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### What omnivores don't eat

*Nonconsumptive ecological effects of phytophagy by *Macrolophus pygmaeus**

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## General discussion

It has long been known that herbivory can induce direct and indirect plant defences that affect the performance and host plant choice of the same or other herbivores, and can also affect the behaviour of natural enemies (Sabelis et al. 2007). Recently, it was discovered that plant feeding by omnivores can induce similar responses as herbivory does, thus affecting herbivores and predators in the food webs associated with the plant (De Puyssseleyr et al. 2011; Pappas et al. 2015; Pérez-Hedo et al. 2015b; Naselli et al. 2016; Bouagga et al. 2018; Zhang et al. 2018 [= CHAPTER 2]). In this thesis, I studied plant defences induced by plant feeding by the omnivorous predator *Macrolophus pygmaeus* and the effects on the performance and the host plant choice of herbivores, as well as effects on the behaviour of predators.

### Omnivore-induced direct plant defences

In CHAPTER 2, I studied the effects of previous exposure of sweet pepper plants to the omnivorous predator on three herbivore species, two-spotted spider mites, green peach aphids and western flower thrips. I found that exposure of plants to the omnivore significantly reduced reproduction of spider mites and thrips, but not of aphids. Furthermore, this decreased reproduction of the two herbivores was not only found on the leaves exposed to the omnivore, but also on the leaves that had not been exposed, suggesting the plant responses induced by the omnivore were systemic. Juvenile survival and the developmental time of spider mites and aphids, and survival of thrips larvae were not affected by plant feeding by the omnivore. Thrips larvae feeding on leaves previously exposed to the omnivore required longer to develop into adults.

To further confirm that the decreased performance was caused by plant defences induced by phytophagy of the omnivore, I measured the levels of plant hormones of the two main biochemical pathways involved in plant defences against herbivores, i.e., the jasmonic acid and salicylic acid pathways. I found that the concentrations of two of the JA-related hormones, i.e., 12-oxo-phytodienoic acid and jasmonic acid-isoleucine, were significantly higher in the attacked leaves than in the unattacked leaves from exposed plants and than in the corresponding leaves from clean plants. Jasmonic acid concentrations showed the same trend, suggesting that the jasmonic acid – related defence pathway was activated. In contrast, similar concentrations of salicylic acid were produced in the leaves from plants with the omnivore and clean plants. Concentrations of abscisic acid, a plant hormone not related to either of the two defence pathways, were significantly higher in both damaged leaves and

undamaged leaves, indicating that the plant showed a systemic response. The results suggest that omnivorous predators can decrease herbivore populations directly by killing them and indirectly by decreasing their performance through induced direct plant defences.

I observed that herbivores had strong tendency of leaving the plants with the omnivore, even though they were restricted in a closed set-up. This inspired me to investigate whether herbivores avoid plants exposed to the omnivore. They might avoid such plants because of the lower plant quality due to the induced direct defences. This would not hold for the aphids, because their performance was not negatively affected on previously exposed plants. In addition, the herbivores might avoid exposed plants because they contain cues associated with an omnivore that might attack them. I found that spider mites and thrips preferred clean plants over plants previously exposed to the omnivore, whereas aphids showed no preference. This was in agreement with their performance as reported in CHAPTER 2. However, significantly higher proportions of aphids left plants exposed to the omnivore than clean plants. Perhaps this was due to non-volatile cues on the plants that were associated with the presence of their omnivorous predator. These results show that omnivorous predators can not only decrease herbivore densities on plants by killing them and by decreasing their performance through induction of direct plant defences, but also by indirectly affecting herbivore host plant selection.

It was still unclear whether volatile cues from the omnivore-exposed plants played a role in the host plant choice of the herbivores, in particular the spider mites and thrips. I therefore subsequently investigated the role of volatiles released by omnivore-exposed plants.

### **Omnivore-induced plant volatiles**

Some evidence has shown that omnivorous predators induced the production of plant volatiles (Moayeri et al. 2007; Bouagga et al. 2018). Inspired by the results of CHAPTER 3, I asked in CHAPTER 4 whether plant feeding by *M. pygmaeus* induced the production of plant volatiles and how this affected the performance of the phytoseiid *Phytoseiulus persimilis*, a predatory mite of spider mites. I chose to use this predator instead of the herbivores because they reliably respond to herbivore-induced plant volatiles in an olfactometer (Sabelis and van de Baan 1983), whereas herbivores perform much more poorly in such a set-up (Pallini et al. 1997; de Kogel et al. 1999). Moreover, I was interested in the possible interference of the omnivore with the searching behaviour of this natural enemy, which is often used together with the omnivore for biological control. I found that the predatory mites preferred volatiles from plants previously exposed to the omnivore over volatiles from clean plants. This was surprising, because these exposed plants did not harbour any food for the

predatory mites. I therefore further investigated whether the omnivore interfered with the attraction of predatory mites to plants with spider mites. I found that the predatory mites were equally attracted by plants previously exposed to the omnivore and subsequently infested by spider mites than to plants infested with spider mites. In contrast, the predators were more attracted by volatiles from plants infested with prey and subsequently exposed to the omnivore than plants infested with prey but not exposed to the omnivore, suggesting that the omnivores indeed can interfere with the searching behaviour of the predatory mites. Subsequently, I investigated whether the predatory mites responded to volatiles of the omnivores themselves by offering them a choice between plants previously exposed to the omnivore, of which one group still harboured the omnivore and the other group not. I found that the predatory mites were also significantly attracted to plants on which the omnivores were still present. This response was unexpected because *M. pygmaeus* can feed on eggs of *P. persimilis*. I therefore investigated whether experience of *P. persimilis* with the omnivore would change its response towards volatiles of exposed plants. I found that such experience resulted in a loss of the preference for volatiles emitted by exposed plants. To confirm that plant volatiles were induced, I also analysed the volatiles from clean and exposed plants with gas chromatography-mass spectrometry. I found that exposed plants indeed produced different volatile blends than clean plants, and that some of the volatile compounds were similar to those induced by spider mites. Together, I showed that the omnivorous predator induced the production of plant volatiles that attracted other predators.

### **Consequences of omnivore-plant interactions on plant and omnivore performance**

Defences induced by herbivores are beneficial for the plants because they decrease the performance of herbivores and attract natural enemies that attack the herbivores damaging the plants (Karban and Baldwin 1997). It is not clear, however, why feeding by omnivores should also induce such defences, and whether these are also beneficial to the plant. It is also not clear what are the effects of these changes in the plant on the performance of the omnivore. This led me to CHAPTER 5, where I investigated plant development and reproduction in the presence of the omnivore. Although exposure to *M. pygmaeus* significantly affected the performance of the plants, especially lowering the numbers of flowers, overall, the plants seemed to benefit from this exposure, which resulted in higher numbers of seeds per fruit. Once plants were flowering, the survival and reproduction of the omnivore were significantly higher, because the omnivores could feed on pollen and nectar. Furthermore, survival and reproduction were positively related with the numbers of open flowers. Hence, the changes induced in the plants by the omnivores do not seem to benefit

the omnivore. Thus, it is still unclear why the omnivores induce these changes in the plant. It is possible that by decreasing their quality for the omnivore through induced defences, plants manipulate the omnivore to feed more on pollen and herbivores, and less on plant tissues. Alternatively, the changes in plant performance could be a result of the plant investing more in fruit production and less in flowering as a response to pollination by the omnivore. Clearly, further investigation of the effects of plant defences on the feeding behaviour of the omnivore and on plant performance is needed.

### **The ecological role of omnivores**

As explained in the introduction, omnivory is a common phenomenon many food webs (Polis et al. 1989; Polis and Strong 1996; Coll and Guershon 2002) and affects the persistence and resilience of food webs (Polis et al. 1989). Most studies, however, have focussed on the effects of omnivores through their feeding on different trophic levels, and plant-mediated interactions of omnivores with herbivores and predators have only received attention recently. Several studies have shown that omnivorous predators can affect herbivores through the induction of plant defences (De Puyssseleir et al. 2011; Pappas et al. 2015; Pérez-Hedo et al. 2015a,b; Bouagga et al. 2018; Zhang et al. 2018 [= CHAPTER 2]; CHAPTER 3), which adds to the importance of their ecological role in food webs associated with plants.

Several interactions among omnivores, plants, herbivores and other species associated with the plant-inhabiting food web deserve further attention. For example, the defences induced by the omnivores may result in the herbivores feeding on these plants being less nutritious for the omnivore, thus affecting the feeding behaviour of the omnivores, but also of other predators of the herbivores (Agrawal et al. 1999; Janssen et al. 2003). Furthermore, the induction of the production of plant volatiles has clear effects on the searching behaviour of predators (CHAPTER 4), but the consequences for population dynamics of these predators and the herbivores remains to be investigated. For the omnivore, it is not beneficial to attract other natural enemies that may compete for food with them. Also, these volatiles may affect the searching behaviour of other, conspecific and heterospecific omnivores. Lastly, the possibility that the omnivore may also play a role in plant pollination needs further study.

### **Implication for biological control**

The interactions of omnivores with plants and their associated food webs also deserve more attention from an applied point of view. During the last decades, an increasing number of omnivore species are released for biological pest control in many crops (Messelink et al. 2012, 2015; van Lenteren 2012). Being phytophagous,

omnivores have the advantage that they can persist in crops by feeding on pollen and plant materials, even in the absence of pests (Perdikis and Lykouressis 2000). Thus, they can be released preventively, before pests are present in the crop.

The interactions of the omnivore with other natural enemies deserve more research. Here, I showed that the predatory mite *P. persimilis*, a specialist predator of spider mites, was attracted by plants with the omnivore even when no spider mites were present (CHAPTER 4). Even after having received experience with volatiles from omnivore-exposed plants, the predatory mites did not avoid these plants. This suggests that the induction of plants by the omnivore may have negative effects on the searching efficiency and pest control of the predatory mite. Both species are released for pest control in crops and both occur in the Mediterranean area. I observed that the omnivore can kill all stages of the predatory mites, and do so even when spider mites, their common prey, are present. This could further affect biological control of spider mites. However, the presence of the omnivore seemed not a serious threat for adult female predatory mites, which could easily escape. The vulnerability of other stages of the predatory mites, such as eggs and larvae, should be further investigated. Possibly, they can use the webs produced by their spider mite prey, in which they preferentially reside, as a refuge (Cloutier and Johnson 1993; Pallini et al. 1998; Venzon et al. 2000; Roda et al. 2000; Lemos et al. 2015; for comparable examples). Understanding the direct and plant-mediated interactions between the omnivore and the predatory mite and other herbivores and natural enemies will provide information to improve biological control.

Plant-associated food webs are very complex, even when considering a limited number of herbivores and predators (Janssen et al. 1998; Ohgushi et al. 2007; Messelink et al. 2012), and omnivores add extra complications to these food webs. Their common occurrence in natural food webs and their increased use as biological control agents necessitates further studies of these interesting organisms.

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