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Use of plant resources by an omnivorous predator and the consequences for effective predation

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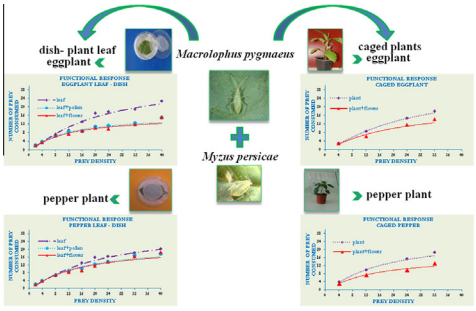
HIGHLIGHTS

- The spatial scale did not affect the functional responses of *Macrolophus pygmaeus*.
- Leaf of high or low quality did not affect the prey consumption.
- Pollen or flower of eggplant or pepper plant reduced the plateau of the functional response.
- On eggplant prey replacement by flower resources was similar at intermediate and high prey densities.
- On pepper plant prey replacement by flower resources only occurred at intermediate prey densities.

GRAPHICAL ABSTRACT



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ABSTRACT

Plant-provided food may enhance survival and establishment of omnivorous predators on target crops but on the other hand they may adversely affect predation rates and thus their potential for biological control of target pests. However, it is not known how predation is affected by plant food quality and prey density. The omnivorous predator *Macrolophus pygmaeus* is commonly used in augmentative releases in greenhouse crops. Experiments have shown its ability to utilize plant resources; eggplant and pepper plant leaves are the most and least suitable, respectively. In this study we searched the effects of floral resources (pollen or flower) of eggplant or pepper plant on the predation rate of *M. pygmaeus*. We used experiments in dishes (leaves) and cages (plants) under a range of densities of its prey, the aphid *Myzus persicae*. We did not find evidence that the consumption rates and the type of the functional responses of *M. pygmaeus* were affected by the plant leaf (eggplant vs pepper plant) or the increase in the spatial scale (leaf vs plant). However, the presence of pollen or a flower of eggplant and to a lesser extent of pepper plant reduced the plateau of the functional response to aphid density and increased the handling time per prey. The extent of prey feeding replacement by flower resources was dependent on the interaction between plant species and prey density. It seems that there is a constant rate of prey consumption replacement at intermediate and high prey densities on eggplant but only at intermediate prey densities on pepper plant. These results indicate the interactions between plant and prey resources in diets of omnivores and may be useful for its efficacy in pest control on eggplant and pepper plant.

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1. Introduction

Omnivorous predators are organisms that feed on both plant and prey tissues. They are common components of food webs (Coll and Guershon, 2002; Denno and Fagan, 2003; Eubanks and Styrsky, 2005). Several omnivores have been used in augmentative or conservation biological control of pests with a high success rate (Alomar and Wiedenmann, 1996; Hodek and Honěk, 1996; McMurtry and Croft, 1997; Dixon, 2000; Coll and Guershon, 2002; van Rijn et al., 2002; Ågren et al., 2012).

Foraging theory predicts that omnivores choose more often a mixed diet to balance energy and nutrient requirements (McMurtry and Rodriguez, 1987; Polis et al., 1989; Bjorndal, 1991; Agrawal and Klein, 2000). It has been proven that plant-feeding can support the omnivores' development (Vacante et al., 1997; Perdikis and Lykouressis, 2000), longevity (Lingren and Lukefahr, 1977; Lee and Heimpel, 2008) and fecundity (Fouly et al., 1995; Nomikou et al., 2002; Perdikis and Lykouressis, 2002; Lee and Heimpel, 2008) as well as affects their dispersal and distribution (Eubanks and Denno, 1999; Wanner et al., 2006). Moreover, omnivorous predators may survive and thereby sustain their populations by feeding on plant resources as alternative food during periods of prey scarcity, which in turn substantially supports their efficacy in pest control (Eubanks and Styrsky, 2005; Perdikis et al., 2011; Ågren et al., 2012).

That omnivorous predators feed on diverse food sources and switch between prey and plant feeding, may also substantially influence their effects on herbivore populations (Agrawal et al., 1999; Agrawal and Klein, 2000; Diehl and Feißel, 2000; Eubanks and Denno, 2000; Snyder and Ives, 2001; Snyder and Wise, 2001; Finke and Denno, 2002, 2005; Bruno and O'Connor, 2005). Plant feeding may cause either short-term effects due to changes of predation rates per day (individual-level) or long-term consequences due to effects on reproduction and numerical responses (population level) (Eubanks and Styrsky, 2005). Plant-provided food may result in reduced consumption of herbivores when alternative food and prey are substitutable food sources (Eubanks and Denno, 2000; Sabelis and Van Rijn, 2005; Koss and Snyder, 2005). It has also been reported that plant food of high quality (such as pollen) may release herbivores from omnivore predation (Wei and Walde, 1997; van Rijn, 2002; Janssen et al., 2003; Badii et al., 2004; Spellman et al., 2006; Robinson et al., 2008), whereas a decreased plant quality would lead to increased predation (Agrawal et al., 1999; Eubanks and Denno, 2000; Coll, 2009; Gillespie et al., 2012; Ågren et al., 2012). In fact, attempts to quantify the contribution of plant resources in the predators' diet are limited. Sabelis and van Rijn (2005) reported that alternative food can bring the pest locally to extinction only when it is substitutable with prey, rather than complementary. Badii et al. (2004) showed that prey consumption by an omnivorous predatory mite was decreased in the presence of pollen at all the prey densities tested; whereas, moth-egg consumption by the mirid *Dicyphus hesperus* Knight (Hemiptera: Miridae) increased when its diet was supplemented with tomato leaves (Gillespie and McGregor, 2000). It has also been reported that consumption of plant derived-water facilitates prey feeding by heteropteran predators (Sinia et al., 2004). However, in most cases, a reduction of prey consumption occurs that is greater at high prey densities (Wei and Walde, 1997; Cottrell and Yeargan, 1998; van Rijn et al., 2002; Lykouressis et al., 2014).

Although the evidence obtained shows that plant-derived resources may interfere with prey consumption, what has been studied less is how prey consumption rates are altered when plant food sources of high quality such as pollen are present in a range of prey densities extending from far below to much higher than the satiation level of the predator. If the aim is to understand these effects it has to be realized that plant-based resources such as pollen in flowers can be considered as being available *ad libitum* and, when present, usually are easily reached by the foraging predator; thus their consumption depends mostly on the nutritional food requirements by the predator.

Aiming to quantify and conceptualize the effects of plant food on prey consumption several approaches have been reported. Murdoch (1969) considering that predator should primarily aim at prey feeding, argued that a prey density threshold should occur above which the omnivore feeds only on prey whereas below this threshold density it feeds on both prey and alternative plant food. van Baalen et al. (2001) predicted that a predator should switch to alternative food when density of preferred prey is sufficiently low. In contrast, Wei and Walde (1997) searched the prey consumption of an omnivore at different prey densities with and without pollen and showed that reduction in prey consumption occurred at higher prey densities. Additionally, Robinson et al. (2008) reported a different association where plant resources had a significant adverse effect on adult lacewing prey consumption only at intermediate prey densities. Thus, the effects of plant recourses on prey consumption seem to be influenced by plant food quality and prey availability.

The omnivorous predator *Macrolophus pygmaeus* (Hemiptera: Miridae) is native to the Mediterranean area and is important for biological control of the South American tomato pinworm, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), whiteflies and other pests of tomato and eggplants in both greenhouses and open fields (Albajes and Alomar, 1999; Lykouressis et al., 1999–2000; Urbaneja et al., 2012). This predator can also successfully develop and reproduce without prey when feeding on plants only (Hansen et al., 1999; Perdikis and Lykouressis, 2000, 2002, 2004a). However, the availability of prey was crucial for its successful establishment on various host plants (Ingegno et al., 2011). Studies have also shown that *M. pygmaeus* nymphs, with access to a water source (moistened cotton), can successfully reach adulthood when fed exclusively on bee pollen (Perdikis and Lykouressis, 2000) and on stamens cut from fully blooming flowers of the weed *Ecballium elaterium* (Cucurbitaceae), without any other plant or prey material (Perdikis and Lykouressis, 2000). Perdikis and Lykouressis (2000) reported that when bee pollen pellets were added to a diet of eggplant leaves, the developmental period of *M. pygmaeus* was significantly shortened and completed within a period similar to that when it was fed on eggplant leaves with the aphid prey *Myzus persicae* Sulzer (Hemiptera: Aphididae). Vandekerkhove and De Clercq (2010) reported that when nymphs were fed only pollen, survival rates and egg production were lower than when provided both pollen and flour moth eggs. Additionally *M. pygmaeus* survival was prolonged on broad bean plants providing extrafloral nectar as compared to broad bean with removed extrafloral nectaries (Portillo et al., 2012). Recently Lykouressis et al. (2014) showed that similar predation rates of *M. persicae* recorded either on plants of lower or higher suitability for development of *M. pygmaeus*. However, the provision of a pepper flower on pepper leaves significantly reduced predation rates, at high prey densities.

Based on the above assessment, here we investigate the nature of interactions between plant food resources of varying quality with the predation rates of *M. pygmaeus* at a range of prey availability extending from low to higher than satiation. Further, we addressed two specific hypotheses: (1) Prey consumption is increased when the available plant resources are of low quality. (2) There is a prey density above which the prey consumption may be replaced by utilizing plant resources. Implications in biological control were also examined.