

**CAIO HENRIQUE BINDA DE ASSIS**

**A CASE OF OMNIVORY: AN IOLINID PREDATORY MITE CAN FEED ON A  
FUNGUS, THE PLANT AND A PEST ON TOMATOES**

Dissertation submitted to the Entomology  
Graduate Program of the Universidade  
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requirements for the degree of *Magister  
Scientiae*.

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## ABSTRACT

ASSIS, Caio Henrique Binda, M.Sc., Universidade Federal de Viçosa, February, 2024. **A case of omnivory: an iolinid predatory mite can feed on a fungus, the plant and a pest on tomatoes.** Adviser: Angelo Pallini. Co-advisers: Arne Janssen and Madelaine Venzon.

The specificity of natural enemies is a central topic in biological control, and the use of specialists or generalists has been extensively discussed since the formal adoption of biological control as a pest management technique in 1889. For a long time, specialist natural enemies were considered superior to generalists and were therefore more widely employed. However, over the last few decades, successful biological control has been achieved through the use of generalist predators in various cultivation systems, making them widely adopted in biological management programs. Generalists can feed on various food sources, enabling them to establish and persist in crops even during periods of prey scarcity, while also allowing for preventive control measures. Some of them can also simultaneously control multiple pests and reduce the costs and complexity of biological control. Predatory mites are among the most important natural enemies employed in the control of crop pests. Several of them are omnivorous, they do not feed only on other arthropods, but also on fungi, pollen, and plant tissue. For instance, many predatory mites have been shown feeding on fungi and even control plant diseases. Some of them can also feed on plant tissue and affect pests directly by attacking them, and indirectly by eliciting plant defences. In this work, I explored the potential of an iolinid predatory mite cf. *Homeopronematus anconai* sp. nov. for the biological control of pests in tomato plants. This predator has been shown to control powdery mildew infections caused by *Oidium neolycopersici* in tomatoes and potentially trigger defence responses in these plants. Hence, the main objective of this study was to assess the mechanism used by the predator to control powdery mildew. In the first chapter, I assess whether it controls this disease by feeding on the fungus, and in the second chapter I evaluate whether the plant feeding by this iolinid mite triggers defence responses in tomato plants, which could subsequently reduce powdery mildew growth. I demonstrate that the iolinid indeed feeds on powdery mildew and can reproduce by feeding on it. I found no evidence of the iolinids inducing plant defences.

Keywords: Omnivory; Biological control; Disease management.

## RESUMO

ASSIS, Caio Henrique Binda, M.Sc., Universidade Federal de Viçosa, fevereiro, 2024. **Um caso de onivoria: um ácaro predador iolinídeo pode se alimentar de um fungo, da planta e de uma praga no tomate.** Orientador: Angelo Pallini. Coorientadores: Arne Janssen e Madelaine Venzon.

A especificidade dos inimigos naturais é um tema central no controle biológico, e o uso de especialistas ou generalistas tem sido extensamente discutido desde a adoção formal do controle biológico como técnica de manejo de pragas em 1889. Por muito tempo, inimigos naturais especialistas eram considerados superiores aos generalistas e, portanto, eram mais amplamente empregados. No entanto, ao longo das últimas décadas, o sucesso no controle biológico tem sido alcançado por meio do uso de predadores generalistas em vários sistemas de cultivo, tornando-os amplamente adotados em programas de manejo biológico. Generalistas podem se alimentar de várias fontes alimentares, permitindo que se estabeleçam e persistam nas culturas mesmo durante períodos de escassez de presas, além de possibilitar medidas de controle preventivo. Alguns deles também podem controlar simultaneamente múltiplas pragas e reduzir os custos e a complexidade do controle biológico. Ácaros predadores estão entre os principais inimigos naturais empregados no controle de pragas agrícolas. Vários deles são onívoros, não se alimentam apenas de outros artrópodes, mas também de fungos, pólen e tecido vegetal. Por exemplo, muitos ácaros predadores foram observados se alimentando de fungos e até mesmo controlando doenças de plantas. Alguns deles também podem se alimentar de tecido vegetal e afetar as pragas diretamente, atacando-as, e indiretamente, provocando as defesas das plantas. Neste trabalho, explorei o potencial de um ácaro predador iolinídeo cf. *Homeopronematus anconai* sp. nov. no controle biológico de pragas em plantas de tomate. Este predador mostrou-se capaz de controlar infecções por oídio causadas por *Oidium neolycopersici* em tomateiros e potencialmente desencadear respostas de defesa nessas plantas. Assim, o principal objetivo deste estudo foi avaliar o mecanismo usado por esse predador para controlar o oídio. No primeiro capítulo, avalio se ele controla essa doença alimentando-se dela, e no segundo capítulo avalio se a alimentação da planta por esse ácaro iolinídeo desencadeia respostas de defesa no tomateiro, o que poderia então reduzir subsequentemente o crescimento do oídio. Demonstro que o iolinídeo realmente se alimenta do oídio e pode se reproduzir ao se

alimentar dele. No entanto, não encontrei evidências de que os iolinídeos induzem defesas nas plantas.

Palavras-chave: Onivoria; Controle biológico; Manejo de doenças.

## SUMMARY

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## General Introduction

Biological control is the use of organisms to control or reduce the impacts of pest organisms such as animals, weeds, and pathogens (Waage and Greathead, 1988; Eilenberg et al., 2001; van Lenteren, 2012; Heimpel and Mills, 2017; Stenberg et al., 2021). This practice has been employed for centuries (Waage and Greathead, 1988; Van Driesche and Bellows, 1996; Gurr et al., 2000). For example, the control of citrus pests through the use of ants has been recorded since 304 A.D. in China (Huang and Yang, 1987). However, the formal adoption of biological control as a pest management technique dates back to 1889, when the Australian ladybird beetle, *Rodolia cardinalis* (Mulsant) (Coleoptera: Coccinellidae), was introduced to California to control *Icerya purchasi* Maskell (Hemiptera: Margarodidae), an important pest of ornamental and citrus plants originating from Australia or New Zealand, which was devastating citrus orchards in that region (DeBach, 1964; Bosch et al., 1982; Caltagirone and Doutt, 1989). Since then, more than 2,700 species of biocontrol agents have been introduced worldwide (Cock et al., 2010).

Biological control is an environmentally safe and economically viable alternative to chemical pest control (Spadaro and Gullino, 2004; Cock et al., 2010; Brodeur, 2012; van Lenteren, 2012; Lahlali et al., 2022). Unlike pesticides, natural enemies are generally specific in the range of prey attacked, there are very few cases of resistance of pests to a biological control agent, and they pose no risks to farmers, consumers, or the environment (Gaugler et al., 1997; Bale et al., 2008; van Lenteren et al., 2018), although there are some issues with the introduction of exotic species in certain areas and the displacement of native fauna (Howarth et al., 1991; Elliott et al., 1996). Moreover, natural enemies can increase the level of control over time, while pesticides are ineffective in the long-term when natural enemies are present (Bale et al., 2008; Janssen and Van Rijn, 2021).

The specificity of natural enemies is a central topic of biological control, and the use of specialist or generalist organisms has been extensively discussed (Hassell and May, 1986; Strand and Obrycki, 1996; Dickens, 1999; Symondson et al., 2002; Brodeur, 2012). Historically, it was believed that for effective biological pest management, natural enemies needed to exhibit traits such as host specificity, synchronization with the pest, and rapid control action (Murdoch et al., 1985; Brodeur, 2012; Messelink et al., 2014), which made specialist organisms the major natural

enemies employed (Murdoch et al., 1985; Albajes and Alomar, 1999; Parrella et al., 1999). In contrast, generalist predators have been underutilized for two main reasons: (1) they exhibit characteristics distinct from those listed above, and (2) as cited before, certain attempts to introduce exotic generalist predators have led to disastrous outcomes, including the extinction of numerous native species (Howarth et al., 1991; Elliott et al., 1996; Albajes and Alomar, 1999; Symondson et al., 2002; Van Lenteren et al., 2003).

Despite these facts, successful biological control using generalist predators has been reported in various cultivation systems over the last few decades (DeClercq, 2002; van Rijn et al., 2002; Calvo et al., 2015; Janssen and Sabelis, 2015), with several species commercialized around the world (van Lenteren, 2012). Unlike specialists, which often decline when pest densities are low, generalist predators feed on various food sources and can establish and persist in crops even during periods of prey scarcity (Symondson et al., 2002; Messelink et al., 2014; Vangansbeke et al., 2014). Several of them can also control multiple pests simultaneously, reducing the complexity and the costs of biological control, and are usually easy to mass-produce on alternative preys (Symondson et al., 2002; Messelink et al., 2008; Calvo et al., 2012; Pirayeshfar et al., 2020).

Many generalist predators are omnivorous, they do not only feed on target prey, but also on other trophic levels (Coll and Guershon, 2002; Sutherland and Parrella, 2009; Goleva and Zebitz, 2013). For example, many predatory mite species are important biological control agents and are able to feed on other arthropods, fungi and plant-provided food such as pollen (Norton et al., 2000; Magalhães and Bakker, 2002; Calvo et al., 2011; McMurtry et al., 2013). Pollen is widely known as a rich alternative food for predatory mites (van Rijn and Tanigoshi, 1999; Gnanvossou et al., 2005; Duarte et al., 2015; Leman and Messelink, 2015), and its addition as alternative food for these predators often results in improved biological control (van Rijn et al., 2002; Nomikou et al., 2010; Delisle et al., 2015). Mycophagy is also relatively common among predatory mites (Hessein and Perring, 1986; Duso et al., 2005; Pozzebon et al., 2009), but despite several studies demonstrating their ability to control plant diseases (English-Loeb et al., 1999; Norton et al., 2000; Pijnakker et al., 2021), research on control of plant-pathogenic fungi by these predators is relatively scarce.

Phytophagy is also common among generalist predators (Coll and Guershon, 2002; Nomikou et al., 2003; Sanchez et al., 2004; Sengonca et al., 2004), which, in

this context, are classified as true omnivores or zoophytophagues (Pimm and Lawton, 1977; Castañé et al., 2011). These predators can feed on plant tissues and trigger plant defence responses similar to those induced by herbivores (Messelink et al., 2015; Bouagga et al., 2018; Cruz-Miralles et al., 2019; 2021; Pérez-Hedo et al., 2021; Zhang et al., 2018; 2022). Plants respond to plant feeding by these predators through diverse signal transduction pathways, which are mediated by phytohormones such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) (Koornneef and Pieterse, 2008; Erb et al., 2012; Pieterse et al., 2012). These responses can directly impact herbivores by decreasing their performance (Kessler and Baldwin, 2004; Howe and Jander, 2008; Zhang et al., 2018) or indirectly by attracting natural enemies through herbivore-induced plant volatiles (HIPVs) (Dicke and van Loon, 2000; Sabelis et al., 2001; Heil et al., 2001; Heil and Ton, 2008; Zhang et al., 2022). Well-known examples of direct plant responses are production of proteinase inhibitors that constrain food digestion of herbivores (Koiwa et al., 1997; Arimura et al., 2005) and secondary metabolites that have antinutritive, deterrent and toxic effects (Bennett and Wallsgrave, 1994).

These tritrophic interactions occur in a complex species-specific way and depend on the plant genotype (McCormick et al., 2012; Pérez-Hedo et al., 2018; Cruz-Miralles et al., 2021). Studies evaluating the effect of omnivores phytophagy have focused on the interaction between heteropteran bugs and greenhouse crops such as sweet peppers and tomatoes (Pappas et al., 2015; Pérez-Hedo et al., 2015; Naselli et al., 2016; Zhang et al., 2018). Predatory mites of the family Phytoseiidae are also known to induce defence responses in citrus plants (Cruz-Miralles et al., 2019; 2021).

Besides induced defences, plants also have constitutive defence mechanisms, which are the result of preformed characteristics and occur independently of herbivore attacks (Arimura et al., 2005; Howe and Jander, 2008). A notable example is trichomes, which occur constitutively and can hinder movement, interfere with feeding, release toxic substances, and capture insects and mites, resulting in their death (Quiring et al., 1992; van Lenteren et al., 1995; Krips et al., 1999; Maluf et al., 2001). Constitutive mechanisms do not only affect the herbivores feeding on plants but may also directly and indirectly affect the natural enemies of the herbivores (Belcher and Thurston, 1982; van Haren et al., 1987; Paspati et al., 2021; Legarrea et al., 2022). Detrimental effects of trichomes have been demonstrated across various groups of natural enemies such as coccinelids, crisopids, parasitoids and predatory mites (van

Haren et al., 1987; Kashyap et al., 1991; Barbour et al., 1993; Riddick and Simmons, 2014; Legarrea et al., 2022).

As a consequence of these defence mechanisms, host plants influence interactions between herbivores and natural enemies, and therefore, have a significant impact on the biological management of pests (Price, 1986; Thomas and Waage, 1996; Agrawal, 2000; Peterson et al., 2016). A well-known example occurs in tomatoes, which are covered with both glandular and non-glandular trichomes and pose several challenges to biological control (Bergau et al., 2015; Riddick and Simmons, 2014). Non-glandular trichomes affect natural enemies by impeding their movement or access to food (Simmons and Gurr, 2005; Bergau et al., 2015), while glandular trichomes produce chemicals such as acyl sugars and terpenoids, which can affect various life parameters of predators and parasitoids, as well as decrease their effectiveness (Kennedy, 2003; Puterka et al., 2003; Simmons and Gurr, 2005; Verheggen et al., 2009; Schillmiller et al., 2010; Legarrea et al., 2022). Therefore, successful biological control in this crop requires the use of natural enemies that are well adapted to these structures.

Some parasitoids and heteropteran predators, such as *Nesidiocoris tenuis* Reuter (Hemiptera: Miridae), are well adapted to tomato trichomes (Pérez-Hedo and Urbaneja, 2016; Bielza et al., 2020; Kennedy, 2003; Luna et al., 2007; Parra and Coelho, 2019) and can control pests (Calvo et al., 2009; 2012; Urbaneja et al., 2012; De Backer et al., 2014). However, predatory mites of the family Phytoseiidae, the key natural enemies employed for controlling phytophagous mites on tomato plants (van Lenteren and Woets, 1988; Drukker et al., 1997; Perdikis et al., 2008), are severely hindered by glandular trichomes, and the successful management of these pests often fails (Belcher and Thurston, 1982; van Haren et al., 1987; Fisher et al., 2005; Riddick and Simmons, 2014; Legarrea et al., 2022). For instance, the tomato russet mite, *Aculops lycopersici* Tryon (Acari: Eriophyidae), is one of the most destructive pests in tomato crops worldwide (Abou-Awad, 1979; de Moraes and Lima, 1983), and several phytoseiid species can successfully feed and reproduce on it in laboratory trials, but none has been able to effectively control this mite on tomato plants (Brodeur et al., 1997; Fisher et al., 2005; Park et al., 2010; Van Houten et al., 2013; Pijnakker et al., 2022). In contrast, predatory mites could successfully control *A. lycopersici* and spider mites on tomato plants without glandular hairs (Legarrea et al., 2022).

Studies exploring alternatives to managing *A. lycopersici* have primarily focused on predatory mites of the Iolinidae family (Hessein and Perring, 1986; Abou-Awad et al., 1979; Kawai and Haque, 2004; Van Houten et al., 2020). These tiny omnivorous predators have demonstrated the ability to: (1) navigate under and between trichomes of tomatoes without contacting the glandular tips, and successfully control the tomato russet mite, (2) manage powdery mildew infections caused by *Oidium neolycopersici*, and (3) feed on plant tissues, potentially triggering defence responses in tomato plants (Hessein and Perring, 1988; Pijnakker et al., 2021; Van de Velde et al., 2021; Vervae et al., 2021; Marcossi et al., in prep.). However, a more comprehensive understanding of the feeding habits and predatory behaviour of these omnivorous predators is needed. Therefore, in Chapter 1, I assessed whether a new species of iolinid mite, which has been shown to suppress both *A. lycopersici* and powdery mildew on tomato plants (Marcossi et al., in prep.), suppresses the fungus by feeding on it, and whether the predator can survive, reproduce and develop when feeding on it. In Chapter 2, I examined whether the leaf-feeding behaviour of this iolinid could trigger defence responses in tomato plants and affect the phytophagous mite *Tetranychus urticae* Koch (Acari: Tetranychidae). Additionally, I evaluated whether this predatory mite can feed on spider mite eggs and the impact of the web produced by this pest on this predator.

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## Chapter 1

### An iolinid predatory mite feeds on powdery mildew on tomato

#### Abstract

Mycophagy, the ability to feed on fungi, is prevalent among invertebrates and relatively common among natural enemies employed in the biological control of pests. Despite reports of arthropods successfully controlling plant diseases, this strategy is nevertheless still underexplored in biological disease management. Iolinids are omnivorous predators that occur naturally on tomato plants and are one of the most promising natural enemies for controlling *Aculops lycopersici*. They also feed on fungi and have been demonstrated to control powdery mildew infections caused by *Oidium neolycopersici* L. on tomatoes. However, how the predator controls this disease remains elusive, and we therefore explored the mechanisms involved in this process. Here, we show that powdery mildew is a suitable food source for the iolinid, allowing its development, survival, and reproduction, much like pollen, another excellent food source for the iolinid. In contrast, feeding on leaf tissue appears to be obligatory for this predator, but did not allow for juvenile development and reproduction. Our findings indicate that feeding is one of the mechanisms employed by this iolinid mite to suppress powdery mildew infections of tomato plants.

**Keywords:** biological control; omnivory; disease biocontrol; generalist predatory mites

## Introduction

Plant diseases are one of the main challenges for agricultural production worldwide. Throughout history, plant pathogens have been responsible for pandemics that have resulted in hunger, malnutrition, and death of millions of people (Padmanabhan et al., 1973; Dyer et al., 1993), and to economic (McCook, 2006) and ecological losses (Brasier, 1991; Rigling and Prospero, 2018). Currently, 20 to 30% of all world crop production is lost due to diseases and pests (Savary et al., 2012; Savary et al., 2019).

Powdery mildew is a widely distributed disease caused by a group of obligate biotrophic fungi that affect over 10,000 plant species, including several important crop groups such as vegetables, cereals and fruits (Gadoury et al., 2001; Vogel et al., 2004; Cowger et al., 2012; Bradshaw and Tobin, 2020; Pijnakker et al., 2021). In tomato, powdery mildew is attributed to several species of fungi (Mieslerova and Lebeda, 1999; Kiss et al., 2001; Jones et al., 2001; Konstantinidou-Doltsinis et al., 2006). Among them, *Oidium neolycopersici* predominates in greenhouses and occurs in growth stages ranging from seedling to mature plants (Jones et al., 2001). Symptoms include white lesions on the adaxial tomato leaf surface and can also occur in petioles and stems (Jones et al., 2001; Jacob et al., 2008). During severe outbreaks, the lesions caused by *O. neolycopersici* can coalesce, leading to chlorosis and premature leaf senescence, as well as a reduction in the quality and size of the fruits (Whipps et al., 1998; Jacob et al., 2008).

Current management practices of powdery mildew include the use of resistant varieties, fungicide applications and technology-based climate control in greenhouse crops (Jarvis, 1992; Castañe et al., 2020; Vielba-Fernandez et al., 2020). However, the constraints associated with the use of fungicides and the lack of resistant cultivars in some crops have demanded alternative methods (Lindhout et al., 1993; Bernard et al., 2004). Biological control of diseases has basically focused on the use of microbial antagonists (bacteria, fungi, oomycetes and viruses) (Collinge et al., 2022), including the use of antagonistic fungi such as species belonging to the genera *Ampelomyces* and *Trichoderma* (Paulitz and Bélanger, 2001; Kiss, 2003; Ownley et al., 2010) and antagonistic bacteria of the genus *Penicillium* and *Bacillus* (Romero et al., 2004; Cal et al., 2008). Despite increasing efforts in recent years, the use of microbial antagonists is still very limited (Alabouvette et al., 2006; Collinge et al., 2022).

A poorly evaluated possibility for the biological control of diseases is the use of fungivores. Mycophagy is widespread among vertebrates and invertebrates (Fogel and Trappe, 1978; Wheeler and Blackwell, 1984; Johnson, 1996). Studies with invertebrates have focused on insects, especially coleopterans, dipterans and collembolans (Visser and Whittaker, 1977; Martin, 1979; Sutherland and Parrella, 2009; Wilding et al., 1989) and mites, particularly soil-dwelling Oribatidae (Mitchell and Parkinson, 1976; Schneider et al., 2005). Although poorly studied, mycophagy is also common among predatory mites that inhabit the aerial parts of plants (Krantz and Lindquist, 1979). Several studies have highlighted this phenomenon within the families Phytoseiidae, Tydeidae and Iolinidae (McCoy et al., 1969; Norton et al., 2000; Pozzebon et al., 2009), emphasizing potential applications in the biological control of plant diseases (English-Loeb et al., 1999; Pijnakker et al., 2021).

Iolinid mites comprise omnivorous organisms that can be free-living in the soil, on plants and associated with insects (Krantz and Walter, 2009). These organisms have been described as predators of mites from the families Tenuipalpidae, Eriophyidae and Tetranychidae (Hessein and Perring, 1988; Abou-Awad et al., 1999; Van de Velde et al., 2021), as alternative food for predators (Flaherty and Hoy, 1971; Calvert and Huffaker, 1974) and as capable of controlling plant diseases (Pijnakker et al., 2021). Although some species have economic importance, this family is poorly known in comparison with other groups of predatory and pest mites (Sadeghi et al., 2012).

Iolinid mites such as *Homepronematus anconai* (Baker) and *Pronematus ubiquitus* (McGregor) (Acari: Iolinidae) are small-sized predatory mites, able to navigate under and among trichomes and can therefore successfully establish on plants with trichomes (Abou-Awad et al., 1999; Johann and Ferla, 2012; Vervaet et al., 2022). These predators occur naturally on tomato plants and are one of the most promising natural enemies for controlling the tomato russet mite, *Aculops lycopersici* (Tryon) (Acari: Eriophyidae), in greenhouses (Hessein and Perring, 1986; Kawai and Haque, 2004; Van Houten et al., 2020; Vervaet et al., 2021). Besides feeding on prey, iolinid mites can also feed on pollen, fungi and plant tissue (without causing noticeable plant damage) (Hessein and Perring, 1986; Duarte et al., 2021; Pijnakker et al., 2022; Vervaet et al., 2022). This generalist habit allows them to establish on plants before the arrival of pests and to persist in periods of prey scarcity (Symondson et al., 2002; Messelink et al., 2014; Van Houten et al., 2020; Van de Velde et al., 2021).

A recent study showed that *P. ubiquitus* was able to simultaneously control *A. lycopersici* and powdery mildew infections caused by *O. neolycopersici* L. on tomatoes (Pijnakker et al., 2021). A similar result was observed by our research group using another species of Iolinidae (cf. *Homeopronematus anconai* sp. nov.). However, our understanding of this control process remained limited. We therefore further investigated the disease control process by this predator by evaluating whether this iolinid mite feeds on powdery mildew. To this end, we assessed its reproduction, development, and survival when fed with fungal structures.

## Materials and methods

### Plant material

Tomato seeds (*Solanum lycopersicum* var. Aguamiel (EX V305), Limagrain®, imported by Vilmorin Seed Generation in Brazil) were sown in polystyrene trays (8 x 16 cells) in a commercial plant substrate (MecPlant, Paraná, Brazil), which we enriched with macro- and micronutrients. This variety is susceptible to powdery mildew but is resistant to various plant-pathogenic viruses. Fifteen days after germination, the seedlings were transplanted to plastic 3 L pots with the same substrate. Bean seeds were sown directly in 3 L pots. The plants were fertilized weekly with a solution of 20g of N-P-K (20-05-20) and 40 g of simple superphosphate in 20 L of water. The plants were kept in an area with natural light, but protected from rain, with temperatures varying between 14 to 28°C. Cattail pollen used in all experiments was collected from *Typha* sp. plants from the campus of the Federal University of Viçosa. The pollen was dried in an oven at 60° C for 24 h and stored in a freezer at -20 °C according to recommendation (Hagedorn and Moeller, 1968; Pernal and Currie, 2000).

### Mite rearing

The iolinids were collected from tomato plants infested with *A. lycopersici* in a residential area in Viçosa (Minas Gerais, Brazil), and were reared on tomato plants with cattail pollen (*Typha* sp.) as food. The tomato plants were kept in cages (1.0 x 1.0 x 1.0 m) manufactured at the Federal University of Viçosa, consisting of a wooden frame covered with a mesh (90 µm). A new clean plant was added every month. Pollen was applied twice a week using a fine brush, spreading a thin layer on the plants. The rearing cages were kept in the same area as above. To obtain young adult females of

approximately the same age, we took infested leaflets from the stock colony and removed all adult individuals. Subsequently, we placed these leaflets on clean tomato plants and added pollen as in the stock colony. After 7 days, we used the females that had reached adulthood.

#### Clean and infected plants

Clean tomato and bean plants were kept in a clean greenhouse with temperatures ranging between 14 and 28 °C. To obtain tomato plants infected with powdery mildew, plants were maintained inside cages (1.0 x 1.0 x 1.0 m) and infection occurred naturally. These plants were kept as above and new plants were added as necessary.

#### Juvenile development, survival, and oviposition

This experiment was designed to verify whether the iolinid can feed, develop, survive, and reproduce on *O. neolycopersici*. First, we assessed this on tomato leaf discs, using natural infections by this fungus. The food sources were leaf discs with powdery mildew, leaf discs with cattail pollen (*Typha* sp.), which is a good food source for the iolinid, and clean leaf discs (control). The arenas consisted of freshly excised tomato leaf discs (1 cm diameter), placed with the upper surface facing up on an agar-water mixture (2 g agar in 100 mL of water) in 4 cm diameter Petri dishes.

To confirm the feeding on fungal structures and eliminate possible feeding on cells infected by *O. neolycopersici*, we also assessed development, survival and reproduction on clean bean leaf discs, which the fungus does not infect (Huang et al., 2000; Jones et al., 2001). The fungal structures were collected from contaminated tomato leaves using a fine brush and put on the bean leaves.

To evaluate the development time and juvenile survival of the predatory mite, larvae from the stock colony were placed individually in the experimental units and development until adulthood was assessed at intervals of 24 h. To evaluate the reproductive capacity on powdery mildew, a single adult female (1 – 7 days after reaching adulthood) was placed on an experimental unit as above and the oviposition rate was recorded daily for 4 days. The eggs were counted daily while removing them from the arenas. Food sources were replaced every two days and there were 13 to 22 replicates for each treatment.

These experiments were conducted in a controlled environmental room at  $25 \pm 1$  °C and  $70 \pm 5\%$  RH. The experiments with tomato and bean leaf discs were conducted with a photoperiod of 16:08 and 12:12 h (L: D), respectively.

### Statistical analysis

Development and survival data were analyzed with a Cox proportional hazards model (package `coxme` Therneau, 2022). The effect of different diets on the oviposition rate was assessed with a linear mixed-effects model (LME) with treatment and time as fixed factors and individuals as a random factor to correct for repeated measures. To prevent possible effects of the previous diet, oviposition from the first experimental day was excluded from the analysis, as suggested by Sabelis (1990) for predatory mites of the Phytoseiidae family. Models were checked with normal error plots and plots of residuals against fitted values. Significance of factors and interactions were determined with log-rank and likelihood ratio (L.R.) tests. Contrasts among treatments were assessed with the function `emmeans` from the package with the same name (Lenth, 2023). All statistical analyses were done using the software R version 4.1.2 (R Core Team, 2021).

### Results

Diet significantly affected immature survival (Fig. 1, Cox proportional hazards: log-rank = 18.5, df = 2,  $p < 0.0001$ ) and development time of the iolinid cf. *H. anconai* sp. nov. (Fig. 1, log-rank = 21.4, df = 2,  $p < 0.001$ ) on tomato discs. Juveniles survived significantly better on a diet of powdery mildew structures or on pollen than on clean leaf discs. The developmental period was similar on discs containing powdery mildew structures and pollen (Fig. 1). All adults survived on a diet of powdery mildew, whereas two died on a pollen diet. On a clean tomato leaf disc, most juveniles reached the protonymph stage and some even became deutonymph, but did not develop into adults.

The oviposition rate on tomato discs differed significantly among diets (Fig. 2, linear mixed effects model, LME: L.R. = 97.8, df = 2,  $p < 0.001$ ) and the variation through time was almost significant (Fig. 2, LME: L.R. = 3.75, df = 2,  $p = 0.053$ ). The oviposition of the predatory mite on tomato discs was higher in the treatment containing fungal structures than in the control and lower than with pollen (Fig. 2). In the treatment

with powdery mildew, the iolinid mite showed a preference for depositing its eggs in the middle of the fungal structures, while they oviposited on the tips of trichomes or on the surface of the leaves in the other treatments.

On bean leaves, survival (log-rank = 42.5, df = 2,  $p < 0.0001$ ) and development time (log-rank = 36.8, df = 2,  $p < 0.0001$ ) of this iolinid mite were affected by diet (Fig. 3). Survival was higher on powdery mildew and pollen than on clean leaf discs. Juvenile development time was longer on a fungal diet than on pollen (Fig. 3). As before, all adults survived on a powdery mildew diet, while only one died on a pollen diet. In the control group, none of the individuals survived until the adult stage.

Oviposition on bean leaves was significantly affected by the interaction between diet and time (Fig. 4, LME: L. R. = 16.0, df = 2,  $p < 0.001$ ). The average oviposition rate of this iolinid mite was similar on a diet of powdery mildew and pollen and higher than on clean leaf discs on all days.

## Discussion

Previous studies demonstrated that cf. *H. anconai* sp. nov. was able to control powdery mildew infections (unpublished data), however, how the predator controls this disease remained undefined. Here, we confirm that it is capable of feeding on *O. neolycopersici* structures (Fig. 1 to 5) and this is a suitable food source for this predator (Fig. 1 to 4). Feeding on powdery mildew allowed for the development, survival and reproduction of this mite (Fig. 1 to 4).

*Oidium neolycopersici* mainly affects plants from the families Solanaceae and Cucurbitaceae (Jones et al., 2001). Despite infecting other families, some plants, such as beans, are immune to this fungus (Huang et al., 2000; Jones et al., 2001). Hence, we evaluated life history parameters of the iolinid on tomato leaf discs naturally infected by this fungus, and on bean leaf discs to which fungal structures were added. On both, powdery mildew proved to be a suitable food source. These results confirm the findings of previous studies showing fungi to be an adequate food for mites of the superfamily Tydeoidea (McCoy et al., 1969; English-Loeb et al., 1999; Duso et al., 2005; Krantz and Walter, 2009).

Fungi are a rich food source and play an important nutritional role in many arthropods (Mueller et al., 2001; Ruess and Lussenhop, 2005; Schneider et al., 2005; Boddy and Jones, 2008). In addition to being a suitable food source for Tydeoid mites,

fungi allow the development, survival and reproduction of several phytoseiid mite species (Zemek and Prenerov, 1997; Pozzebon and Duso, 2008; Pozzebon et al., 2009; Momen and Abdelkhader, 2010; Ajila et al., 2018). We obtained a high oviposition rate of the iolinid when fed with powdery mildew on tomato and bean discs. These results differ from the findings of Duarte et al. (2021), who obtained low oviposition of the iolinid *P. ubiquitous* feeding on *O. neolycopersici*. Similarly, Hessein and Perring (1986) observed survival, but not reproduction, of *H. anconai* feeding on *Cladosporium cladosporioides*.

Our data confirm that pollen is an adequate food source for this iolinid mite. We observed fast development and high survival and oviposition on this food. Pollen is an excellent food source for many predatory mites (van Rijn and Tanigoshi, 1999; Gnanvossou et al., 2005; Duarte et al. 2015; Leman and Messelink, 2015) and is often used as alternative food to improve biological control (van Rijn et al., 2002; Nomikou et al. 2010; Delisle et al. 2015). It has been demonstrated that its use improves the establishment and persistence of predatory mites in crops (Messelink et al., 2012; Symondson et al., 2002), even before the occurrence of pests and during periods of prey scarcity (Messelink et al., 2014; Vangansbeke et al., 2014). In a previous study, pollen supplementation allowed for rapid population growth of this predatory mite before infestation by *A. lycopersici*, which resulted in effective control of this pest (in prep.), and similar results were obtained for *P. ubiquitous* and *H. anconai* (Pijnakker et al., 2022; Vervaet et al., 2022).

Omnivores can feed on more than one trophic level and obtain resources that can complement their nutritional needs (Pimm and Lawton, 1977; Coll and Guershon, 2002). For instance, many predatory insects and mites can simultaneously feed on other arthropods and plant tissues, allowing them to obtain varied nutritional resources (Armer et al., 1998; Magalhães et al., 2002; Nomikou et al., 2003; Sanchez et al., 2004; Sengonca et al., 2004; Castañé et al., 2011; Cruz-Miralles et al., 2021; Pérez-Hedo et al., 2022). Although we frequently observed the iolinid feeding on plant tissue without causing apparent damage, the predator did not develop on healthy leaf discs without other food. Most individuals reached the protonymph and sometimes even the deutonymph stage, however, all of them died after a few days (Fig. 1 and 3). Likewise, oviposition was low on both plant species (Fig. 2 and 4), and was probably based on the previous diet of the adult mites. Phytophagy is common among iolinid mites (Krantz and Walter, 2009), however, many studies have also shown that this food source alone

cannot support their development and reproduction (Flaherty and Hoy et al., 1971; Hessein and Perring, 1988; Duarte et al., 2021). We observed that the iolinid feeds on plant tissue even in the presence of pollen and fungal structures. Moreover, attempts to keep them without leaf tissue were unsuccessful. Therefore, we suggest that phytophagy in this species may be obligatory and not facultative.

Tydeoid mites have been described as controlling plant-pathogenic fungi (English-Loeb et al., 1999; Norton et al., 2000; Pijnakker et al., 2021). However, none of the previous studies have indeed explored the mechanisms involved in controlling these diseases. The results of our study show that feeding is one of the mechanisms involved in suppressing powdery mildew infections of tomato plants by this iolinid mite (Fig. 6). Pijnakker et al. (2021) also report feeding by *P. ubiquitus* and propose that this could be a likely mechanism for controlling powdery mildew infections. However, a subsequent study revealed that *O. neolycopersici* was not as suitable a food source for this predatory mite as shown here for cf. *H. anconai* sp. nov. (Duarte et al., 2021).

Considering the leaf-feeding behavior of this iolinid mite, it is possible that this feeding induces plant defenses, which may also affect the development of powdery mildew on the tomato plants. Many omnivorous predators have been shown to trigger defense responses in plants and consequently affect pest populations (Sanchez et al., 2008; Bouagga et al., 2018; Pappas et al., 2015; Cruz-Miralles et al., 2019; Zhang et al., 2019). Furthermore, potential induction of plant defenses by iolinid mites have been demonstrated in tomato plants (Van de Velde et al., 2021; Pijnakker et al., 2021). Therefore, the induction of plant defenses through herbivory by this iolinid merits further investigation.

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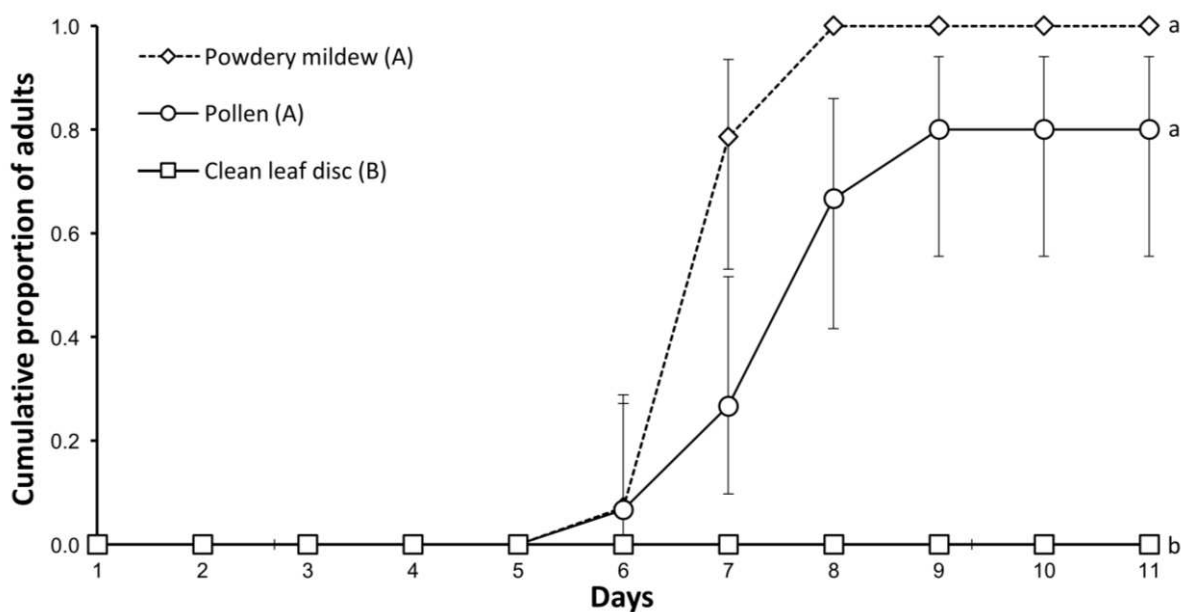
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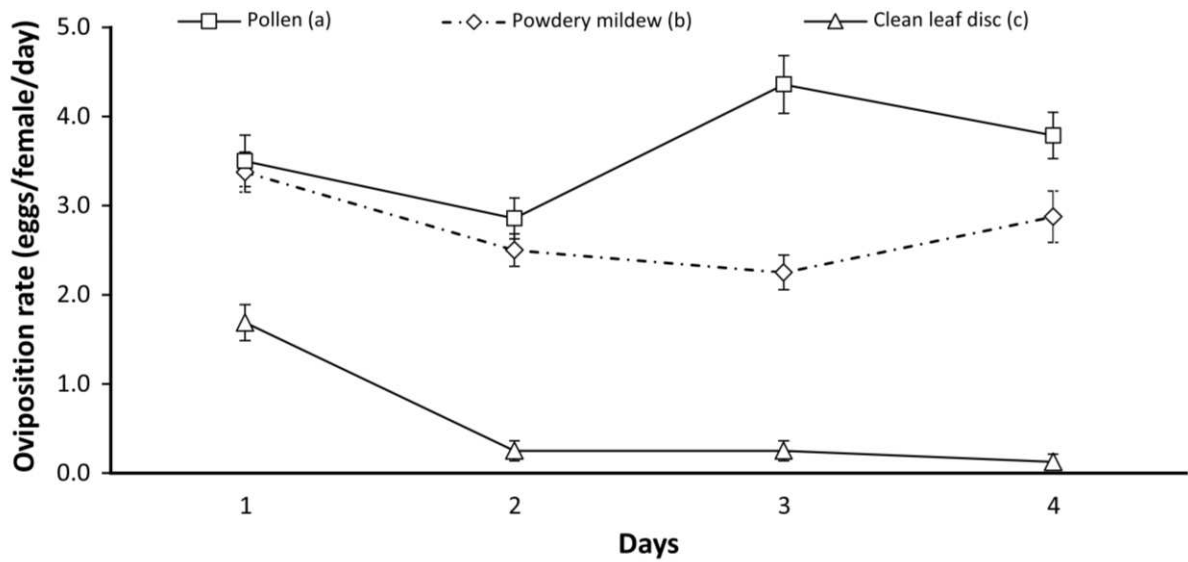
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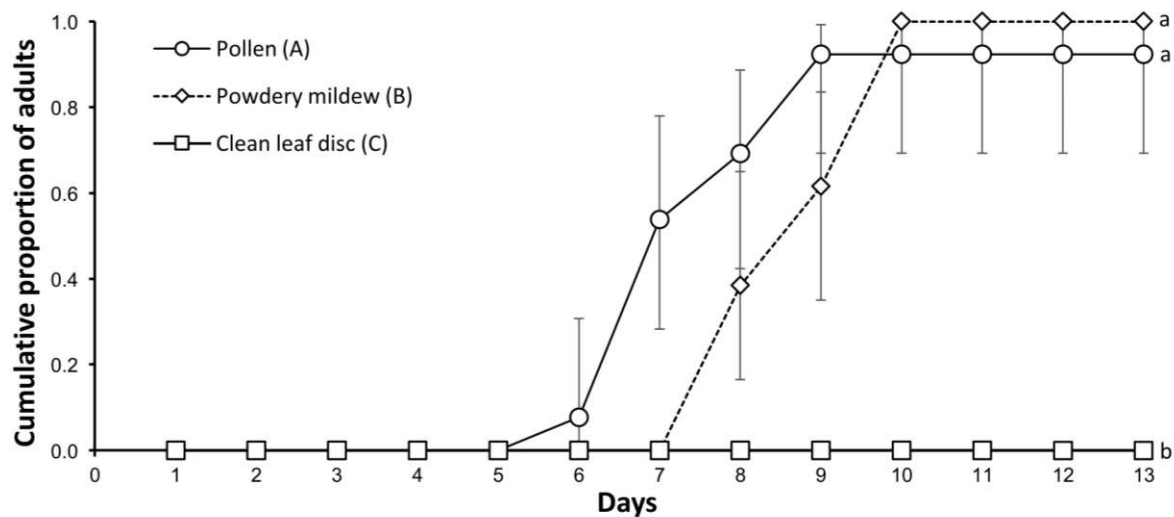
**Figure 1.** Juvenile development and survival of cf. *Homeopronematus anconai* sp. nov. on tomato leaf discs with powdery mildew structures or pollen (*Typha* sp.) and on clean leaf discs. Shown is the cumulative proportion ( $\pm$  CI) of adults as a function of time. Total survival is the final cumulative proportion of individuals that reached adulthood (i.e., the points at day 11); individuals that did not become adult died. Different uppercase and lowercase letters indicate significant differences in development and survival between the treatments, respectively (contrasts after survival analysis,  $p < 0.0001$ ).



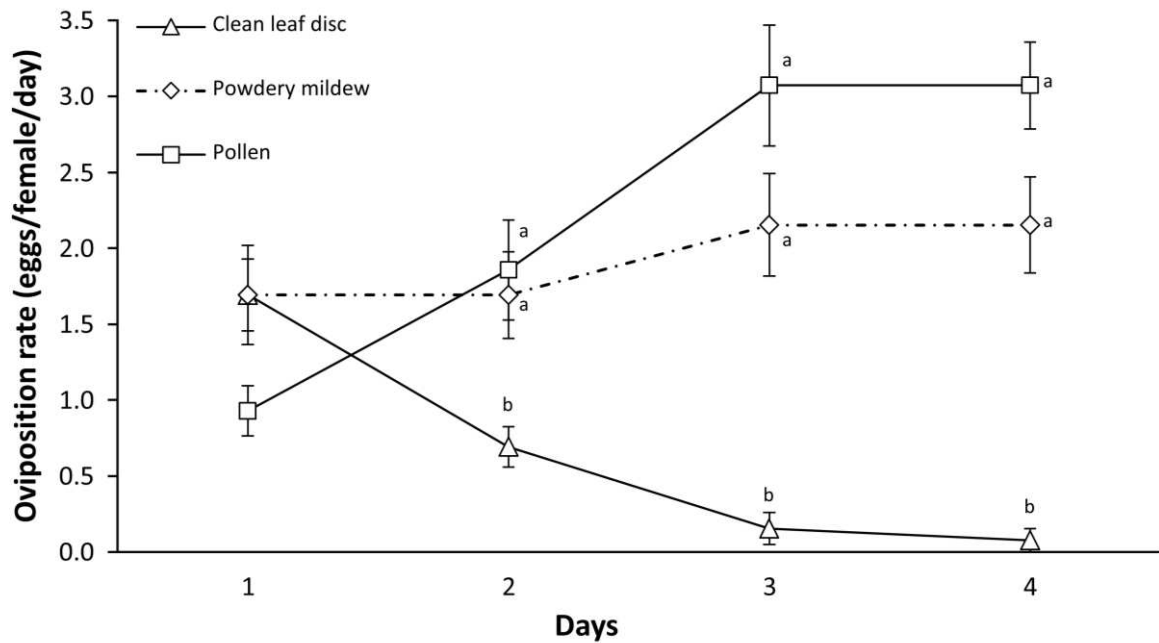
**Figure 2.** Oviposition rates ( $\pm$  SE) of cf. *Homeopronematus anconai* sp. nov. fed with tomato leaf discs containing powdery mildew structures or pollen (*Typha* sp.) and clean leaf discs after 4 days. Oviposition rates did not differ significantly among days. Differences between diets are indicated by different letters in the legend (contrasts after lme,  $p < 0.0001$ ).



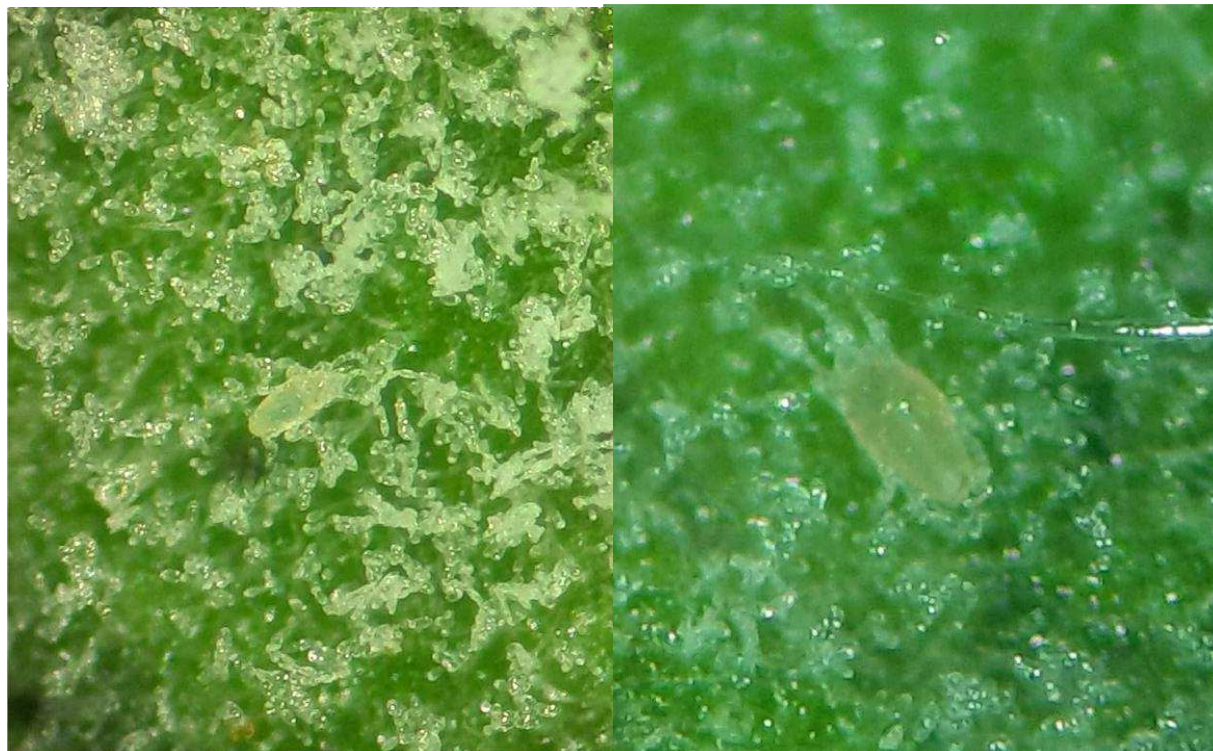
**Figure 3.** Juvenile development and survival of cf. *Homeopronematus anconai* sp. nov. on bean leaf discs containing powdery mildew structures or pollen (*Typha* sp.) and on clean leaf discs. Shown is the cumulative proportion ( $\pm$  CI) of adults as a function of time. See legend to Fig. 1 for further explanation.



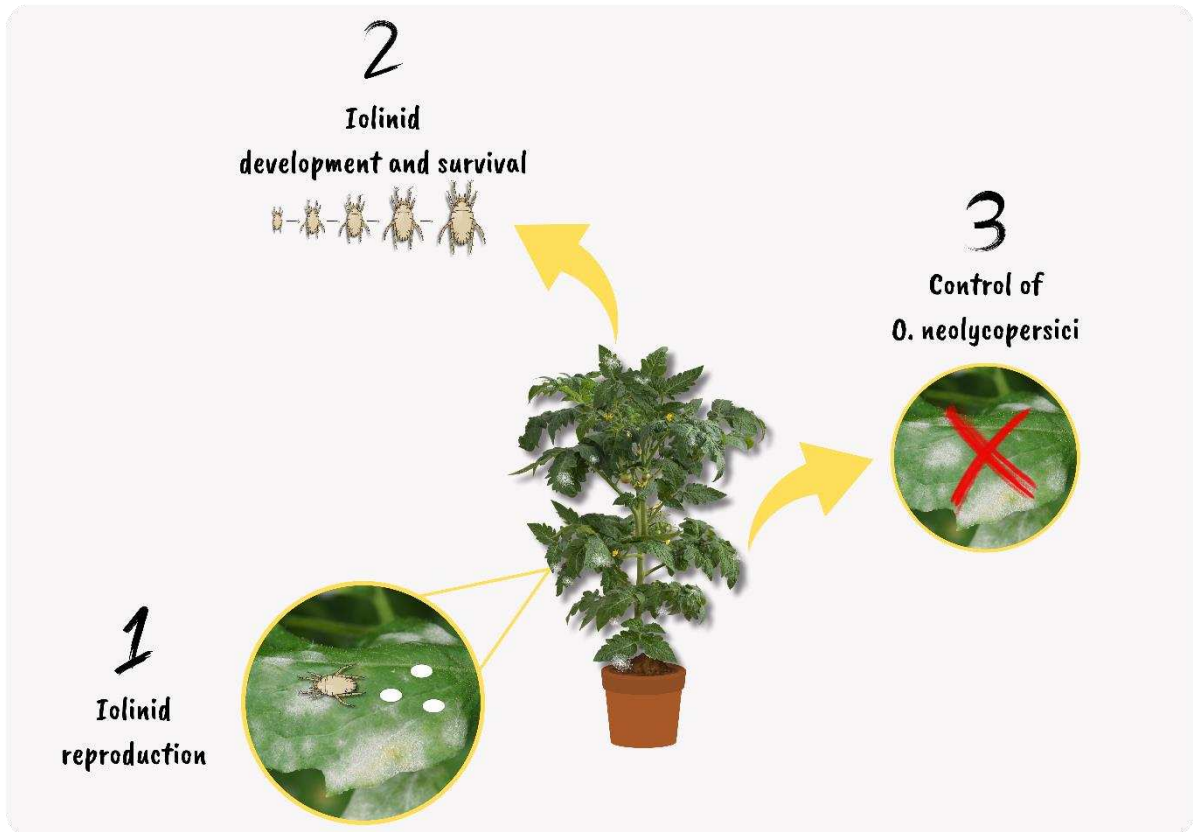
**Figure 4.** Oviposition rates ( $\pm$  SE) of *cf. Homeopronematus anconai* sp. nov. fed with bean leaf discs containing powdery mildew structures or pollen (*Typha* sp.) and clean leaf discs after 4 days. Oviposition rates did not differ significantly among days. Different letters indicate significant differences in oviposition rates between the treatments (contrasts after lme,  $p < 0.0001$ ).



**Figure 5.** The iolinid mite (225–280  $\mu\text{m}$ ) feeding on *Oidium neolycopersici* structures.



**Figure 6.** The iolinid mite feeding on *Oidium neolycopersici*. (1) allows its reproduction and (2) development and survival and (3) contributes to the control of powdery mildew on tomato plants.



## Chapter 2

### Phytophagy of an omnivorous iolinid mite does not affect oviposition of the two-spotted spider mite on tomato plants

#### Abstract

Iolinid mites are omnivorous predators capable of feeding on other arthropods, fungi, and plant-provided sources like pollen. This plasticity enables them to establish and persist more effectively in the environment and allows preventive control of these natural enemies against pests and diseases. Iolinids can also feed on plant tissue, which apparently is obligatory in this group. As it is known that herbivory in general induces defence responses in plants, here, we investigated the induction of defence responses by the iolinid cf. *Homeopronematus anconai* sp. nov. in tomato plants. To verify this induction, we measured oviposition by the spider mite *Tetranychus urticae*, which is sensitive to both types of plant defence, the Jasmonic Acid and Salicylic Acid pathways. Additionally, we also evaluated whether this iolinid is able to feed on eggs of two-spotted spider mite, as well as the impact of the web produced by this pest on this predation. Oviposition by *T. urticae* females was not affected by phytophagy of the iolinid, and we discuss some reasons for this. We observed no effect of the web produced by *T. urticae* on the iolinid mite; however, the predation rate of spider mite eggs was low. Despite these findings, we suggest that this predator may combat initial infestations of *T. urticae* and potentially contribute to the biological management of this pest in tomatoes.

**Keywords:** zoophytophagues; omnivory; iolinid; biological control; plant defence

## Introduction

Omnivory, the capacity to feed on organisms from more than one trophic level, is prevalent in ecological systems (Rosenheim et al., 1995; Polis and Strong, 1996; Eubanks and Denno, 2000), and allows omnivores to obtain varied nutritional sources (Pimm and Lawton, 1977; Coll and Guershon, 2002). This feeding behaviour is widespread among natural enemies employed in biological control (Momen and Elsayay, 1993; Nomikou et al., 2003; Sengonca et al., 2004; Pappas et al., 2015), and although it is now considered a positive trait, it was previously regarded as a sign that predators were not well adapted to the pest, making them underutilized (Huffaker et al., 1969; Murdoch et al., 1985; Parrella et al., 1999; Janssen and Sabelis, 2015). Currently, omnivorous predators are widely used in biological management programs (van Rijn et al., 2002; Calvo et al., 2015; van Lenteren, 2012). Their ability to feed on arthropods, fungi, and plant-provided sources like pollen and nectar (Symondson et al., 2002; Goleva and Zebitz, 2013; McMurtry et al., 2013; Leman and Messelink, 2015; Janssen and Sabelis, 2015) enables them to establish populations more effectively, allows preventive control measures and contributes to their persistence during periods of prey scarcity (Eubanks and Denno, 1999; Magalhães and Bakker, 2002; Symondson et al., 2002; Perdikis et al., 2011; Messelink et al., 2014; Pappas et al., 2016).

Some omnivores, also called zoophytophagous, do not only feed on prey, but also on plant tissues, including plant sap and cellular contents (Castañé et al., 2011). As a result, they can impact prey populations both through direct attacks and indirectly by eliciting plant defences (Kessler and Baldwin, 2004; Pérez-Hedo et al., 2015a; Zhang et al., 2018). Plants defend themselves through constitutive and induced mechanisms, which can act directly against herbivores, impairing their performance, and indirectly by attracting natural enemies (Sabelis et al., 2001; Heil et al., 2001; Karban and Myers, 1989; Fürstenberg-Hägg et al., 2013; Kant et al., 2015). Constitutive mechanisms are the result of preformed traits, for example, reproductive tissues generally accumulate large amounts of chemical compounds (Arimura et al., 2005; Howe and Jander, 2008). In contrast, induced mechanisms only occur following an attack, occur locally or are expressed systemically throughout the plant, and can be triggered by herbivores as well as by the phytophagy of zoophytophagous predators (Ryan, 2000; Bostock, 2005; Heil and Ton, 2008; Zhang et al., 2019).

Studies of zoophytophagous have mainly focused on heteropteran bugs (Messelink et al., 2015; Bouagga et al., 2018; Pérez-Hedo et al., 2021; 2022). Mirid bugs such as *Nesidiocoris tenuis* Reuter and *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) are widely used in biological control in Europe and have been extensively studied for their zoophytophagous behaviour (Calvo et al., 2012; De Backer et al., 2014; van Lenteren et al., 2020; Naselli et al., 2016; Zhang et al., 2022). Predatory mites have also been reported as feeding on plant tissues (Hessein and Perring, 1988; Magalhães and Bakker, 2002; Nomikou et al., 2003; Sengonca et al., 2004). Nevertheless, research on the impact of zoophytophagous mites feeding on plants, plant defences, and other arthropods have remained relatively scarce. Only two studies have addressed the induction of plant defences by phytoseiid mites and their effect on other arthropods (Cruz-Miralles et al., 2019; 2021).

Iolinid mites (Acari: Iolinidae) are omnivorous predators capable of feeding on other arthropods (Hessein and Perring, 1986; Abou-Awad et al., 1999), pollen (Duarte et al., 2021) and fungi (Chapter 1). They also feed on plant tissue, which apparently is obligatory in some species (Flaherty and Hoy et al., 1971; Hessein and Perring, 1988; Krantz and Walter, 2009; Chapter 1), and as with other zoophytophagous, this plant feeding can potentially trigger defence responses on plants (Van de Velde et al., 2021; Pijnakker et al., 2021). Unlike phytoseiids, which are hampered by glandular trichomes on tomato plants (van Haren et al., 1987; Koller et al., 2007; Sato et al., 2011; van Houten et al., 2013), iolinids can successfully establish on these plants because they are small and can move in between the trichomes without touching the glandular cells. Furthermore, they can reach high densities when pollen is supplemented (Pijnakker et al., 2022; Vervaet et al., 2022).

The iolinids can successfully control the tomato russet mite, *Aculops lycopersici* (Tryon) (Acari: Eriophyidae) (Hessein and Perring, 1986; Kawai and Haque, 2004; Van Houten et al., 2020; Vervaet et al., 2021; Marcossi et al., in prep.), which is also small enough to move in between the trichome stalks. Species like *Homeopronematus anconai* (Baker) and *Pronematus ubiquitous* (McGregor) have also been reported to feed on spider mites (Dean, 1957; Knop and Hoy, 1983) and *P. ubiquitous* potentially affected *Tetranychus urticae* Koch (Acari: Tetranychidae) densities by eliciting tomato defence responses (Van de Velde et al., 2021). However, information regarding the interaction between iolinid predators and spider mites is still very limited. Here, we

investigated the effect of the iolinid cf. *Homeopronematus anconai* sp. nov. on the performance of the two-spotted spider mite, *T. urticae*.

*Tetranychus urticae* is one of the most important pests worldwide (Van Leeuwen et al., 2010; Gotoh et al., 2015) and can feed on over 1,500 different plant species (Migeon and Dorkeld, 2024), causing significant reduction of agricultural production (Attia et al., 2013; Nyoike and Liburd, 2013). Its importance as an agricultural pest, along with traits such as a short generation time, easy rearing, and a high-quality genome sequence, has made *T. urticae* a widely used model organism (Helle and Sabelis, 1985; Grostal and Dicke, 1999; Grbic et al., 2007; 2011; Dermauw et al., 2013; Santamaria et al., 2020).

Given the leaf-feeding habit of the iolinid cf. *H. anconai* sp. nov., we expected that its phytophagy would induce defence responses in tomatoes and affect the performance of herbivores. Therefore, as a first step we investigated the induction of plant defences by this iolinid using *T. urticae* as a test species. To this end, we evaluated the impact of the feeding of the iolinid on oviposition of *T. urticae*. The spider mite is known to induce and be affected by inducible plant defences of both the Jasmonic Acid (mainly associated with defence against herbivory) and the Salicylic Acid (associated with defence against pathogens) pathways (Ament et al., 2004; Kant et al., 2004; 2008; Zhang et al., 2018). Furthermore, we evaluated whether the iolinid is able to feed on eggs of the two-spotted spider mite, as well as the impact of the web produced by this pest on predation.

## Materials and methods

### Plant material

Tomato seeds (*Solanum lycopersicum* var. Aguamiel (EX V305), Limagrain®, imported by Vilmorin Seed Generation in Brazil) were sown in polystyrene trays (8 x 16 cells) in a commercial plant substrate (MecPlant, Paraná, Brazil), which we enriched with macro- and micronutrients. Fifteen days after germination, the seedlings were transplanted to plastic 3 L pots with the same substrate. The plants were fertilized biweekly with a solution of 20g of N-P-K (20-05-20) and 40g of simple superphosphate in 20L of water. The plants were kept in an area with natural light, but protected from rain, with temperatures varying between 14 to 28°C. The cattail pollen used for the predator rearing was collected from *Typha* sp. plants on the campus of the Federal

University of Viçosa. The pollen was dried in an oven at 60° C for 24 h and stored in a freezer at -20 °C according to recommendation (Hagedorn and Moeller, 1968; Pernal and Currie, 2000).

#### Mites rearing

The iolinids were collected from tomato plants infested with *A. lycopersici* in a residential area in Viçosa (Minas Gerais, Brazil), and were reared on tomato plants with cattail pollen (*Typha* sp.) as food. The tomato plants were kept in cages (1.0 x 1.0 x 1.0 m) manufactured at the Federal University of Viçosa, consisting of a wooden frame covered with a mesh (90 µm). A new clean plant was added every month. Pollen was applied twice a week using a fine brush, spreading a thin layer on the plants. The rearing cages were kept in conditions as above. To obtain young adult female iolinids of approximately the same age, we took infested leaflets from the stock colony and removed all adult individuals. Subsequently, we placed these leaflets on clean tomato plants and added pollen as in the stock colony. After 7 days, we used the females that had reached adulthood.

*Tetranychus urticae* individuals were collected from infected soybean (*Glycine max* (L.) Merrill) plants at the University Federal of Viçosa. They were initially kept on tomato plants in cages (as above) for about 120 days. During the experiments, we maintained the population on arenas made with black PVC sheets (15 × 10 cm) on top of foam pads (h = 3 cm), which were kept in plastic trays (29 × 14 × 4 cm) filled with water. A wet cotton barrier was added to the edges of the arenas to prevent mites from escaping. New tomato leaves were added daily. The trays were kept in a room with natural light at 23 ± 3 °C and 70 ± 10% relative humidity. To obtain age-standardized females, we transferred some females from the rearing trays to clean tomato leaves and allowed them to oviposit for 24 hours. Subsequently, we removed the females and allowed the eggs to develop. Within 7 to 10 days, we obtained young adult females of approximately the same age.

#### Effect of iolinid feeding on *T. urticae* oviposition

This experiment was performed to verify whether phytophagy by the iolinid affects oviposition by *T. urticae* through the induction of local and systemic defence responses in tomato. Using plants with at least six true leaves, we divided the terminal leaflet of

leaves 3 and 5 into two sections using a thin barrier composed of a mixture (50:50 v/v) of insect glue (Colly, São Paulo, Brazil) and lanolin (União química, São Paulo, Brazil). Entomological glue + lanolin was also applied on the petiole of the leaflets. In one group of plants, we released 100 mobile iolinids on a section of leaflets on both leaves, while the other section remained uninfested (Fig. 1). In the other group, all leaflets remained uninfested but had an insect glue/lanolin barrier, and served as control. We evaluated oviposition of *T. urticae* in infested leaflet sections, in uninfested leaflet sections, and on clean plants. The predatory mites were kept on the section for 4 days without food or prey. The mite release section (tip or base of the leaflet) was changed between repetitions (Fig. 1). The tomato plants were kept in cages as above.

We assessed the performance of the two-spotted spider mite through the oviposition of young adult females, which is a good stand-in measure for spider mite performance (Sabelis and Janssen 1994). We use arenas consisting of freshly excised tomato leaf discs (3 cm<sup>2</sup>), placed with the lower surface facing up on an agar-water mixture (2 g agar in 100 mL of water), in 4 cm diameter Petri dishes. The leaf discs were prepared using the sections of leaflets that had either been exposed to the iolinids or not and clean leaflets from clean plants (Fig. 1). All predatory mites were removed from the infected leaflet sections with a fine brush. The brush was also passed over the discs that did not have predatory mites to induce the damage caused to the trichomes. Each treatment had ten replicates. A single adult female, 1 to 4 days old, was placed on each arena and oviposition was recorded daily for 4 days at 25 ± 2° C, 70 ± 10% RH, 12:12 L:D. The eggs were counted daily without removing them from the arenas. The oviposition of the first day was not included in the analysis because of the possible effect of the diet of the preceding days (Sabelis, 1981). The effect of different diets on the oviposition rate was assessed with a linear mixed-effects model (LME) with treatment, time, leaf and site (tip or base of the leaflet) as fixed factors and replicates as a random factor to correct for repeated measures. Contrasts among treatments were assessed with the function `emmeans` from the package with the same name (Lenth, 2023). All statistical analyses were done using the software R version 4.1.2 (R Core Team, 2021).

### Oviposition of iolinid females

We investigated the ability of the predatory mite to oviposit by feeding on *T. urticae* eggs. In arenas as described above, we placed two spider mite adult females and allowed them to oviposit for 24 hours. After that, we removed the prey females and kept five eggs per arena. An iolinid adult female (1 – 7 days after adulthood) was added to the arenas, and the oviposition rate and consumption of *T. urticae* eggs were recorded daily for 4 days. Clean tomato leaf discs with no food were used as control treatment. The predators were moved to new experimental units after two days to prevent the eggs from hatching. Ten replicates were carried out per treatment. The tests were performed under conditions as above.

We analysed the total oviposition of the iolinid females. Owing to the large number of zeros in the results, we conducted the analysis in two steps. First, we compared the proportion of ovipositing females in both treatments using a generalized linear model (GLM) with a quasi-binomial error distribution. Then, the number of eggs laid per ovipositing female was compared using a GLM with a quasi-Poisson error distribution. As above, to prevent possible effects from the previous diet, oviposition of the first day was excluded from the analysis.

### Predation on *T. urticae* eggs and effect of the web

This experiment was designed to assess *T. urticae* egg predation using a higher predator density as above and to investigate the effect of the spider mite web on the predator. In arenas as described above, we divided the discs into 2 parts using a thin strip of wet cotton wool as barrier. On one of them, we placed leaflets infested with iolinids and allowed them to move down onto the discs. These leaflets remained in the arenas for 24 hours, and after this time, we reduced or increased the number of predators to 18 individuals per disc by carefully removing or adding predators using a fine brush. This density was observed in a previous experiment (in prep.). On the other side of the disc, we placed 10 *T. urticae* adult females. The predators were starved for 24 hours on one side of the barrier while the prey females remained ovipositing and producing web on the other side. Afterwards, we removed the adult female spider mites and the web with a fine brush from half of the arenas, while we used a very thin needle to gently prod the females until they left the web in the other half, and then we removed them, leaving the web intact as much as possible. We then removed the cotton strip,

giving the predators access to the spider mite eggs. Predation was scored 24 hours later. There were 10 repetitions for each treatment (discs with and without web), and the test was performed in conditions as above. The proportion of damaged eggs in both treatments were compared using a generalized linear model (GLM) with a quasi-Poisson error distribution.

## Results

### Effect of iolinid feeding on *T. urticae* oviposition

The previous infestation of leaflet halves did not have a significant effect on the oviposition rate of *T. urticae* (Fig. 2, LME: L.R. = 1.26, df = 2, p = 0.53). The two-spotted spider mite oviposition was only affected by the interaction between leaf and site (LME: L.R. = 7.55, df = 1, p = 0.006). Females oviposited more at the tip of leaflet of leaf 5 than on the base, while no difference in oviposition was observed between base and tip on the leaflet of leaf 3.

### Oviposition of iolinid females

The consumption of *T. urticae* eggs by a single iolinid female was low (0.1 eggs/female/day) and the oviposition by the predator was therefore probably based on the previous diet of the predators (Fig. 3A). There was no significant difference in the occurrence of oviposition between the treatments (Fig. 3B, GLM:  $F_{1,22} = 2.57$ , p = 0.12). Likewise, the average number of eggs laid per ovipositing female was similar in both treatments (Fig. 3C, GLM:  $F_{1,10} = 0.35$ , p = 0.56).

### Predation on *T. urticae* eggs and effect of the web

The web produced by *T. urticae* did not affect the consumption of *T. urticae* eggs by iolinids (Fig. 4, GLM:  $F_{1,18} = 0.08$ , p = 0.78). The average predation ( $\pm$  s.e.) of spider mite eggs by 18 individuals was 3.40 ( $\pm$  0.82) and 3.10 ( $\pm$  0.66) in arenas with web and without web, respectively.

## Discussion

We previously showed that the iolinid cf. *H. anconai* sp. nov. feeds on plant tissues in an apparent obligatory way, and hypothesized that this phytophagous habit could potentially trigger defence responses in tomato plants (Chapter 1). Contrary to our

hypothesis, we did not find a significant effect of the phytophagy of the iolinid on oviposition by *T. urticae* (Fig. 2), and therefore, our findings did not provide evidence that this predator triggered defence responses in tomatoes under the conditions of our experiment.

Tomato defence responses elicited by zoophytophagues have primarily been demonstrated for mirid predators (Naselli et al., 2016; Pérez-Hedo et al., 2018; Esmaeily et al., 2021; Silva et al., 2022). Exposing tomato plants to species like *N. tenuis* and *M. pygmaeus* resulted in the activation of signalling pathways such as abscisic acid (ABA) and jasmonic acid (JA), attracting natural enemies and repelling pests (Pérez-Hedo et al., 2015ab; Naselli et al., 2016), as well as decreasing herbivore performance, including reduction in oviposition by *T. urticae* (Pappas et al., 2015; Esmaeily et al., 2021; Silva et al., 2022). We propose several explanations for the non-significant effect on oviposition by *T. urticae* in our experiments. First, it is possible that this predatory mite does not induce defence responses in tomatoes. Second, the iolinid may induce defences in tomato, but the numbers of iolinids used here may do so at a level that does not affect oviposition by the spider mite. Third, perhaps the set-up used in our experiment was not suitable for assessing the impact of iolinid phytophagy on the oviposition by two-spotted spider mites. In the only study investigating the potential of an omnivorous predatory mite to trigger defence responses in tomatoes, Van de Velde et al. (2021) observed that *T. urticae* females laid fewer eggs on tomato leaf discs previously exposed to the iolinid *P. ubiquitous*. However, the methodology employed in their study was quite different from ours; besides using a different iolinid species, they also released a different number of iolinids onto the plants and provided pollen as supplementary food.

Whether a predator attacks a specific prey depends on various factors, such as life stage, ability to execute a successful attack, level of satiation and body size ratio (Oaten and Murdoch, 1975; Cohen et al., 1993; Sabelis, 1992; Walzer et al., 2004). Despite being considered unlikely due to their diminutive size, iolinids have been reported as potential predators of tetranychids in natural settings (Dean, 1957; Metwally et al., 2014). However, these studies merely document the co-occurrence between predator and prey (Metwally et al., 2014), or report iolinids feeding on tetranychid individuals (Dean, 1957), without providing clear information on whether these predators indeed play a role in controlling these pests. As expected, we observed a low consumption of *T. urticae* eggs by adult females of the iolinids (0.1

eggs/female/day), and their oviposition in the presence of these eggs was similar to that on clean tomato leaf discs (Fig. 3). Low consumption of spider mite eggs was also reported for *P. ubiquitous* and *H. anconai*, and the latter was unable to oviposit when feeding on these eggs (Knop and Hoy, 1983; Van de Velde et al., 2021).

In the experiment with a higher predator density and presence of *T. urticae* webs, we found no effect of the web on the predation rate of spider mite eggs by the iolinid mite (Fig. 4), although we frequently observed some iolinids trapped, which suggests some effect of the web on the predator. During this trial, we observed that all developmental stages of the predator could feed on two-spotted spider mite eggs, and the consumption rate was slightly higher than that of single females: 18 iolinids consumed an average of 3.40 ( $\pm 0.82$ ) ( $\pm$  s.e.) eggs with web presence (0.19 eggs/female/day).

The observed predation rate is very low compared to phytoseiid mites specialized in feeding on tetranychids, which can consume up to 30 eggs per day (Janssen and Sabelis 1992). However, it is known that small predators are more abundant than large predators due to their lower metabolic needs (Brown et al., 2004; White et al., 2007), and although they have a low individual feeding rate, their high abundance can result in a significant negative impact on prey densities (Schneider et al., 2012). Iolinids can reach high densities on tomatoes (e.g., 200 to 250 mobile individuals per leaflet; Pijnakker et al., 2021; Marcossi et al., in prep.), and despite their low individual consumption rates, they have been shown to successfully control pests (Brodeur et al., 1997; Vervaet et al., 2022). For instance, despite females of cf. *H. anconai* sp. nov. consuming only 0.8 adults of *A. lycopersici* per day, they successfully controlled the pest in tomato plants (Marcossi et al., in prep.). Therefore, this predator may combat initial infestations of *T. urticae*. However, to confirm this, it is necessary to investigate the long-term interaction between these mites on tomato plants. Future studies should also assess whether combined inoculative releases of this iolinid and phytoseiid predators can enhance the biological control of *T. urticae* and other tomato pests.

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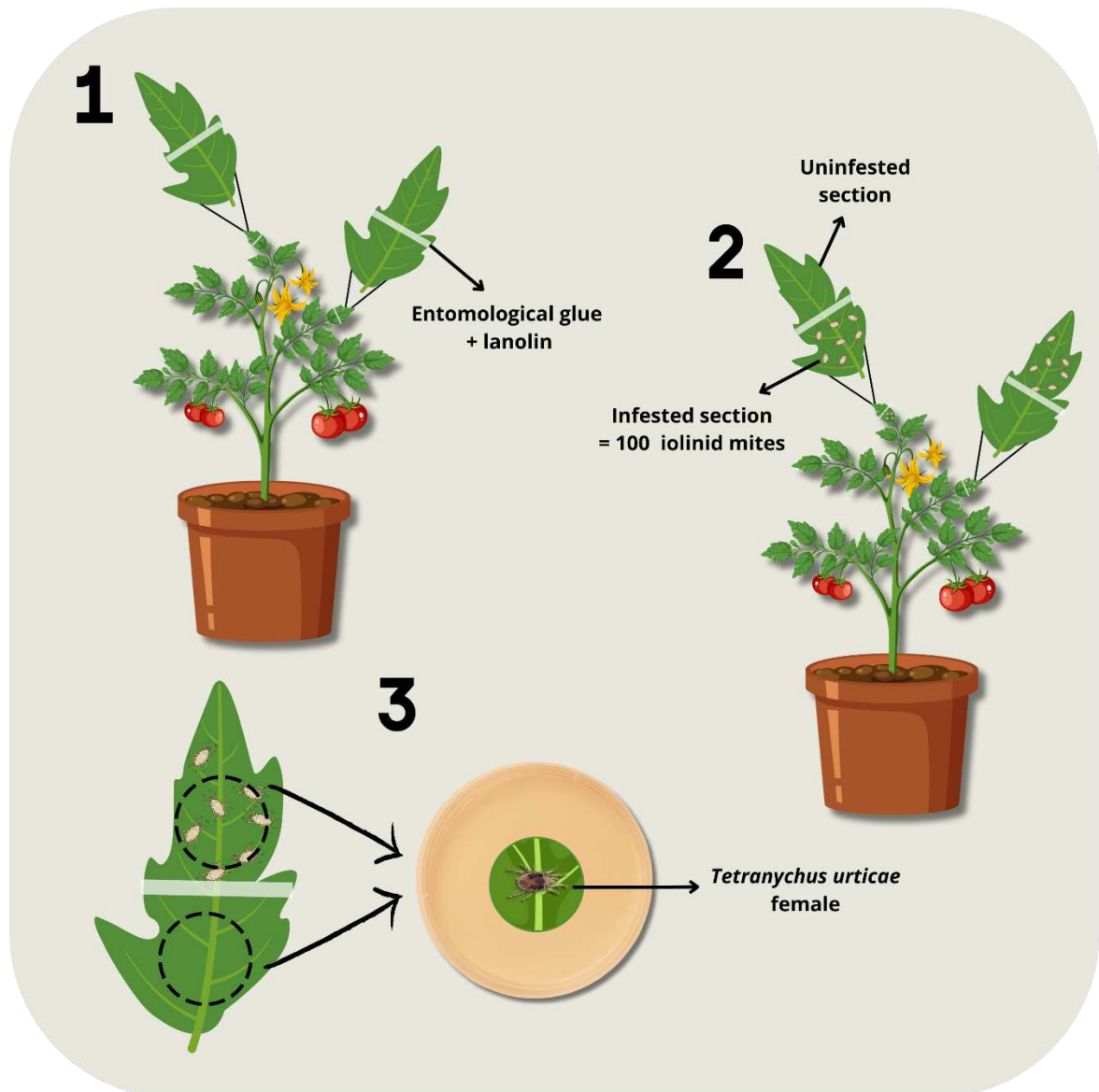
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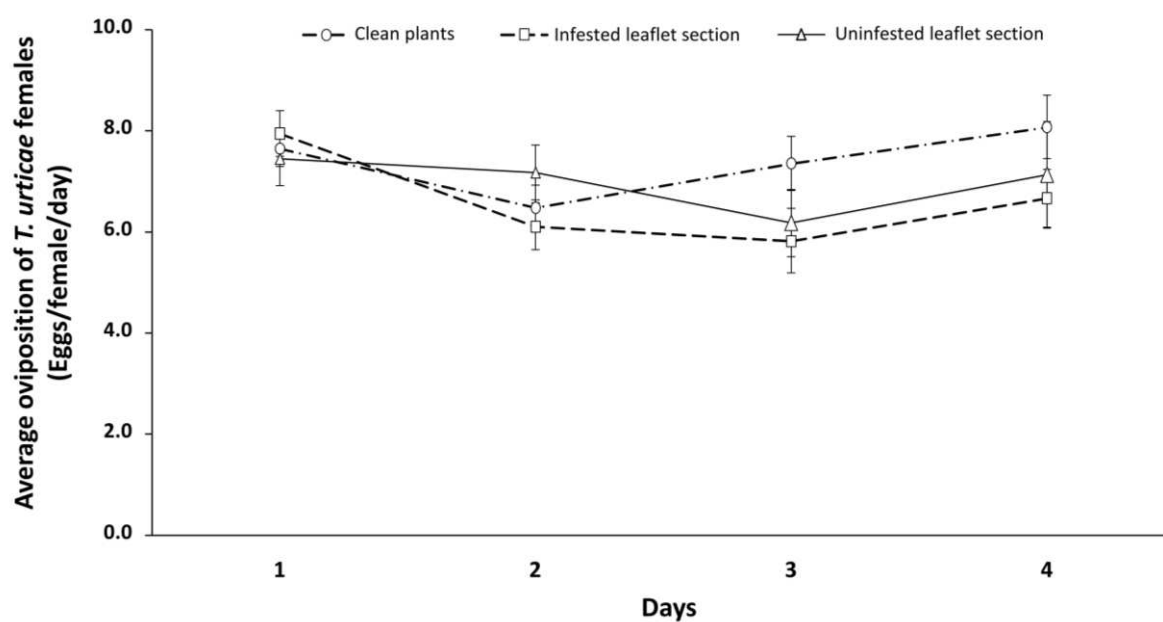
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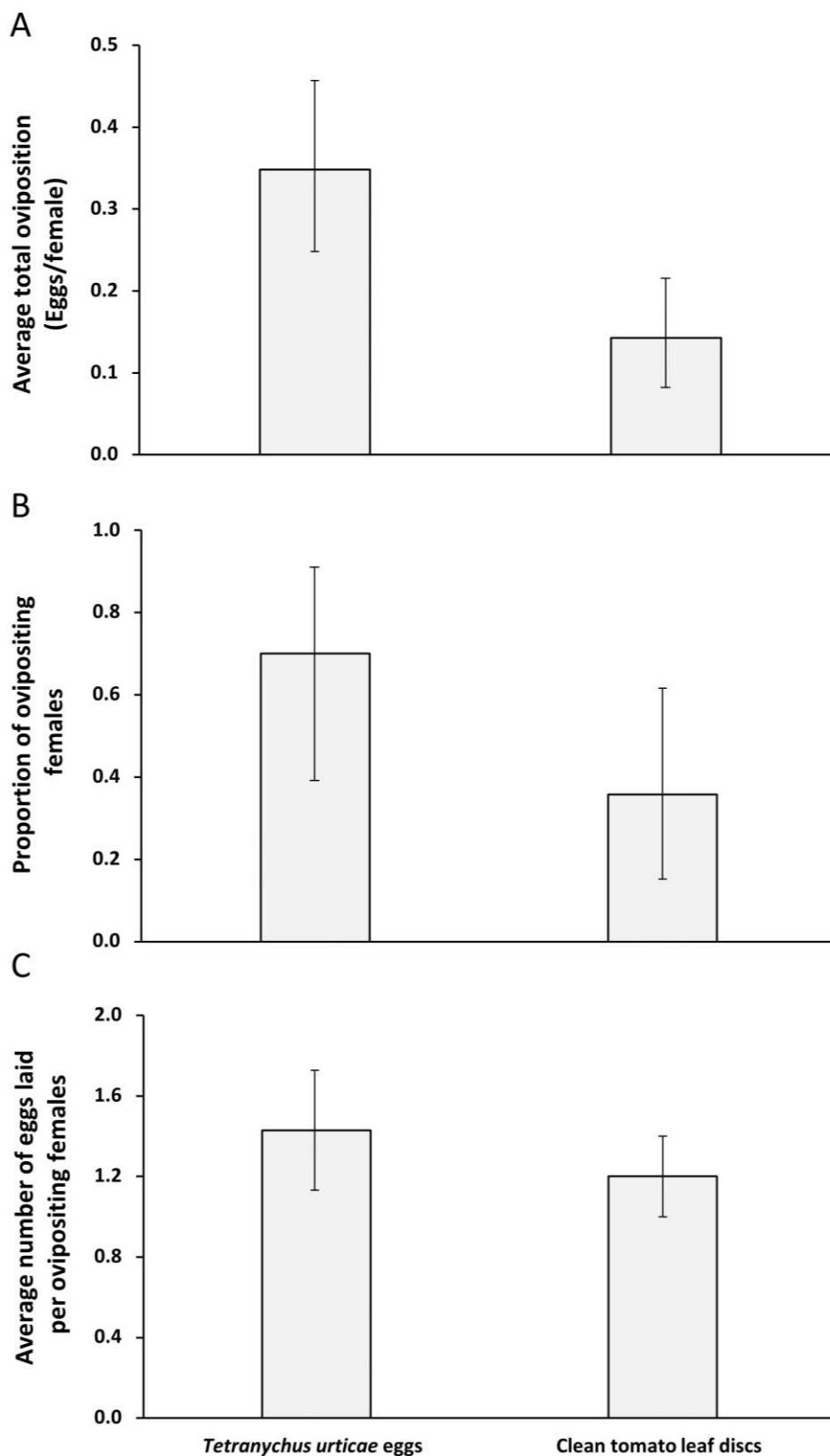
**Figure 1.** Set-up used in the test to assess the effect of plant feeding by cf. *Homeopronematus anconai* nov. sp. on oviposition by *Tetranychus urticae*. (1) Control plants without iolinid mites, (2) iolinid release scheme on leaflets, and (3) assembly of arenas to assess two-spotted spider mite oviposition.



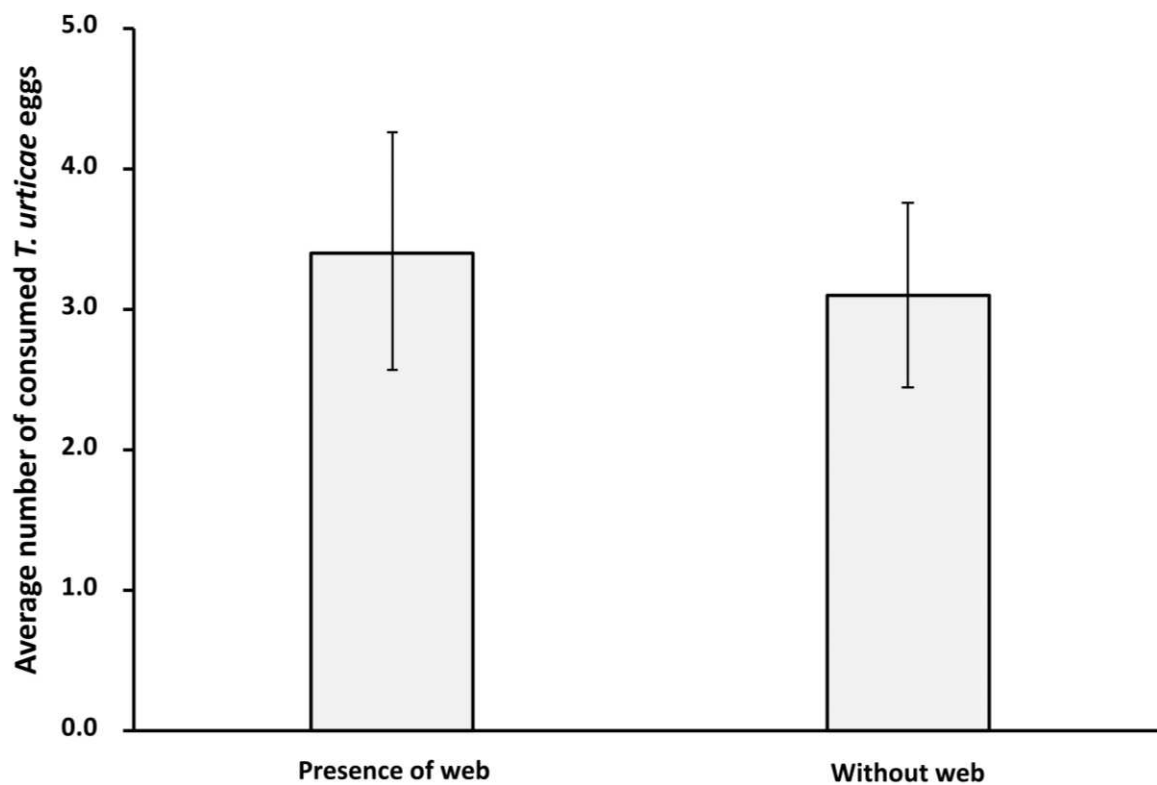
**Figure 2.** Oviposition rate ( $\pm$  SE) of *Tetranychus urticae* on discs pre-infested or not with the iolinid mite cf. *Homeopronematus anconai* nov. sp. after 4 days. Tomato leaflets were divided into two sections and predators released on only one (infested leaflet section). Clean plants did not receive mites on any leaflet. Oviposition rates did not differ significantly among treatments.



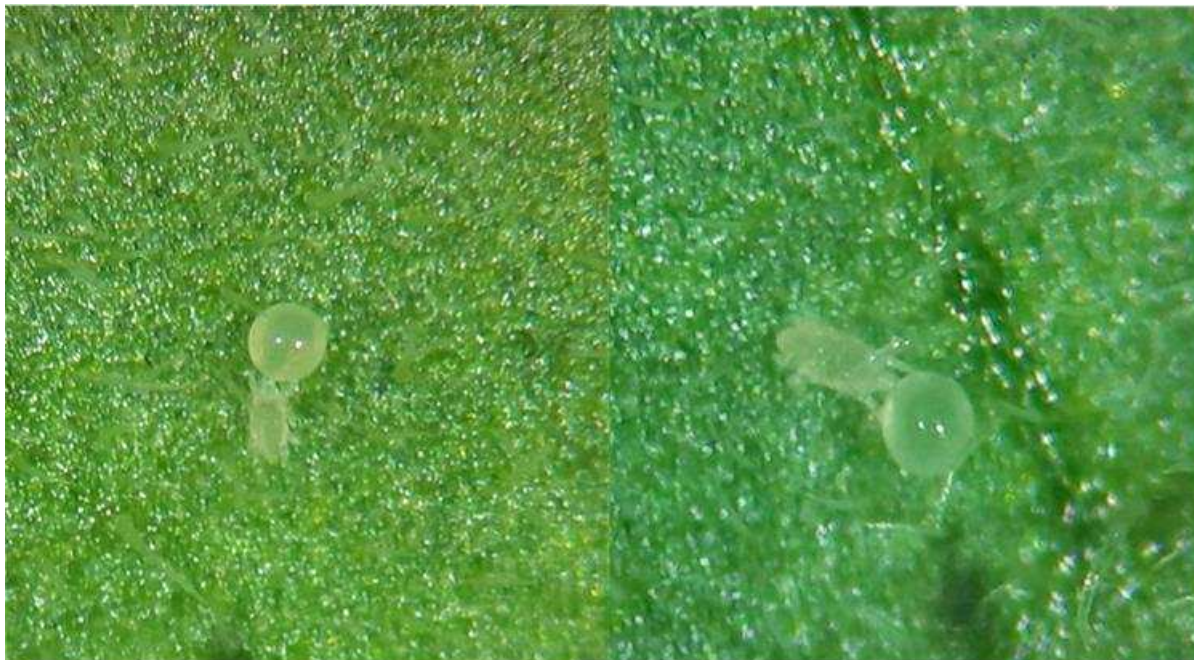
**Figure 3.** Average total oviposition ( $\pm$  SE) (A), proportion of ovipositing females ( $\pm$  CI) (B), and average number of eggs laid per ovipositing females ( $\pm$  SE) (C) of cf. *Homeopronematus anconai* nov. sp. fed with *Tetranychus urticae* eggs and clean tomato leaf discs. The proportion of ovipositing females (B) and the average number of eggs laid per ovipositing females (C) did not differ significantly between treatments.



**Figure 4.** Predation rate ( $\pm$  SE) of 18 iolinid mites on *Tetranychus urticae* eggs with and without the web produced by the two-spotted spider mite. The difference in egg consumption between the treatments was not significant.



**Figure 5.** Juveniles of the iolinid mite (225–280  $\mu\text{m}$ ) attempting to feed on *Tetranychus urticae* eggs.



## General Conclusion

In this dissertation I explored the potential of the iolinid, cf. *Homeopronematus anconai* nov. sp., in the biological management of pests on tomato plants. This predator has been demonstrated to effectively control tomato russet mites (*Aculops lycopersici*) and powdery mildew infections caused by *Oidium neolycopersici* L. on tomatoes (Marcossi et al., in prep.). However, the mechanism of control of powdery mildew is thus far unknown. I demonstrate that the mite feeds on fungal structures and is capable of developing, surviving and reproducing when feeding on it (Chapter 1). Conversely, the leaf-feeding habit of this predator appears to be obligatory but did not allow for development and reproduction.

Considering the phytophagy of cf. *H. anconai* nov. sp. in tomatoes, in Chapter 2, I investigated whether this could trigger defence responses in tomatoes and affect the reproduction of *Tetranychus urticae*. Despite phytophagous behaviour being common among iolinid mites (Flaherty and Hoy et al., 1971; Hessein and Perring, 1988; Krantz and Walter, 2009) and previous work suggesting potential defence inductions triggered by these predators on tomato plants (Van de Velde et al., 2021; Pijnakker et al., 2021), I did not observe a significant effect of its leaf-feeding habit on oviposition by the two-spotted spider mite, a species that is sensitive to tomato plant defences. I also quantified predation of two-spotted spider mite eggs by this iolinid, which was found to be low. Nevertheless, I suggest that, because of the high densities of the iolinids commonly found on tomato plants, it could still have a negative impact on spider mite densities on tomatoes.

In conclusion, this study presents promising findings regarding the use of this iolinid predatory mite in the biological management of pests in tomatoes. In addition to providing a better understanding of powdery mildew suppression in this crop, it also offers evidence that these predators can combat initial infestations of *T. urticae*.

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