenology and morphology, resulting in changes in flowering time (Hanley and Fegan, 2007; Hoffmeister et al., 2016; Poveda et al., 2003; Strauss et al., 1996), a decrease of the numbers of flowers (Karban and Strauss, 1993) and of flower size (Hoffmeister et al., 2016; Strauss, 1997; Strauss et al., 1996). For example, foliar herbivory by cabbage white butterfly larvae delayed flowering and decreased flower size of wild radish plants, but did not affect plant size and biomass, or the lifetime flower production and total number of fruits and seeds (Lehtilä and Strauss, 1999). Herbivory on leaves and flowers may also change pollen and nectar characteristics. For instance, foliar herbivory on wild radish plants by cabbage white butterfly larvae reduced the amount and size of pollen

(Lehtilä and Strauss, 1999). A perennial shrub exposed to a pollen beetle produced fewer functional inflorescences than unexposed plants, and flowers damaged by beetles produced less than one third of the amount of nectar per flower than undamaged flowers (Krupnick et al., 1999), and tobacco leaf consumption by tobacco hornworm larvae increased alkaloids in nectar, but not in leaves (Adler et al., 2006). Furthermore, herbivory on leaves and flowers can change the emission of plant volatiles (Kessler and Halitschke, 2009). Bruinsma et al. (2014) showed that the emission of volatiles from flowers changed significantly upon attacks of black mustard leaves by caterpillars. Leaf herbivory is also known to change flower volatile emissions (Hoffmeister et al., 2016).

These changes in flower phenology can affect plant performance. Delayed flowering time may cause plants missing the peak of pollinator activity, resulting in lower flower visiting rates (Sharaf and Price, 2004). Leaf damage by herbivores can decrease the size and number of flowers, causing different attractiveness for different pollinator species (Lehtilä and Strauss, 1997). At early developmental stages of plants, herbivory can accelerate flowering phenology and alter floral morphology and scent, which affects interactions with flower visitors (Hoffmeister et al., 2016). However, these changes in the flower visitor

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network did not affect plant reproduction (Hoffmeister et al., 2016). A study by Strauss et al. (1996) shows that foliar herbivory delayed flowering time, decreased flower size and pollen production, resulting in reduction in the number and duration of visits of pollinators. Foliar herbivory can also result in reduced attraction of bumblebee pollinators by the damaged plants, even though it does not result in changes in flower size and number (Kessler and Halitschke, 2009). Phenological, morphological and physiological changes caused by herbivory can also affect other organisms on the plant, such as other species of herbivores, predators and flower visitors, including pollinators, which may alter plant reproduction (Ohgushi et al., 2007).

Plants are not passive victims when facing herbivore attacks; they employ different strategies to reduce the negative effects of herbivory. In response to herbivory, plants defend themselves through constitutive as well as induced defences (Kant et al., 2015; Karban and Baldwin, 1997; Sabelis et al., 1999). These defences can lower the performance of herbivores directly by the induction of production of specific secondary compounds, referred to as induced direct plant defences (Karbon and Baldwin, 1997). The induction of plant defences may go at the expense of other plant traits: resources may be reallocated from growth and development to defence, resulting in changes in plant phenology (Herms and Mattson, 1992). Thus, changes in plant performance may partly be caused by trade-offs between defence and other life-history traits.

Besides herbivores, zoophytophagous omnivores may also cause changes in plant performance when they feed on plants. Such omnivores are increasingly used for biological control of various pests in different crops (Messelink et al., 2012). The advantage of these predators is that their populations can be established and persist in crops by feeding on plant tissues, pollen and nectar, even when pest densities are low (Castañé et al., 2011). Several recent studies show that omnivores that cause limited or no damage when feeding on plants do nevertheless induce plant defences (Bouagga et al., 2018; De Puyssleir et al., 2011; Pappas et al., 2015; Pérez-Hedo et al., 2015; Zhang et al., 2018). Hence, like herbivory, plant feeding by omnivores may also cause changes in plant phenology, which is what we tested here. We previously showed that the omnivorous predator *Macrolophus pygmaeus* induces defences in sweet pepper plants, resulting in negative effects on performance of two herbivore species, i.e. the spider mite *Tetranychus urticae* and the thrips *Frankliniella occidentalis* (Zhang et al., 2018). Furthermore, these two herbivores avoided plants previously exposed to the omnivore (Zhang et al., 2019). A third species, the aphid *Myzus persicae*, was unaffected (Zhang et al., 2018, 2019).

The omnivorous predator *M. pygmaeus* is one of the most widely used biocontrol agents for control of whiteflies (Montserrat et al., 2000), aphids (Alvarado et al., 1997) and spider mites (Hansen et al., 1999). It also attacks other important agricultural pests such as thrips (Riudavets and Castañé, 1998), leaf miners (Arnó et al., 2003), as well as Lepidoptera species (Urbaneja et al., 2009). *Macrolophus pygmaeus* also feeds on plants, piercing plant tissue and sucking out liquid contents (Castañé et al., 2011), and can complete its development feeding on plant tissue only (Perdikis and Lykouressis, 2000). When the density of the predator is very high, plant damage was observed on several plant species (Castañé et al., 2011). Here we investigated the effects of plant feeding by this omnivorous predator on plant performance by evaluating plant growth and reproduction. We also assessed the effects of these plant changes on survival and reproduction of the omnivore.

## 2. Materials and methods

### 2.1. Plant and predator rearing

Sweet pepper plants (*Capsicum annum* L. Spider F1, Enza Zaden Beheer B.V., The Netherlands) were grown from seeds in pots ( $\varnothing = 14$  cm) with soil in a climate room dedicated to growing clean plants ( $25 \pm 1^\circ\text{C}$ , 60–70% RH, 16: 8 L: D). Water was supplied twice a

week. Four-week-old plants with 6–8 true leaves (about 20 cm high) were used for experiments.

A culture of *M. pygmaeus* was established with fifth-instar nymphs obtained from a commercial company (Koppert Biological Systems BV, Berkel en Rodenrijs, The Netherlands). They were reared in plastic containers (height = 45 cm,  $\varnothing = 35$  cm) in a climate room (conditions as above) with *Ephestia kuehniella* eggs as food and green bean pods as both food supply and oviposition substrate. New *E. kuehniella* eggs and beans were added twice a week. Old beans with *M. pygmaeus* eggs were transferred to new containers, and kept until the eggs hatched, whereupon *E. kuehniella* eggs and bean pods were supplied twice a week. Old pods from which nymphs no longer hatched were removed from the containers. Adults of 4–8 days old were used for experiments.

### 2.2. Experimental protocol

Four-week-old clean plants with six to eight true leaves were transferred to insect-proof cages (BugDorm-44590DHF,  $93.0 \times 47.5 \times 47.5$  cm, mesh size: 160  $\mu\text{m}$ ) that were equally distributed on three benches in a compartment in the greenhouse ( $25 \pm 1^\circ\text{C}$ , 60–70% RH, 16: 8 L: D). Plants were watered twice per week and fertilized once per week. In half of the cages, five adult females and five adult males of *M. pygmaeus* were released, and plants in the other half of the cages were clean, serving as control plants. There were no other arthropods present in the cages. To minimize the effect of variation in abiotic factors among locations, plants with different treatments were alternated, and the sequence of treatments of the plants was alternated on different benches. Thereafter, numbers of females and nymphs of *M. pygmaeus* were assessed twice per week. No extra food was supplied for *M. pygmaeus* during the experiments. To keep densities of the omnivores similar throughout the experiment, the cages that contained fewer than five females of *M. pygmaeus* received new females and the same number of males twice per week, adding up to five females in each cage. This also resulted in assessment of survival of the omnivores. Leaves bigger than 8 cm were counted twice per week. After the first open flower appeared on one of the plants, the open flowers and fruits on the plants were counted on a daily basis, and the dates on which the first flower and fruit appeared on each plant were also recorded. Because *M. pygmaeus* feeds on pollen and nectar (Messelink et al., 2011; Vandekerckhove and De Clercq, 2010), we compared the survival of females and the numbers of nymphs (resulting from reproduction of the omnivores) on the plants before and during flowering. Subsequently, we assessed the effects of the numbers of flowers on adult survival and on the number of nymphs, omitting the data before flowering. The survival of females and the numbers of nymphs on plants with and without flowers were also assessed.

Sixteen to seventeen days after the onset of flowering, all plants were harvested, and leaves and stems and fruits of each plant were put in separate paper bags. The fresh weight and the length and diameter of each fruit were measured, and the numbers of seeds in fruits heavier than 3 mg were assessed. Thereafter, all plant material was dried separately in an oven (Ehret KLT/S 2, Emmendingen, Germany) ( $80 \pm 1^\circ\text{C}$ ) for about 2 weeks. Subsequently, dry weight of leaves and stems and fruits were recorded. The experiments were conducted in two blocks in time (block A: October–November 2016; block B: March–April 2017), with 9 plants per treatment per block.

### 2.3. Data analysis

The numbers of leaves, open flowers and fruits (all square-root transformed) on plants exposed to *M. pygmaeus* and clean plants were each compared using linear mixed-effect models (LME) with treatment, time and their interaction as fixed factors, and block and individual plant as random factors. The distribution of the residuals was checked for normality. Non-significant interactions and factors were removed until a minimal adequate model was reached (Crawley, 2013).

Contrasts were assessed with the Tukey method (function `glht` of the package `lsmeans` in R, Lenth, 2016). We furthermore compared the time of the first flower appearing between treatments with a generalized linear model (GLM) with treatment and block as factors and a Poisson error distribution. Because flowers were not marked and followed through time individually, we estimated the time to fruit set as the difference between the appearance of the first flower and the first fruit per plant. These data were compared between treatments with a GLM with a Poisson error distribution and block and treatment as factors.

The total dry weight of the stem and leaves (untransformed) and the dry weight of the fruits ( $\log(x + 0.1)$ -transformed) per plant were each compared between treatments with an LME with block and individual plant as random factors as explained above.

The numbers of seeds per fruit may have been affected by the presence of *M. pygmaeus* and the volume of the fruit; therefore, we calculated the volume of all fruits heavier than 3 mg using half the volume of an ellipsoid as an approximation of the shape of a sweet pepper fruit. The numbers of seeds per fruit (square-root transformed) were compared using an LME as described above, with treatment and fruit volume and their interaction as fixed factors, and block and each individual plant as random factors.

The proportions of female omnivores surviving and the numbers of nymphs ( $\log(x + 1)$  transformed) on plants before and during flowering were compared using an LME as described above, with the presence of flowers as a fixed factor, and block and plant as random factors. Survival of adult females as a function of the number of flowers was analysed with a generalized mixed effects model (GLMER) with a binomial error distribution (logit link) and with block and plant as random factors. The analysis of the numbers of nymphs as a function of the numbers of flowers was done with an LME as above, with block as a random factor. All statistical analyses were performed with R (R Development Core Team, 2017).

### 3. Results

Plants exposed to *M. pygmaeus* had significantly lower numbers of leaves than clean plants (Fig. 1a, LME:  $\text{Chi}^2 = 5.75$ ,  $d.f. = 1$ ,  $P = 0.0165$ ), and the numbers of leaves from both groups of plants increased with time (LME:  $\text{Chi}^2 = 513.2$ ,  $d.f. = 1$ ,  $P < 0.0001$ ). The numbers of leaves differed between the two blocks (Fig. 1a), which was probably caused by the two blocks having been conducted at different seasons. There was no significant difference between treatments in the timing of the first flower (clean plants: average =  $30.3 \pm 0.61$  days, *M. pygmaeus*-treated plants:  $31.6 \pm 0.79$  days, GLM:  $\text{Chi}^2 = 1.89$ ,  $d.f. = 1$ ,  $P = 0.491$ ). The numbers of open flowers on plants with and without *M. pygmaeus* increased differently with time, (Fig. 1b, LME: interaction of treatment and time,  $\text{Chi}^2 = 7.4$ ,  $d.f. = 1$ ,  $P = 0.0064$ ). Plants exposed to *M. pygmaeus* had lower numbers of flowers than clean plants (Fig. 1b, contrasts after LME). The numbers of fruits on plants of both treatments increased differently with time (Fig. 1c, LME:  $\text{Chi}^2 = 4.5$ ,  $d.f. = 1$ ,  $P < 0.034$ ), but overall did not differ significantly between treatments (Fig. 1c, contrasts after LME). The difference in time between appearance of the first flower and the first fruit was approximately half on exposed plants than that on clean plants (*M. pygmaeus*-treated plants:  $2.5 \text{ day} \pm 0.26 \text{ days}$ ; clean plants:  $4.8 \text{ day} \pm 0.29 \text{ days}$ , GLM:  $\text{Chi}^2 = 13.8$ ,  $d.f. = 1$ ,  $P < 0.001$ ).

Plants with and without *M. pygmaeus* had similar dry weight of leaves plus stems (Fig. 2a, LME:  $\text{Chi}^2 = 0.07$ ,  $d.f. = 1$ ,  $P = 0.795$ ) and there was a non-significant trend of the total dry weight of fruits from plants with *M. pygmaeus* being lower than that of clean plants (Fig. 2b, LME:  $\text{Chi}^2 = 3.2$ ,  $d.f. = 1$ ,  $P = 0.072$ ).

Interestingly, plants exposed to *M. pygmaeus* produced five times higher numbers of seeds per fruit than clean plants did (Fig. 3ab, LME:  $\text{Chi}^2 = 41.6$ ,  $d.f. = 1$ ,  $P < 0.0001$ ), which was not affected by the volume of the fruits (LME:  $\text{Chi}^2 = 2.11$ ,  $d.f. = 1$ ,  $P = 0.146$ ).

The survival rate of female *M. pygmaeus* was higher when plants

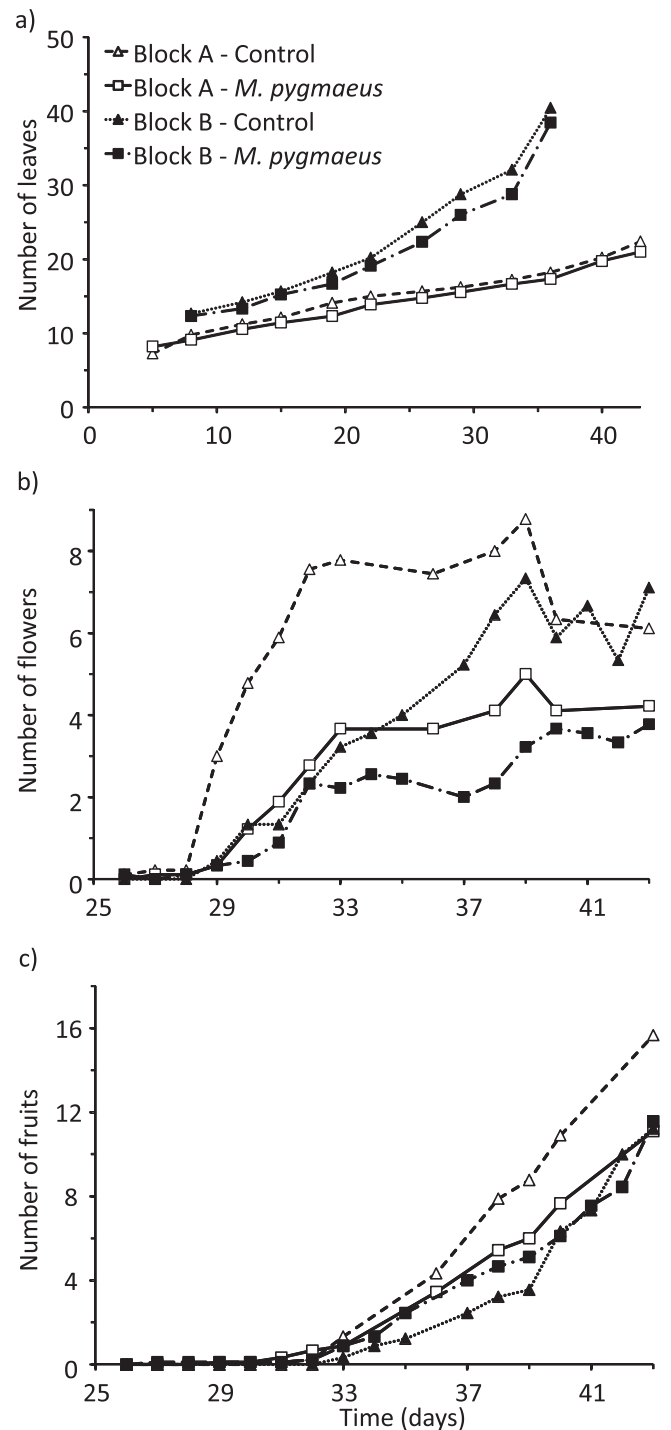
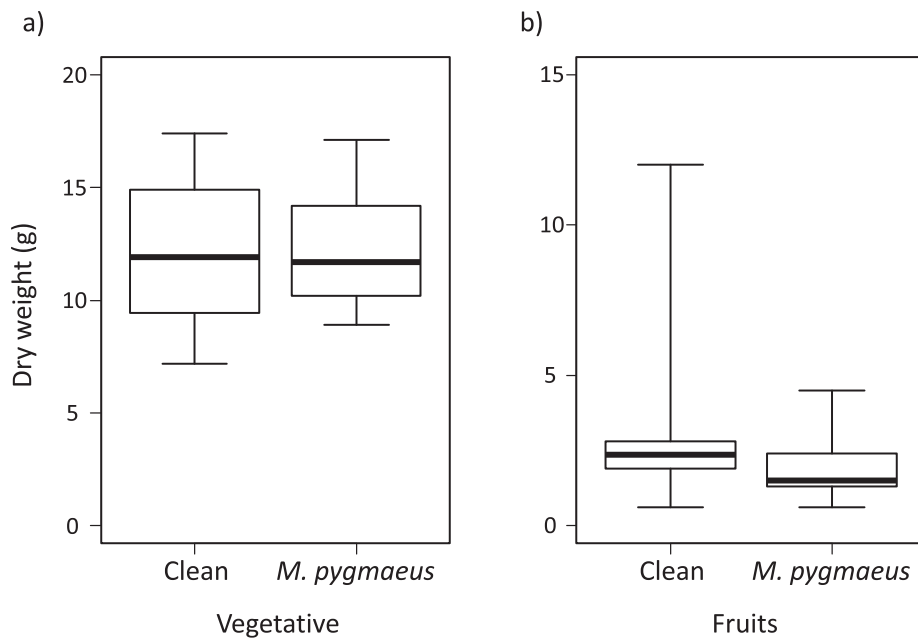


Fig. 1. The average numbers of leaves (a), flowers (b) and fruits (c) on sweet pepper plants exposed to *M. pygmaeus* and clean plants over time in two experimental blocks performed in different seasons. Triangles indicate clean plants (block A: open triangles; block B: closed triangles); Squares indicate plants exposed to *M. pygmaeus* (block A: open squares; block B: closed squares). Standard errors are not shown for reasons of clarity.

were flowering than before flowering (Fig. 4a, LME:  $\text{Chi}^2 = 51.0$ ,  $d.f. = 1$ ,  $P < 0.0001$ ), and there were also more nymphs on plants during flowering than before flowering (Fig. 4b, LME:  $\text{Chi}^2 = 24.6$ ,  $d.f. = 1$ ,  $P < 0.0001$ ). Adult survival increased with the numbers of flowers (Fig. 4c, GLMER:  $\text{Chi}^2 = 11.75$ ,  $d.f. = 1$ ,  $P = 0.0006$ ), as did the number of nymphs (Fig. 4d, LME:  $\text{Chi}^2 = 9.15$ ,  $d.f. = 1$ ,  $P = 0.0025$ ).



**Fig. 2.** The median dry weights of leaves plus stems (a) and fruits (b) on plants exposed to *M. pygmaeus* and clean plants. Vertical thick lines show medians, boxes show 25th and 75th percentiles and whiskers give minima and maxima.

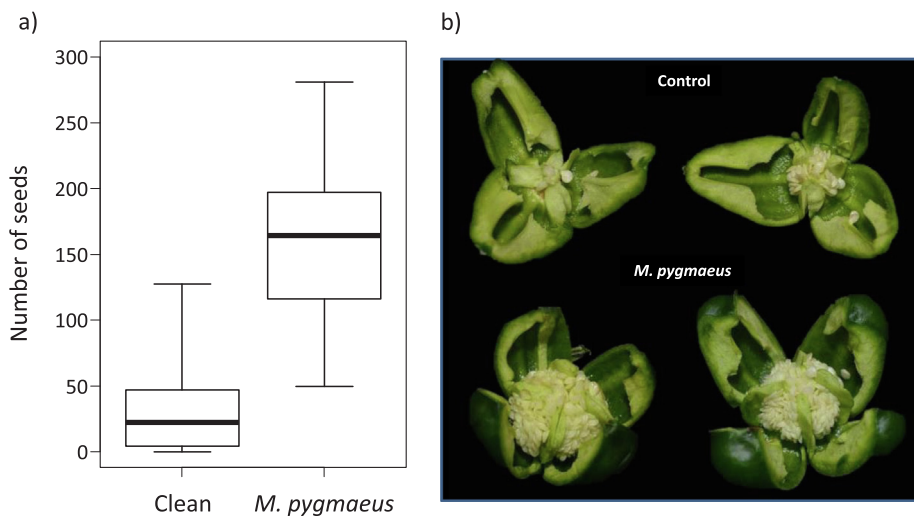
**4. Discussion**

We show that plant feeding by the omnivorous predator *M. pygmaeus* affected performance of sweet pepper plants. Plants exposed to the omnivores had significantly fewer leaves than unexposed plants, but the difference was not large (Fig. 1a), and it is questionable whether this would have affected plant performance significantly. However, the numbers of flowers of exposed plants were considerably lower than those of clean plants, suggesting that the presence of *M. pygmaeus* had a negative effect on these plants. Similar numbers of fruits and similar dry weights of leaves plus stems and fruits were found on plants exposed to the omnivore and clean plants, showing no negative effects on plant performance. More importantly, omnivore exposure significantly shortened the time from the first flower to the first fruit, and resulted in five times higher numbers of seeds per fruit on plants with omnivores than on clean plants, suggesting that the presence of the omnivore is not costly but beneficial for plant fitness. For logistic reasons, we did not measure plant performance throughout individual plant lifetimes. Possibly, effects of *M. pygmaeus* on plant growth and flowering can be

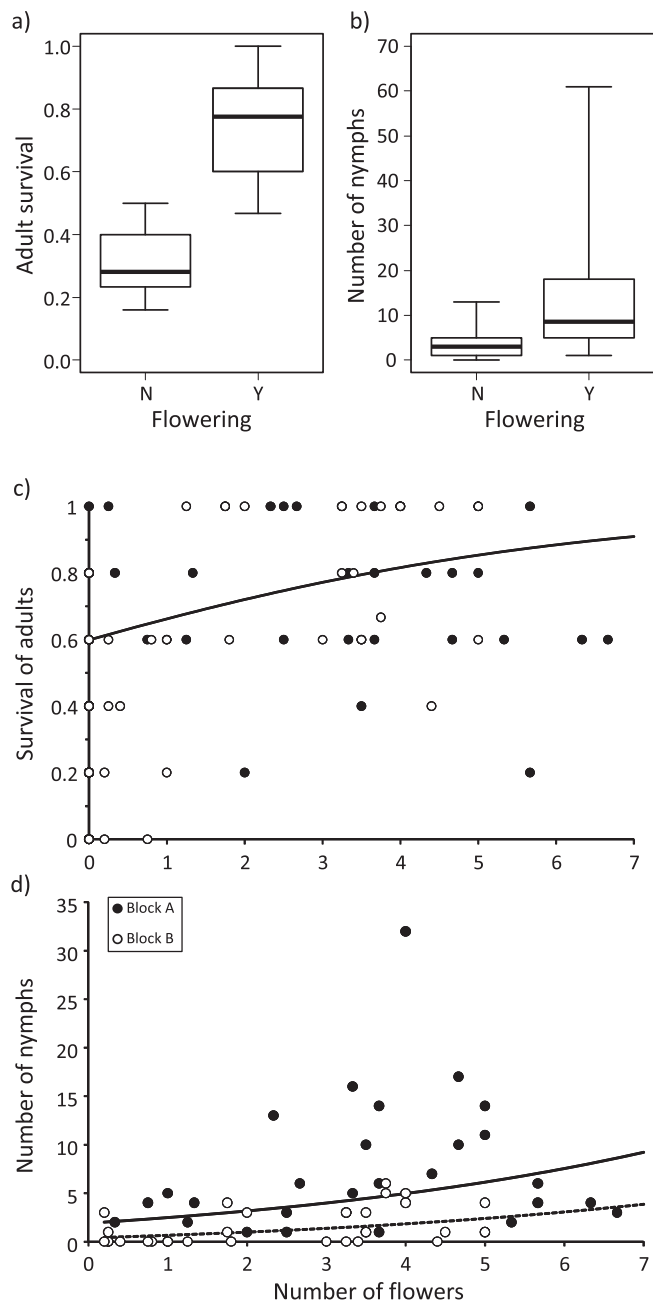
partly compensated later in the plant’s life.

Before the plants started flowering, the omnivores could only use leaves and stems as food source. After the plants started flowering, they could also feed on pollen and nectar, which resulted in increased survival and development of the omnivore, as was found previously (Perdikis and Lykouressis, 2000). This shows that the omnivores benefit from the resources offered by the flowers. Indeed, *M. pygmaeus* is often found in the flowers of sweet pepper plants (Messelink and Janssen, 2014). The results presented here show that the presence of this omnivore resulted in earlier fruit development and in higher numbers of seeds per fruit, suggesting that *M. pygmaeus* may also act as a pollinator. Sweet pepper is self-pollinating, but movement of flowers releases pollen, resulting in increased pollination. Under greenhouse conditions, wind causes sufficient movement, thus growers do not need to release pollinators, but in the cages used in our experiment, there was no wind, so pollination may have occurred less in cages without the omnivore.

The other changes in plant phenology, i.e. lower numbers of flowers and leaves, may have been a consequence of the exposed plants allocating more resources to fruits than to flowers and leaves. In our



**Fig. 3.** The median numbers of seeds in each fruit from sweet pepper plants exposed to *M. pygmaeus* and clean (control) plants (a) and a picture showing numbers of seeds in two fruits from control plants (top) and *M. pygmaeus*-exposed plants (bottom) (b). Vertical thick lines show medians, boxes show 25th and 75th percentiles and whiskers show minima and maxima.



**Fig. 4.** The median proportion of surviving females (a) and the median numbers of nymphs (b) of *M. pygmaeus* on plants with (Y) and without (N) flowers. Vertical thick lines show medians, boxes show 25th and 75th percentiles and whiskers show minima and maxima. c) The proportion of females surviving in two blocks (block A: closed circles; block B: open circles). The solid line is the fitted curve of a generalized linear mixed effects model on data of both blocks together (blocks did not differ significantly). d) The numbers of nymphs in two blocks. Lines are fitted curves of a linear mixed effects model on data per block (block A: solid line; block B: dashed line).

experiments, plants may have invested in fruits rather than flowers because the presence of *M. pygmaeus* probably increased pollination. Additionally, the phenological changes could also have been a consequence of the plant investing more in induced plant defences. Earlier, we showed that plant feeding by the omnivore resulted in the induction of direct plant defences, which affected the performance of the spider mite *Tetranychus urticae* and the thrips *Frankliniella occidentalis*, but not the aphid *Myzus persicae* (Zhang et al., 2018). The induction of such plant defences can result in the allocation of fewer resources to

vegetative growth and flower production. Induced plant defences are often assumed to be costly because of this reallocation (Agrawal, 2000; Zangerl et al., 1997), but there is mixed evidence for such costs (Gianoli and Niemeier, 1997; Karban, 1993; Strauss et al., 2002; Thaler, 1999). The results presented here suggest that plant performance is not negatively affected by the presence of *M. pygmaeus* on the plant or by the induction of plant defences by the omnivore. Clearly, the ultimate proof for costs of induced plant defences and other changes in the plant caused by the omnivore should involve ecological costs because of changes in interactions within the entire food web associated with the plant (Sabelis et al., 2007). One may wonder why plant defences are induced by plant feeding by *M. pygmaeus*. This omnivore does not cause significant damage to plants, and can effectively protect plants against herbivores, making induced plant defences largely redundant. Perhaps in nature, the omnivore mainly visits plants that have already been attacked by herbivores, and further induction by the omnivore will then have little effect on plant defences and plant fitness. Furthermore, it is known that omnivores feed more on prey and less on the plant when plant quality is low (Agrawal et al., 1999; Janssen et al., 2003). Possibly, the induction of plant defences by *M. pygmaeus* lowers plant quality, resulting in a preference for pollen, nectar and herbivores in the omnivores, thus promoting fruit development and seed production as well as reducing plant damage. It has also been suggested that the omnivores induce defences to trigger the production of plant volatiles (induced indirect defence), which then serve as signal for conspecifics, for example to attract mates (Moayeri et al., 2007; Rim et al., 2018).

One remaining question is how *M. pygmaeus* interacts with other pollinators and how this affects fruit and seed production (Bruinsma et al., 2014, 2008; Lehtilä and Strauss, 1997; Strauss et al., 2002). As explained above, sweet pepper plants are self-pollinating, and are not dependent on pollinators in greenhouses or in the field. However, on other plant species, the omnivore could directly interact with pollinators by attacking them in the flowers, and indirectly by inducing plant defences. It is known that herbivory can affect pollinator behaviour (Kessler and Halitschke, 2009), and the induction of plant defences by *M. pygmaeus* may have similar effects. Possibly, plant feeding by the omnivore can affect pollen and nectar characteristics, which may influence the behaviour of pollinators. This clearly needs further investigation.

The survival of *M. pygmaeus* on flowering plants was higher than plants without flowers. Furthermore, there was a positive relation between the survival and reproduction of the omnivore and the number of open flowers. Because plants exposed to the omnivore produced fewer flowers, this suggests that the changes in flowering as a result of this exposure do not benefit the omnivore. This may further cause the omnivores to feed on herbivores instead of on pollen and nectar. Thus, it appears that the changes in plants as a result of exposure to the omnivore benefit the plant and not the omnivore.

*Macrolophus pygmaeus* is commercially used for pest control in greenhouses. The large advantage of plant feeding by this omnivore for biological pest control is that its population can be established in a crop before pest outbreaks (Castañé et al., 2011). Here we show that such plant feeding has no effect on fruit biomass while it increases seed production.

#### CRediT authorship contribution statement

**Nina Xiaoning Zhang:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Visualization, Funding acquisition. **Gerben J. Messelink:** Conceptualization, Supervision, Writing - review & editing. **Sunny Verdonkshot:** Investigation, Writing - review & editing. **Arne Janssen:** Conceptualization, Methodology, Investigation, Data curation, Writing - original draft, Writing - review & editing, Formal analysis, Visualization, Supervision, Project administration.

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