Universität für Bodenkultur Wien

Master Thesis

Aggregation as an anti-predator response in the two-spotted spider mite *T. urticae*

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…dedicated with love and gratitude to my parents.

...meinen Eltern in Liebe und Dankbarkeit gewidmet.

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Contents

1 Introduction

The phytophagous two-spotted spider mite *Tetranychus urticae* is a ubiquitous plant pest with a significant economic impact in agriculture. The web spinning mite has an extremely broad host plant range of more than a thousand host plant species (Bolland et al. 1998; Migeon and Dorkeld 2006) and possesses the ability to develop resistances against pesticides very rapidly (Dermauw et al. 2012, Van Leeuwen et al. 2010). Therefore, biological control and integrated pest management of *T. urticae* become more and more important in diverse agricultural and horticultural crops, primarily by using predatory mites of the family Phytoseiidae as the prime natural enemies of spider mites (Nicetic et al. 2001; Rhodes et al. 2006; Skirvin & De Courcy Williams 1999).

The specialist predatory mite *Phytoseiulus persimilis* feeds exclusively on tetranychid spider mite prey and can deal very well with the dense webs of *T. urticae* (Shimoda et al. 2009). It is an effective predator and plays an important role in biological control of spider mites in greenhouse cultivations (Opit et al. 2004) and in the open field (Decou 1994). *Phytoseiulus persimilis* as a natural enemy is used in augmentative biocontrol in two ways to control *T. urticae*. In inoculative pest management, a relatively low number of natural enemies is released with the purpose of establishing a long-term pest control of the pest population, which is very effective in some cultivations to control *T. urticae* (e.g., Abad-Moyano et al. 2010; Opit et al. 2004). Inundative pest control is the release of a high number of predators to flood the crop infested by the pest population and to achieve an immediate short-term, but not necessarily persistent, pest control (Gacheri et al. 2015).

Phytoseiulus persimilis is usually a very efficacious biocontrol agent of tetranychid pests, but many biotic and abiotic factors like crop plant species, plant nutrition, temperature, humidity, formation of spider mite hotspots, use of pesticides and other factors can influence the efficacy of *P. persimilis* in pest management (Camps et al. 2014; Collings 1995; El-Laithy 1992, Oomen et al. 1991). All these factors may decisively influence the interaction between the predators and their prey and consequently the success of biological control. Predator-prey interactions do not necessarily always lead to death of prey. Predators may also exert non-lethal effects on prey morphology, physiology or behavior (Lima 1998). Prey species can react to their predators with special behaviors, so called anti-predator behaviors, to minimize or avoid predation and to increase their survival chances, respectively. These anti-predator behaviors are widespread in the animal kingdom and can have many different forms. For example, in *T. urticae* web spinning is an effective anti-predator behavior that works well as a protection against generalist predators, which are not able to deal with these dense webs (Lemos et al. 2010; Yano 2012). At the individual level, these behaviors may negatively affect the predator's killing rate, but, at the population level, may have positive effects on biological control, for example, by making the prey feeding less or leaving the host plant. To study the behavior of *Tetranychus urticae* and the interaction between predator and prey, respectively, can provide fundamental knowledge about this widespread plant pest. Behavioral studies are highly important for improvement and optimization of biological control.

Production of, and living inside, the webbing is an appropriate anti-predator strategy of *T. urticae* against generalist predators but not against specialized spider mite predators such as *P. persimilis*. Due to the shared co-evolutionary history, *P. persimilis* is morphologically and behaviorally well-adapted to move through the web of spider mites (Sabelis and Bakker 1992). While *T. urticae* is relatively defenseless against the specialist predatory mite *P. persimilis*, once the predators have detected it, the spider mites also evolved primary anti-predator behaviors to reduce the chance of detection by this predator. For example, it is known, that *T. urticae* is able to recognize the past or immediate presence of phytoseiid predators including *P. persimilis* because of the chemical traces left by the predators on the plant surface (e.g., Dicke and Grostal 2001). For example, the spider mites avoid plants or plant parts occupied by *P. persimilis* (Pallini et al. 1999; Grostal and Dicke 1999). In addition, they are able to assess the relative risk of predation when exposed to chemical cues of different generalist and specialist predatory mite species (Fernandez-Ferrari and Schausberger 2013; Hackl and Schausberger 2014).

My study is concerned with a specific type of anti-predator behavior of *T. urticae*, when it is exposed to chemical cues of the specialist predatory mite *P. persimilis*, namely aggregation. Modifying the level of aggregation is a typical form of anti-predator behavior observed in many group-living animals (Larsson 1986; Spieler 2003; Creel and Winnie 2005; Frommen et al. 2009) but has been scarcely studied in spider mites such as *T. urticae* (Yano 2012).

1.1 Anti-predator behavior

Predation has a strong influence on prey morphology, life history and/or behavior. In response to predation, prey organisms commonly evolve special behaviors to avoid or minimize predation risk (Beauchamp 2014; Lima and Dill 1990), which, accordingly, are then called anti-predator behaviors. Anti-predator behaviors comprise all the strategies of an organism aiming at preventing detection by predators, defending itself against predators or otherwise avoiding predation. Across animal taxa, prey evolved numerous diverse anti-predator strategies, reaching from habitat selection, especially in nesting behaviors, over increased vigilance for an early detection of the predator, to have a chance to escape from or avoid predators, as well as to active defense mechanisms that confuse or repel the predator (e.g., Beauchamp 2014).

1.1.1 Aggregation as an anti-predator behavior in group-living animals

Living in groups is a widespread phenomenon in both vertebrate and invertebrate animals. Group-living can have simple passive backgrounds, like spatially and/or temporally limited habitats, food resources or nesting sites, or be the result of mutual attraction (Krause and Ruxton 2002). Ultimately, group-living must yield net fitness benefits to individual group members to be evolutionary stable (Alexander 1974; Krause and Ruxton 2002; Earley and Dugatkin 2010). Ultimate reasons for group-living can be facilitation or enhancement of mate finding, labor division, food acquisition, thermal storage and/or protection against predators (Farabaugh et al. 1992; Gazda et al. 2005; Krause and Ruxton 2002). Enhanced anti-predator functions are considered an important driver of living in groups. Different strategies like cooperative defense (Farabaugh et al. 1992), increased vigilance of one or more group members (Jayakody et al. 2008), sometimes combined with alarm signals or alarm pheromones (Klump and Shalter 1984; Kunert 2005), or confusion of the predator (Krakauer 1995) have evolved. To aggregate with conspecifics can reduce the risk for an individual group member of being predated (Treisman 1975). Also for organisms that are unable repelling a predator actively or do not benefit from the increased vigilance in a group, living in aggregations can have the simple positive function of dilution (Turner and Pitcher 1986). The likelihood of being attacked is reduced in aggregations, as there are other individuals that could be the ones that are attacked instead. The individual risk of being attacked decreases with increasing group size. Another possibility is the avoidance or encounter effect, meaning that a single individual in an aggregation of conspecifics is less likely found than a single individual among an equal number of scattered individuals in the same area (Turner and Pitcher 1986). Due to Turner and Pitcher (1986) the combined effects of dilution and avoidance - called attack abatement – can reduce the risk of being captured by a predator.

1.1.2. Threat-sensitive anti-predator behavior

Anti-predator behaviors can be fixed, and thus similar under every circumstance, or can be risk dependent. Many animals perform different behaviors under low and high predation risks (Lima 1998). In addition to the benefits, which are mostly enhanced survival of the prey individuals themselves or their progeny, every anti-predator behavior also incurs costs. Energy is spent for enhanced motion, vigilance or defense, which otherwise could be used for food acquisition or reproduction (Liam and Dill 1990). For example, Monserrat et al. (2007) observed that females of the predatory mite *Neoseiulus cucumeris* are able to retain their eggs inside their body when they perceive the presence of the intraguild predator *Iphiseius degenerans*, which feeds on their juveniles. This led to lower oviposition rates in *N. cucumeris*. Persons et al. (2002) detected that the wolf spider *Pardosa* *milvina*, which is normally living on the soil surface, changes its location in presence of silk and excreta of another, larger wolf spider species, *Hogna helluo*, which frequently preys on the smaller *P. malvina*. The small wolf spider uses vertical structures, when exposed to *H. helluo* cues, and benefits of higher survival rates, when the predator is present. However, this anti-predator behavior implies high costs as well. Persons et al. (2002) found out, that *P. milvina* capture less prey in presence of cues of *H. helluo*, they lose body weight and their egg sacs contain fewer eggs than in the control group without *H. helluo* cues and in the treatment with cues of conspecifics of *P. milvina*.

Therefore, due to the inherent costs of any anti-predator behavior, prey are expected to be able to evaluate the level of predation risk upon perceiving visual, auditory, tactile and/or chemical cues, indicating the presence of predators and the associated predation risks. Anti-predator behaviors adjusted in type or intensity to the level of predation risk are called threat-sensitive behaviors (Sih 1982; Helfman 1989; Ferrari and Douglas 2009). Threat-sensitive anti-predator behaviors were also observed in *T. urticae* by Grostal and Dicke (2000), Skaloudova et al. (2002) and Fernandez-Ferrari and Schausberger (2013). Fernandez-Ferrari and Schausberger (2013) tested the threat-sensitive behavior of *T. urticae* in presence of cues of three different predatory mites, differing in the risk posed to the spider mites, in two spatial contexts. They found out, that, in presence of predatory mite cues on the leaf discs, the *T. urticae* females spent more time moving than on leaf discs without predator cues. On leaf discs with cues of *P. persimilis* they laid their first egg later than in presence of cues of the generalist predatory mites *Amblyseuis andersoni* and *Neoseiulus californicus* and on leaves without predator cues. Furthermore, the total number of eggs laid within 24 h was lower in presence of *P. persimilis* and *A. andersoni* cues than on the leaf discs without predator cues and with *N. californicus* cues, respectively. In a choice test, the spider mites avoided leaf discs with predatory mite cues but in an artificial area they preferred the site with predatory mite cues. Fernandez-Ferrari and Schausberger (2013) concluded that, in an artificial area, the predatory mite cues may indicate cues for the spider mites guiding them to a possible host plant. Grostal and Dicke (2000) considered the responses of spider mites to nine different mite species, which were either predators of spider mites or predators/parasites of other animals or fungivores and pollen feeders. They detected that the spider mites avoided leaves with cues of predators and parasites and the cues of one pollen-feeding predatory mite that can also feed on spider mites. The cues of fungivorous and other pollen-feeding mite species had no influence on the spider mite behavior. Spider mites are able to distinguish between cues of different predatory mite species and adapt their behavior to the possible predation risk. Skaloudova et al. (2006) observed that in presence of caged *P. persimilis* or *P. persimilis* cues, the spider mites had an increased activity level and their fecundity decreased under predation risk. To account for threat sensitivity of the spider mites, in my study the spider mites were experimentally exposed to different predation risk levels, posed by the predatory mite *P. persimilis*.

1.2 Study organisms

1.2.1 *Tetranychus urticae*

1.2.1.1 Taxonomy

Table 1: Taxonomy of the spider mite *Tetranychus urticae* (Helle and Sabelis 1985a)

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	Arachnida
Subclass:	Acari
Order:	Trombidiformes
Family:	Tetranychidae
Genus:	*Tetranychus*
Species:	*Tetranychus urticae* C. L. Koch 1836

Figure 1.1: Left: *Tetranychus urticae* females, juveniles and egg. Right: adult *T. urticae* female. © www.agrobestgrup.com

1.2.1.2 Life history and pest status

The two-spotted spider mite *Tetranychus urticae* is a globally distributed plant pest feeding on more than a thousand host plant species and causing significant economic losses in many agricultural and horticultural crops (Bolland et al. 1998; Migeon and Dorkeld 2006).

The pattern of leaf damage caused by spider mites is visibly starting as small whitish yellow dots, which then merge to larger yellowish patches on the leaf surface. These necrotic areas are caused by the spider mites sitting on the underside of leaves, piercing the leaf surface and extracting the nutritious cell contents from the parenchyma tissue. Sucking by the spider mites leads to a reduction in photosynthesis rates as well as water loss, which may finally result in the death of the host plant (Helle and Sabelis 1985a).

The spider mite *Tetranychus urticae* reproduces via male-producing parthenogenesis (arrhenotoky). Unfertilized eggs become haploid males, fertilized eggs become diploid females. The temperature preference of *T. urticae* is between 13 and 35°C. The developmental time from egg to adult depends on temperature, humidity and host plant species and nutrition and takes about eight days at an average temperature of 21°C. At 25 °C, a female lays up to ten eggs per day and on average about 200 in her life (Helle and Sabelis 1985a).

The developmental stages of the spider mites are egg, larva, protonymph, deutonymph and adult. In between the larval and nymphal stages there are periods of quiescence for growing and molting, called chrysalis: the larval stage is followed by the protochrysalis, the protonymphal stage is followed by the deutochrysalis and between deutonymph and adult the phase of inactivity is called teliochrysalis (Helle and Sabelis 1985a).

1.2.1.3 Group-living

The small spider mites (about 0.5 mm body length of adult females) are group-living organisms and form colonies consisting of a few to thousands of individuals on their host plants. They have silk producing glands in their palps and constantly spin silk threads whenever they walk (Saito 1977). These webs have great importance for the protection against natural enemies, for regulating the local micro-climatic conditions on the leaf surface and for protection against wind, rain, dust and other environmental hazards (Helle and Sabelis 1985a; Sabelis and Bakker 1992; Yano 2012). Additionally, the webs fulfill a role in intraspecific communication of the spider mites such as mate finding and dispersal to new host plants. Spider mites are able to perceive non-volatile chemical cues of conspecifics in feces and in the silk (Clotuche et al. 2014; Yano 2008). The silk has also a function in strain recognition. In a choice test, Clotuche et al. (2012) found out, that the spider mite females prefer the silk trails laid by related individuals that belong to their own strain and discriminate against silk trails of genetically more distantly related individuals of another strain. As group-living organisms, *T. urticae* also follow the silk trails produced by their conspecifics. The silk threads may lead them to their colony, to food sources or to new host plants. However, silk trails lose their attractiveness for the mites after approximately ten days. Fresh trails of multiple mites appear more attractive to followers than trails of single mites (Yano 2008; Astudillo-Fernandez et al. 2012b). Le Goff et al. (2012) observed that trail following depends on the satiation state. Satiated spider mites are attracted to the silk of conspecifics, while starved mites are not. They concluded that starved mites avoid overcrowded areas to find new feeding sites. Spider mites have several options to disperse to new host plants. They may disperse from one plant to another by walking, phoresy (Helle and Sabelis 1985a) and passive aerial dispersal, which is called ballooning (Bell et al. 2005). Ballooning is the collective forming of a silk ball at the tip of the leaves and dispersing passively within the silk ball using the wind (Clotuche et al. 2011). Triggers for such dispersal behavior are, among others, mite density and plant desiccation. Clotuche et al. (2011) found out that the inner layers of a silk ball consist of dead mites, trapped by silk and dying in the formation process, and the outer layers consist of living, mostly immature, mites. Forming of the silk ball starts after a certain amount of silk trails was laid to the tip of the plant and Clotuche et al. (2011) concluded that it could be a kind of recruitment process with trail-bound pheromones involved in the recruitment. Oku et al. (2005) observed that trail-bound pheromones guide the males of *Tetranychus kanzawai* to unmated females. Such pheromones could be involved in the collective dispersal processes as well. Spider mites could benefit of collective dispersal in silk balls because of Allee effects (Astudillo-Fernandez et al. 2012a). The group of mites founding a new colony, benefit of their conspecifics because of a faster population growth, denser webs on the new host plant and, as a consequence, a better protection against predators. Le Goff et al. (2010) found out that grouped females produced more webs per mite and more eggs per mite than single females; single females also suffered from a higher mortality rate. Altogether, living in groups largely has positive effects on the spider mites' life history parameters. The more mites, the denser the webs, the better is the protection against abiotic factors and generalist predators (Lemos et al. 2012; Yano 2012).

Figure 1.2: Damage caused by *Tetranychus urticae* on a bean leaf. © www.forestryimages.org

1.2.2 *Phytoseiulus persimilis*

1.2.2.1 Taxonomy

Table 2: Taxonomy of the predatory mite *Phytoseiulus persimilis* (McMurtry and Croft 1997)

Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	Arachnida
Subclass:	Acari
Superorder:	Parasitiformes
Order:	Mesostigmata
Family:	Phytoseiidae
Genus:	*Phytoseiulus*
Species:	*Phytoseiulus persimilis* Athias-Henriot 1957

Figure 1.3: *Phytoseiulus persimilis* female with eggs. © www.photo.net

1.2.2.2 Life history and status as natural enemy

Phytoseiulus persimilis is a predatory mite specialized on tetranychid spider mite prey and plays an important role in biological control of spider mites in diverse agro-ecosystems. It is similarly sized as the spider mites (about 0.5 mm body length as adult females), and has relatively high reproduction and prey consumption rates. At 30 °C, a young *P. persimilis* female produces up to five eggs per day. To produce one egg the female has to consume at least six eggs, 3.5 deutonymphs or one adult female of *T. urticae* (Helle and Sabelis, 1985b).

Phytoseiulus persimilis outlive their prey. At 25 °C, adult longevity averages about 36 days and a female can produce, on average, 3.7 eggs per day and 79 eggs throughout life. Like its prey *T. urticae,* the predatory mites also develop from egg through larva, protonymph, deutonymph to the adult mite. Different from the spider mites, they have no quiescence phases in between the nymphal stages. The developmental time of *P. persimilis* from egg to adult depends on temperature, humidity and food availability and takes about seven days at 25 °C and 60% relative humidity (Helle and Sabelis, 1985b).

Unlike spider mites, insemination has to occur for egg production. *Phytoseiulus persimilis* is pseudo-arrhenotokous, which means, that both males and females develop from fertilized eggs, but during development the males lose the paternal set of chromosomes and become haploid (Helle and Sabelis, 1985b).

Phytoseiulus persimilis is blind but light-sensitive and therefore not able to use visual cues for hunting and for orientating itself. It predominantly uses tactile and chemical cues for orientation and for locating its prey. For example, spider mite-infested plants emit volatiles (synomones) that attract *P. persimilis* and, accordingly, guide them to the habitat of its prey colonies (Sabelis and Dicke 1992). On the plant, the foraging predators orient themselves on kairomones emitted by the spider mites (Helle and Sabelis 1985b).

1.3 Study aims and objectives

Increasing the level of aggregation as an anti-predator behavior is a widespread phenomenon in the animal kingdom (Frommen et al. 2009; Forsman et al. 1998; Spieler 2003). For *T. urticae,* Yano (2012) suggested that more tightly aggregated spider mites benefit from the denser web but, the anti-predator function of aggregation itself, in absence of webbing, has not yet been scrutinized.

Accordingly, the first aim of my study was finding out if adult *T. urticae* females respond to predation risk posed by cues of *P. persimilis* with tighter aggregation and, if so, if their responses vary with the level of predation risk. The second aim was finding out if aggregated distribution of the spider mites indeed enhances their survival chances under immediate risk posed by living predatory mites, as compared to solitary sitting spider mites.

2 Materials and methods

Two experiments were conducted in the laboratory to investigate (1) the aggregation level of spider mites *Tetranychus urticae* in response to cues of the predatory mite *Phytoseiulus persimilis,* and (2) the survival chances of aggregated spider mites, as compared to those being solitary, in physical presence of a predatory mite female. In both experiments, common bean plants *Phaseolus vulgaris,* two-spotted spider mites *Tetranychus urticae* and predatory mites *Phytoseiulus persimilis* were used. All rearing and experimental units were stored in climate chambers at 25 ± 1 °C, 60 ± 5 % RH and 16:8 h L:D.

2.1 Rearing of bean plants, spider mites and predatory mites

2.1.1 Rearing of bean plants

Common bean plants *Phaseolus vulgaris* were reared in a walk-in climate chamber (25 ± 2°C, 60 ± 10 % relative humidity, and a photoperiod of 16:8 h L:D). The plants were grown in a substrate mixture containing 75% soil and 25% expanded clay. For the experiments clean trifoliate leaves were used.

2.1.2 Rearing of spider mites

Two-spotted spider mites *Tetranychus urticae* were reared on whole bean plants (*P. vulgaris*) under room conditions (23 ± 2°C, 60 ± 10% relative humidity and 16:8 h L:D). Infested plants were kept in a separate room from the clean plants that were used for the experiments.

2.1.3 Rearing of predatory mites

The laboratory population of the predatory mite *Phytoseiulus persimilis*, originally founded by specimens collected in Oregon, USA, was reared on a detached bean leaf arena and fed *T. urticae*. The detached leaf arena consisted of a leaf on a water-saturated foam cube (15 x 15 x 4 cm), covered with filter paper, placed into a plastic box (20 x 20 x 5 cm), half-filled with tap water. A primary leaf of *P. vulgaris* was placed upside down onto the filter paper and the edges of the leaf were covered with moist tissue to function as a barrier for the mites (Fig. 2.1). The plastic box was again placed into a larger plastic box (45 x 34 x 9 cm), half-filled with tap water and a drop of dishwashing detergent was added to reduce the surface tension and prevent the mites from escaping. Every second to third day the predatory mites were fed with spider mites *T. urticae* from the stock population, which were brushed off infested leaves onto the rearing arena.

Figure 2.1: Detached leaf arena used for rearing the predatory mite *P. persimilis.*

2.2 Experiment 1: Aggregation of spider mites

In the first experiment, the aggregation level of adult females of the spider mite *T. urticae* and the placement of their eggs in dependence of predator cues left by *P. persimilis* on the leaf surface were examined. The predator cues represented three different risk levels, described in detail in 2.2.2.

2.2.1 Experimental setup

Aggregation of the spider mites was assessed using standardized circular bean leaf discs as experimental arenas. Leaf discs (Ø 2.2 cm) were punched out of trifoliate bean leaves (Fig. 2.2). To create standardized leaf discs, the leaf vein had to be in the middle of the disc. The leaf discs were placed upside down onto foam cuboids inside cylindrical compartments of plastic cartridges (Fig. 2.3). Each plastic cartridge (12.5 x 8 x 2 cm) contained six cylindrical compartments (Ø 3.5cm, 2 cm high). Foam cuboids of about 2 x 2 x 1.5 cm were singly fixed to the bottom of each compartment with petroleum jelly (Fig. 2.4) and the compartments were filled with tap water up to the upper edge of the foam cuboids. Thus, the leaf discs were completely surrounded by water creating a barrier for the mites.

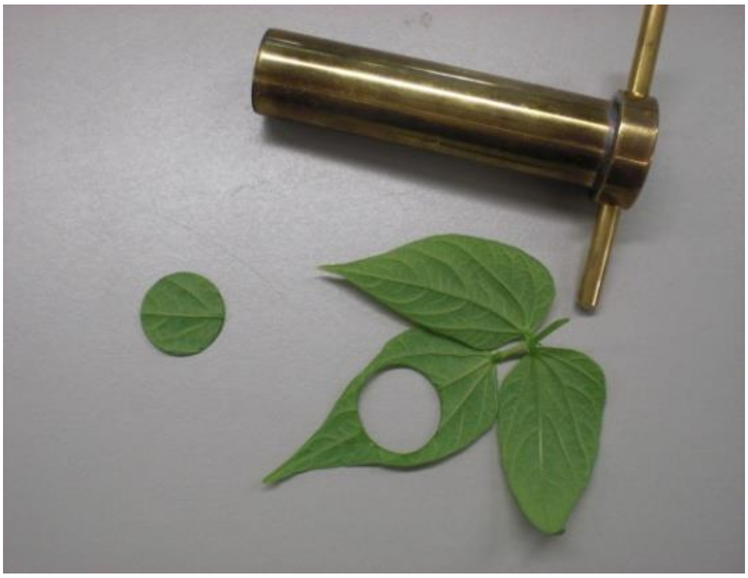

Figure 2.2: Leaf disc punched out from a trifoliate bean leaf, *P. vulgaris.*

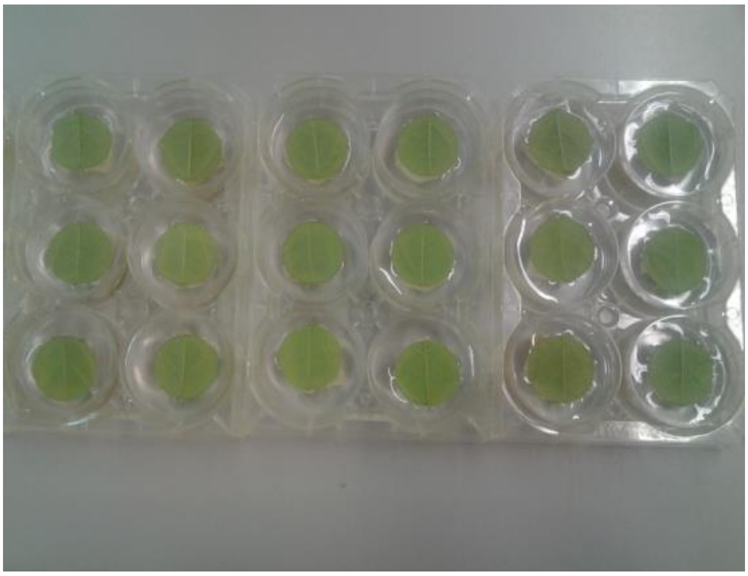

Figure 2.3: Standardized circular bean leaf discs on top of foam cuboids surrounded by water inside cylindrical compartments in plastic cartridges.

Figure 2.4: Foam cuboids fixed with petroleum jelly in cylindrical compartments inside plastic cartridges.

2.2.2. Pre-experimental procedure

To prepare the leaf discs for the experiment, each leaf disc either received one well-fed gravid female of *P. persimilis*, transferred from the rearing arena by using a fine moistened brush, or left without a predator. After 15 h, the predatory mite females were again removed from the leaf discs. The females did not receive prey on the leaf discs but left traces (metabolic waste products, possibly chemical footprints and eggs) on the discs, all of which are indicators of predator presence for the spider mites (Pallini et al. 1999; Grostal & Dicke 2000; Fernandez-Ferrari & Schausberger 2013). Four different types of leaf discs, differing in the level of predation risk, were prepared: (1) discs with predator traces and five predatory mite eggs, representing high predation risk (PP traces + 5 eggs), (2) discs with predator traces and two predatory mite eggs, representing medium predation risk (PP traces + 2 eggs), (3) discs with predators traces but without eggs, representing low risk (PP traces), and (4) discs without any predatory mite cues, representing no risk and serving as a control group (control). For treatment (1), some eggs had to be added manually because the females did not produce that many eggs during 15 h. For treatments (1), (2) and (3), only those leaf discs that still had a predatory mite female on it after 15 h were kept for the experiment. The cartridges were stored in a climate chamber at 20 ± 1°C, 60 ± 5 % relative humidity and 16:8 h L:D until use in experiments.

2.2.3 Experimental procedure

Five adult spider mite females, randomly withdrawn from the stock population, were transferred onto each leaf disc. The spider mites were observed every 30 min for 3.5 h in total, and then again after 24 h. At each observation, the position and activity (moving/stationary) of the spider mites were recorded. The position of the mites was marked on paper sketches of the leaf discs and their inter-individual distances measured after the experiment. After 3.5 and 24 h also the total number of eggs and the position of the laid eggs were recorded. Spider mite females that had left the leaf disc during the experiment were replaced by new females or, if still alive, rescued from the water and returned onto the leaf disc. Leaf discs that harbored only one spider mite female after 24 h were excluded from the experiment.

2.3 Experiment 2: Survival chances in dependence of aggregation

In the second experiment, the detectability and survival chances of fixed aggregated and fixed solitary spider mites in presence of a gravid predatory mite female *P. persimilis* was examined. Two treatments were compared: (1) four solitary spider mite females on each leaf disc, and (2) four spider mite females in a group on each leaf disc. To assess detectability and survival chances of the spider mites, one gravid predatory mite female was released onto each disc and the time of the first encounter with the spider mites and the time of the first successful attack on the spider mites were recorded.

2.3.1 Experimental setup

The basic experimental setup was the same as in the first experiment, i.e. circular bean leaf discs (Ø 2.2 cm) floating on top of foam cuboids inside cylindrical compartments (Ø 3.5 cm, 2 cm high) filled with tap water. Four adult spider mite females, randomly taken from the stock population, were fixed with a drop of petroleum jelly onto each leaf disc. The petroleum jelly was applied to the bean leaf using the tip of a dissection needle. The mites stayed alive after fixation. Two different treatments were prepared: (1) four solitarily placed spider mite females, each of them fixed in the middle of one quarter of the leaf, halfway between the edge and the middle of the leaf disc (Fig 2.5a); (2) the second treatment consisted of a group of four spider mite females, aggregated at a mutual pairwise distance of 1 mm; the group of spider mites was fixed in one quarter of the leaf disc, halfway between the edge of the leaf disc and the middle of the leaf disc (Fig. 2.5b).

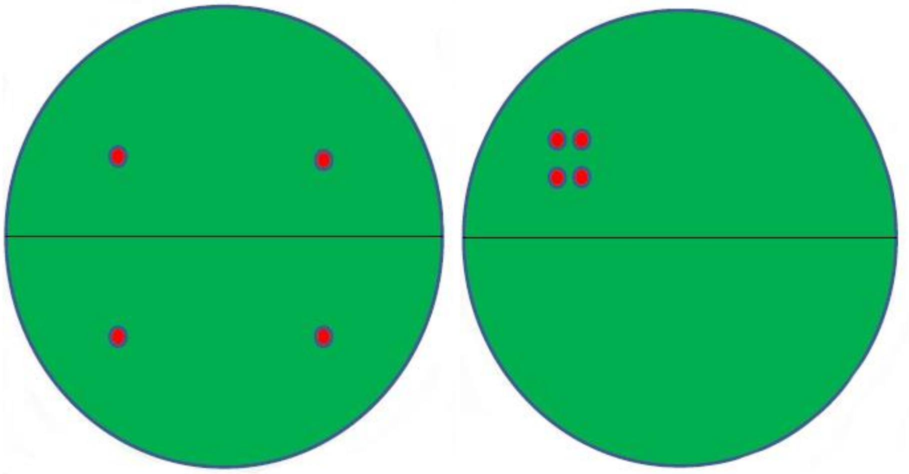

Figure 2.5: Distribution pattern of four spider mite females, either solitary (a) or aggregated (b), fixed with petroleum jelly on circular bean leaf discs.

2.3.2 Pre-experimental preparation of the predatory mite female

Gravid predatory mite females of *P. persimilis*, to be used in the experiment, were singly placed for 15 to 18 h before the experiment took place into acrylic cages without prey for starvation. Each cage consisted of an acrylic plate of 8 x 3.5 x 0.3 cm, with a cylindrical circular chamber (Ø 1.5 cm, 0.3 cm high) drilled into the plate. On one side the chambers were closed with gauze, the upper sides were closed with a microscope slide fixed with rubber bands (Fig. 2.6; Schausberger 1997). Each *P. persimilis* female was transferred with a fine moistened brush into the chambers. To prevent dehydration of the mites, the acrylic cages were stored on top of a grid fixed above tap water inside a plastic box (25 x 16.5 x 5 cm). These boxes were kept in a climate chamber at 20 ± 1°C, 60 ± 5 % relative humidity and 16:8 h L:D.

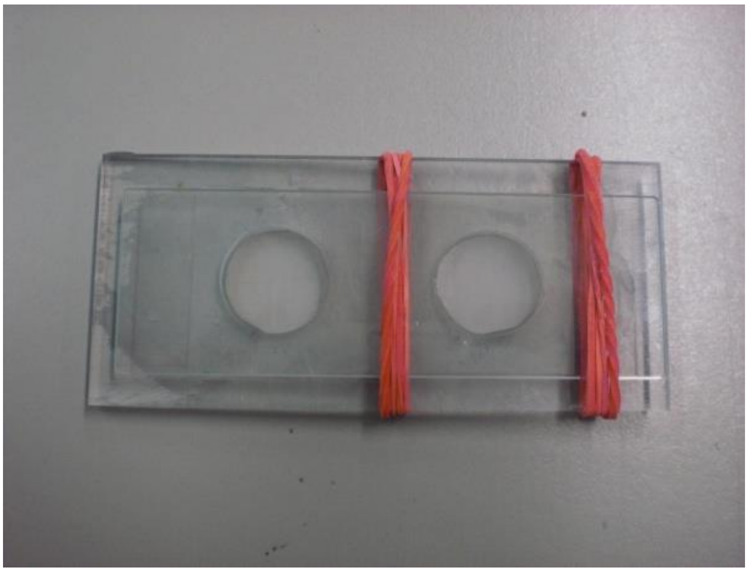

Figure 2.6: Acrylic cage (Schausberger 1997) used to starve gravid females of the predatory mite *Phytoseiulus persimilis* before use in experiment 2.

2.3.3 Experimental procedure

To start the experiment, one starved gravid female of *P. persimilis* was transferred onto each leaf disc using a fine moistened brush. After releasing the predator female, the time of the first encounter of the predator and the spider mites, the time of the first attack on a spider mite and the activity of the predator females was recorded for three h in total, every 10 min during the 1st h and every 20 min during the 2nd and 3rd h.

2.4 Statistical analyses

IBM® SPSS® Statistics Version 21 (IBM Corp., USA) was used to analyze the results of the two experiments.

In experiment 1 (aggregation experiment), I used generalized estimating equations (GEE; normal distribution, identity link) to compare the mean inter-individual distances between the stationary spider mite females among the four treatments over time (used as auto-correlated inner subject). The inter-individual distances were multiplied by a correction factor depending on the number of spider mite females present on the leaf disc at each point of observation. The correction factor for five present females was 1, for four present females 0.89, for three present females 0.77 and for two present females 0.62. The correction factor was calculated from the virtual area available to each individual on the leaf disc (radius of 11 mm). Assuming a virtual circle around each individual the radii of the individual circles were related to each other in dependence of the number of individuals on the disc.

The aggregation level of the eggs after 3.5 and 24 h was analyzed by a generalized linear model (GLM; binomial distribution, counts of events, log link). The egg aggregation level was estimated by an egg aggregation index. To estimate the egg aggregation index, the leaf disc was divided by a virtual raster into 16 sectors and the number of sectors harboring at least one egg was determined (Fig. 2.7).

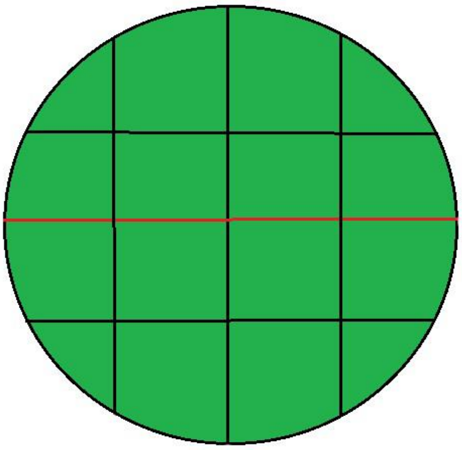

Figure 2.7: Virtual raster on the leaf disc to estimate the egg aggregation level (in red: main leaf vein).

In experiment 2 (survival experiment), cox hazard regression was used to compare the first encounter time and the first attack time between the two treatments, solitary and grouped spider mites. A generalized linear model (GLM, Poisson distribution) was used to analyze the number of killed spider mites during the experimental period of 3 h.

3 Results

3.1 Experiment 1: Aggregation of spider mites

3.1.1 Distance between spider mite females

Both with and without data correction, the aggregation of the spider mites was significantly affected by predatory mite cues on the bean leaf discs. Without data correction, the *T. urticae* females were aggregated more tightly in presence than absence of *P. persimilis* cues (GEE: Wald $\chi_3^2 = 14.546$, P = 0.02), no matter of the type of cues present and the associated level of predation risk (table 3.1, fig. 3.1). The different risk levels of the treatments with *P. persimilis* cues did not differ among each other (table 3.1). Additionally, development of the spider mite aggregation levels varied differently over time in dependence of treatment (Wald $\chi_{28}^2 = 50.046$, P = 0.006). The aggregation level of the females in the control group did not change much over time. Predator traces alone strongly affected spider mite aggregation within the first 2 h, after 2.5 h the females became less aggregated. Spider mite aggregation developed similarly in the two other predator risk treatments. The spider mite females in the treatments with *P. persimilis* traces plus 2 eggs and *P. persimilis* traces plus 5 eggs were the most strongly aggregated after 0.5 h. After 1 h, the distances between the females increased, whereas after 3.5 h they decreased again (Fig. 3.1).

Table 3: Results of least significant difference (LSD) tests, following GEE, on the pairwise comparisons of the mean distances between females over time between the treatments with and without (control) *Phytoseiulus persimilis* (PP) cues, and with and without data adjustment.

Treatment	**Pairwise comparison**	**P level** (without data adjustment)	**P level** (after data adjustment)
Control	PP traces	<0.001	<0.001
	PP traces + 2 eggs	0.026	0.015
	PP traces + 5 eggs	0.003	0.001
PP traces	Control	<0.001	<0.001
	PP traces + 2 eggs	0.174	0.206
	PP traces + 5 eggs	0.331	0.394
PP traces + 2 eggs	Control	0.026	0.015
	PP traces	0.174	0.206
	PP traces + 5 eggs	0.609	0.597
PP traces + 5 eggs	Control	0.003	0.001
	PP traces	0.331	0.394
	PP traces + 2 eggs	0.609	0.597

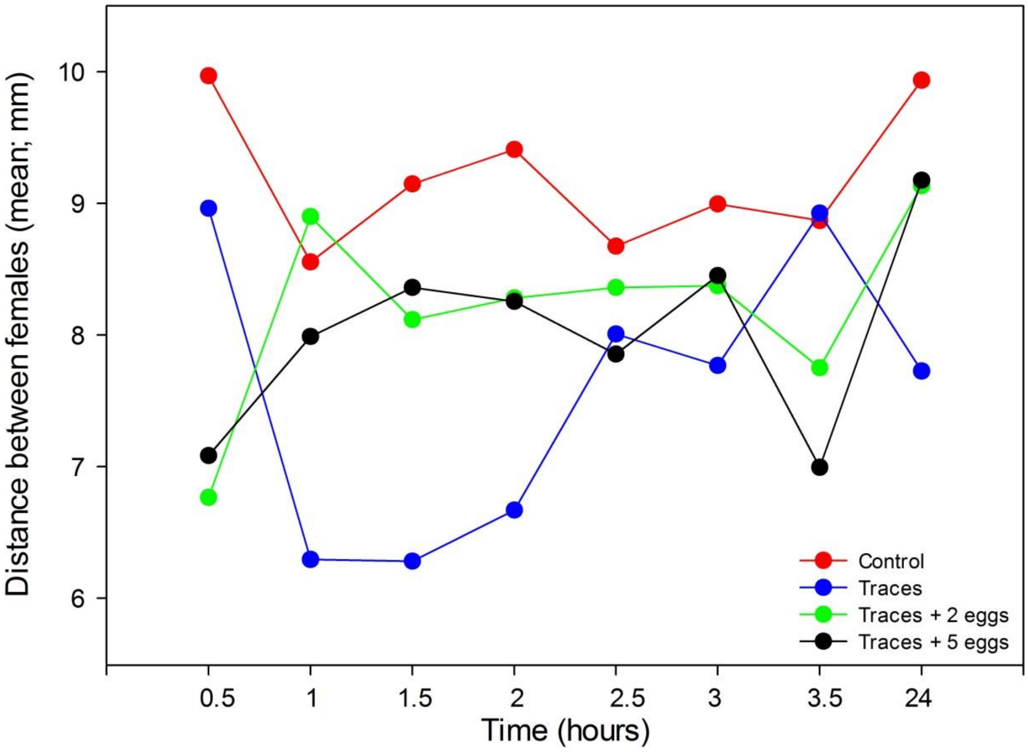

Figure 3.1: Distance of spider mite females over time without data correction.

After data correction, GEE showed an even clearer difference between treatments without (control) and with *P. persimilis* cues (Wald $\chi_3^2 = 17.368$, P = 0.001). As in the analysis without data adjustment, the spider mite females on the leaf discs with predatory mite cues were aggregated more tightly than the spider mite females on the leaf discs without predator cues (Fig. 3.2). In contrast to the analysis without data adjustment, development of the spider mite aggregation levels did not vary differently over time in dependence of treatment (Wald $\chi_{28}^2 = 37.406$, P = 0.11).

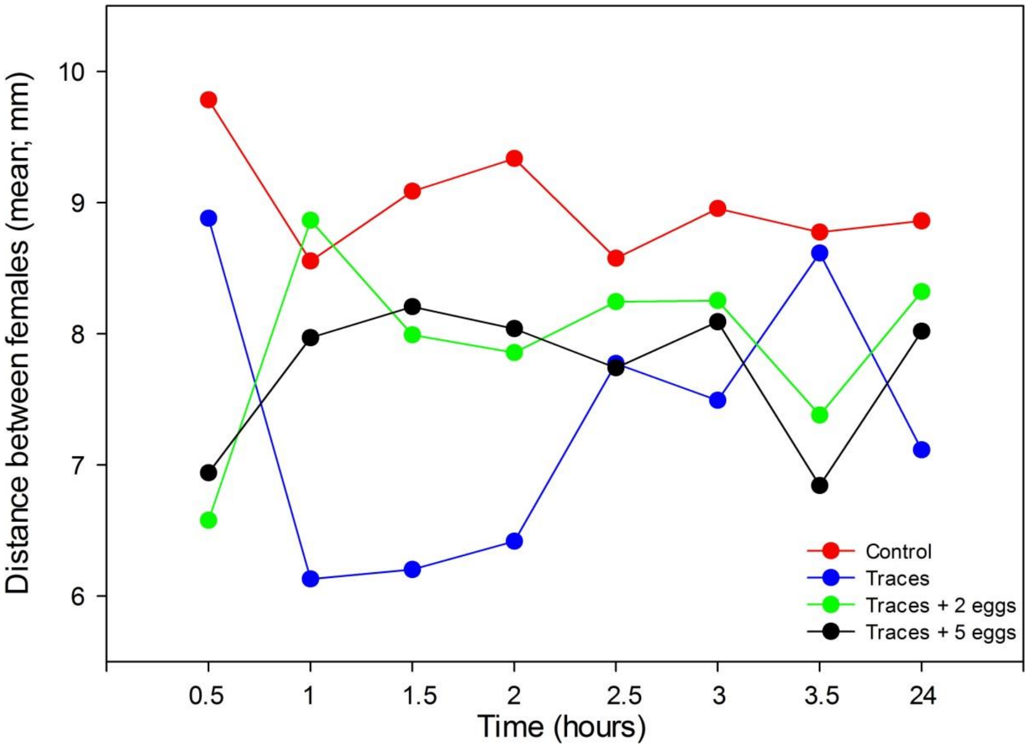

Figure 3.2: Distance of spider mite females over time after data correction.

3.1.2 Activity

The activity of the spider mite females was affected by the presence of predatory mite cues (GEE: Wald $\chi_3^2 = 39.02$, $P < 0.001$) and developed also differently among treatments over time (Wald $\chi_{28}^2 = 387.12$, $P < 0.001$). The *T. urticae* females were more active in presence than absence of *P. persimilis* cues, no matter of the type of cues. Pairwise comparisons revealed that the control treatment differed from all predatory mite cue treatments ($P < 0.001$), whereas the latter three treatments did not differ among each other ($P > 0.22$ for each pairwise comparison). Except after 24 h, the females were much more active in the treatments with predatory mite cues than in the control treatment. After 1 h (*P. persimilis* traces and *P. persimilis* traces plus 5 eggs) and 1.5 h (*P. persimilis* traces plus 2 eggs), respectively, the spider mites gradually reduced their activity (Fig. 3.3).

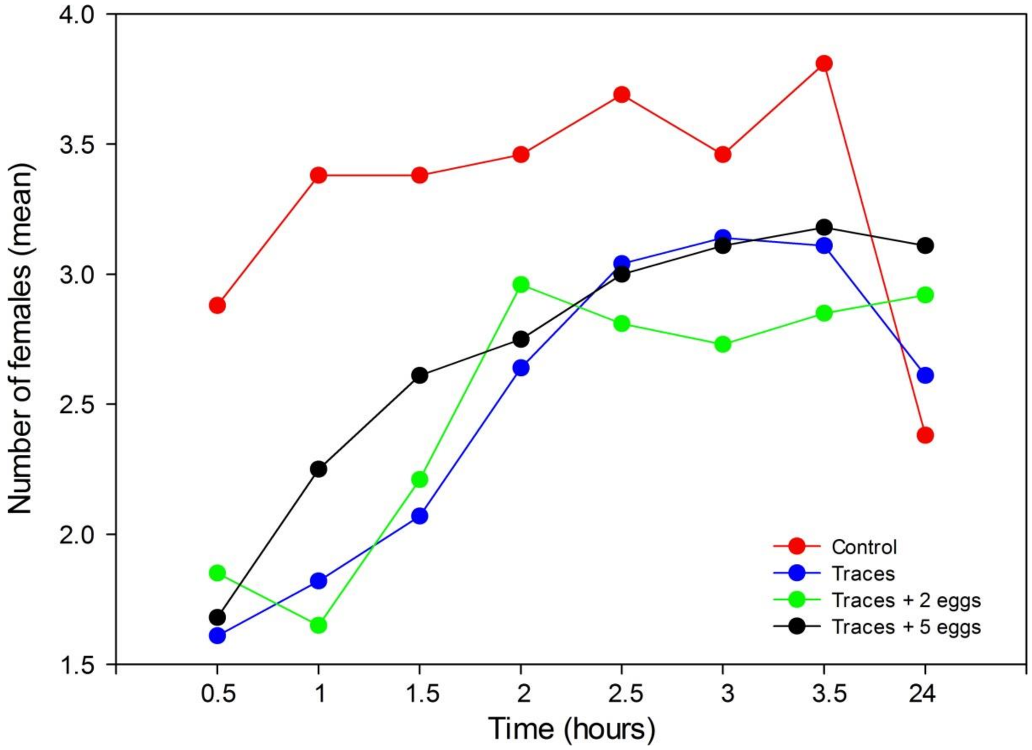

Figure 3.3: Number of stationary females out of all present females over time.

3.1.3 Presence of spider mite females

Albeit slightly lower in treatments with predatory mite cues, the presence of *T. urticae* females on the leaf discs was not significantly affected by presence/absence of predatory mite cues (GEE: Wald χ_3^2 = 5.084, P = 0.166) but varied significantly over time (Wald χ_3^2 = 88.359, P < 0.001). The presence of females of all four treatments was constantly high until 3.5 h but decreased strongly after 24 h (Fig. 3.4).

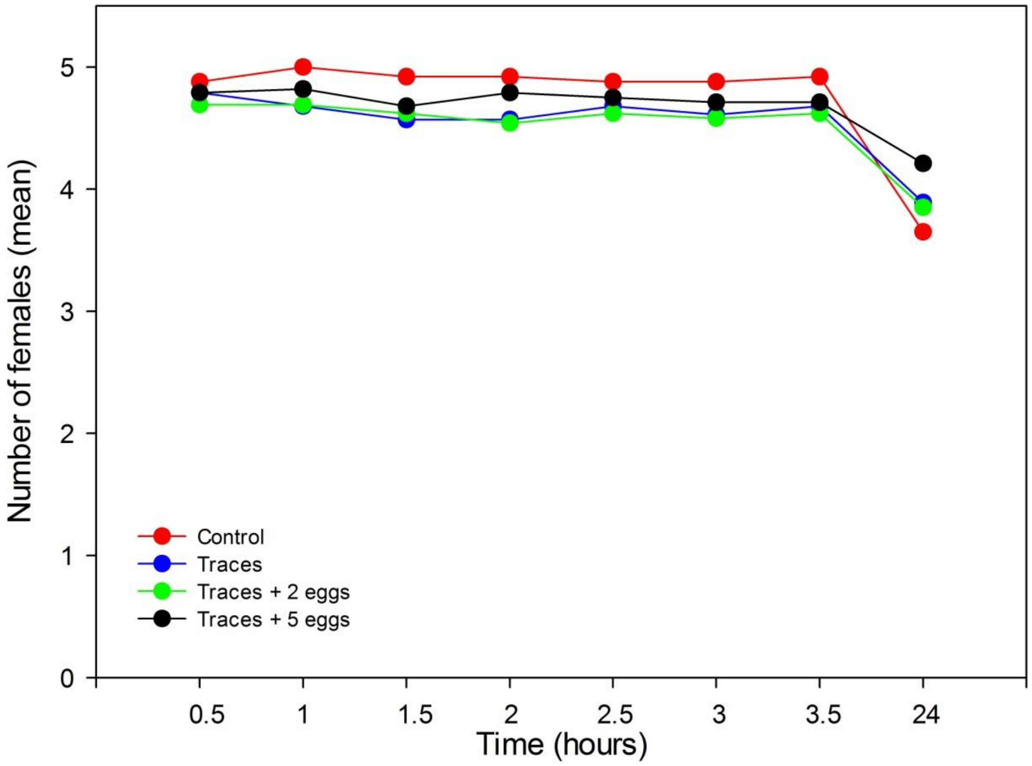

Figure 3.4: Presence of spider mite females over time on leaf discs with and without predatory mite traces and eggs.

3.1.4 Number of eggs per female after 3.5 and 24 h

The number of eggs produced by each spider mite female within 3.5 and 24 h was slightly, but not statistically significant, higher in the control treatment than in treatments with predatory mite cues (GLM: 3.5 h: Wald $\chi_3^2 = 3.393$, $P = 0.335$; 24 h: Wald $\chi_3^2 = 3.179$, $P = 0.365$) (Fig. 3.5, 3.6).

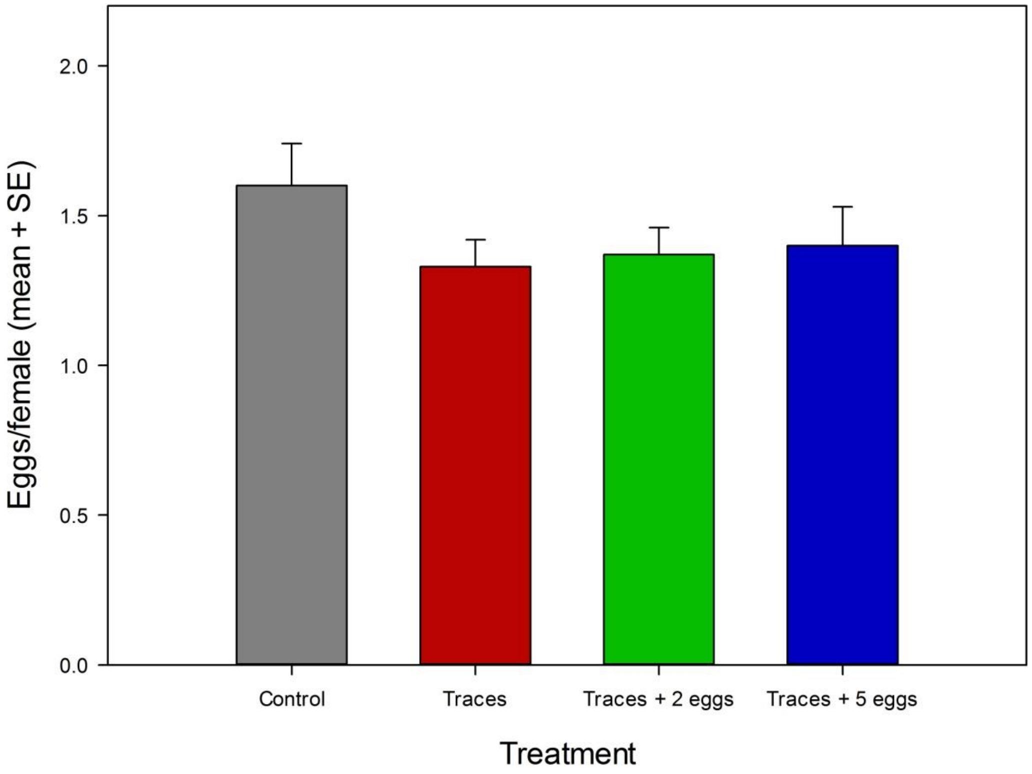

Figure 3.5: Total number of eggs per female after 3.5 h of observation.

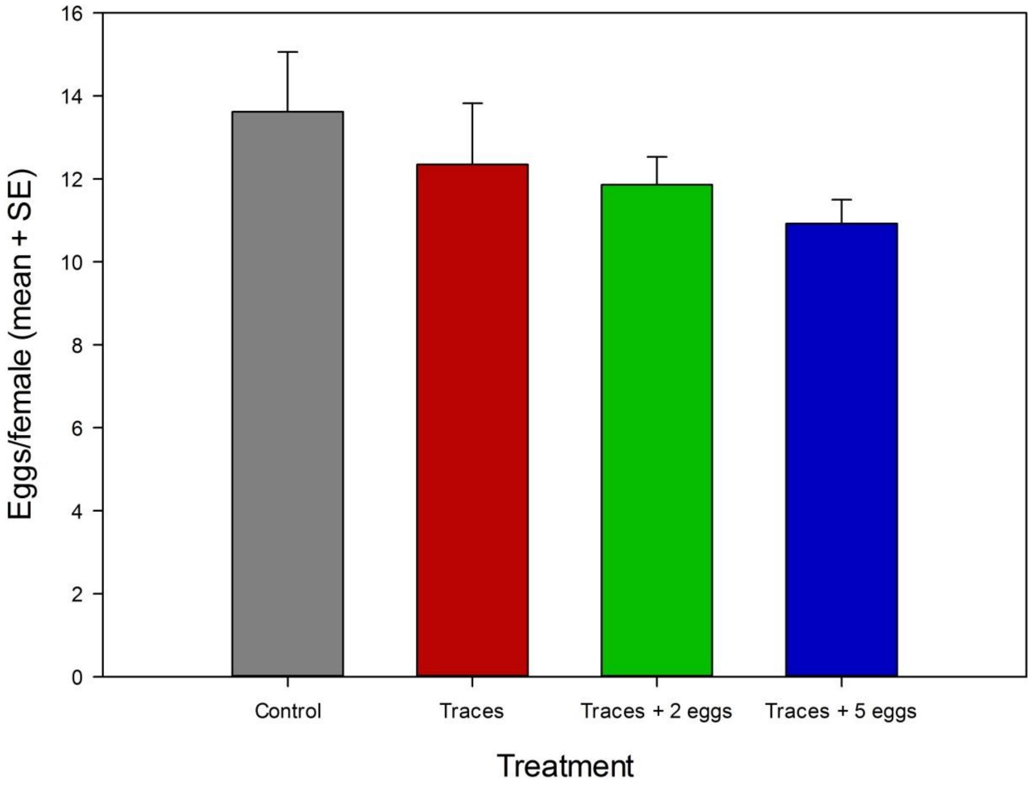

Figure 3.6: Total number of eggs per spider mite female after 24 h of observation.

3.1.5 Egg aggregation after 3.5 and 24 h

Egg aggregation was slightly, but not statistically significantly, tighter in treatments with than without predatory mite cues within 3.5 h (GLM: Wald $\chi_3^2 = 5.351$, $P = 0.148$) (Fig. 3.7), but did not differ among treatments after 24 h (Wald $\chi_3^2 = 0.858$, $P = 0.836$) (Fig. 3.8).

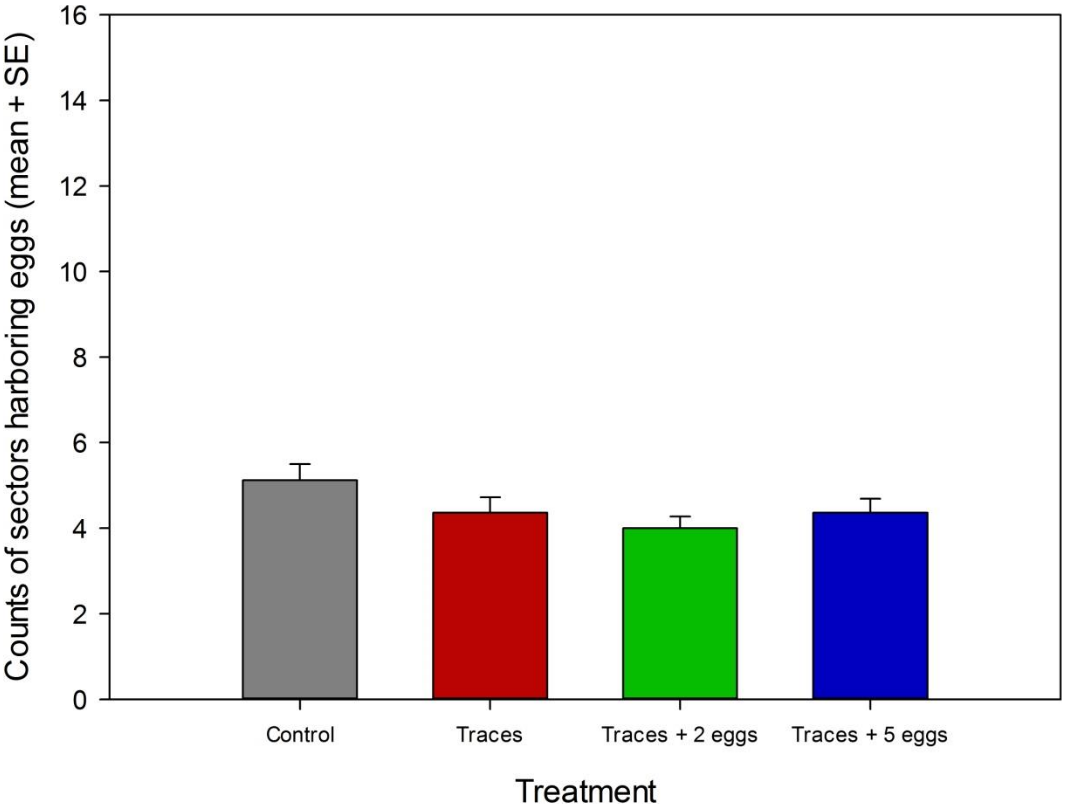

Figure 3.7: Number of leaf disc sectors (out of 16) harboring at least one egg after 3.5 h.

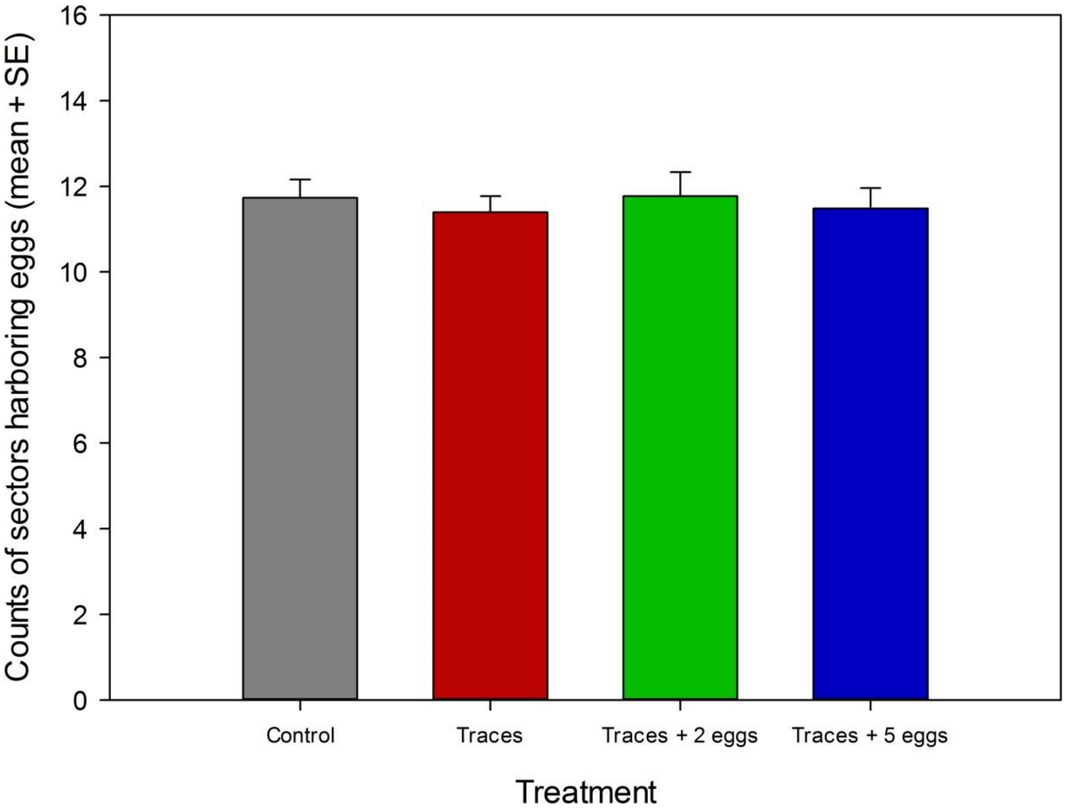

Figure 3.8: Number of leaf disc sectors (out of 16) harboring at least one egg after 24 h.

3.2 Experiment 2: Survival chances in dependence of aggregation

3.2.1 First encounter

The first grouped spider mite female was significantly later found by the predatory mites than the first solitary spider mite female (Cox regression: Wald $\chi_1^2 = 3.752$, $P = 0.05$). Within ten minutes after release, the predatory mites had encountered the first spider mite on 45% of the leaf discs harboring four solitary mites but only on 27% of the leaf discs harboring four grouped spider mites (Fig. 3.9).

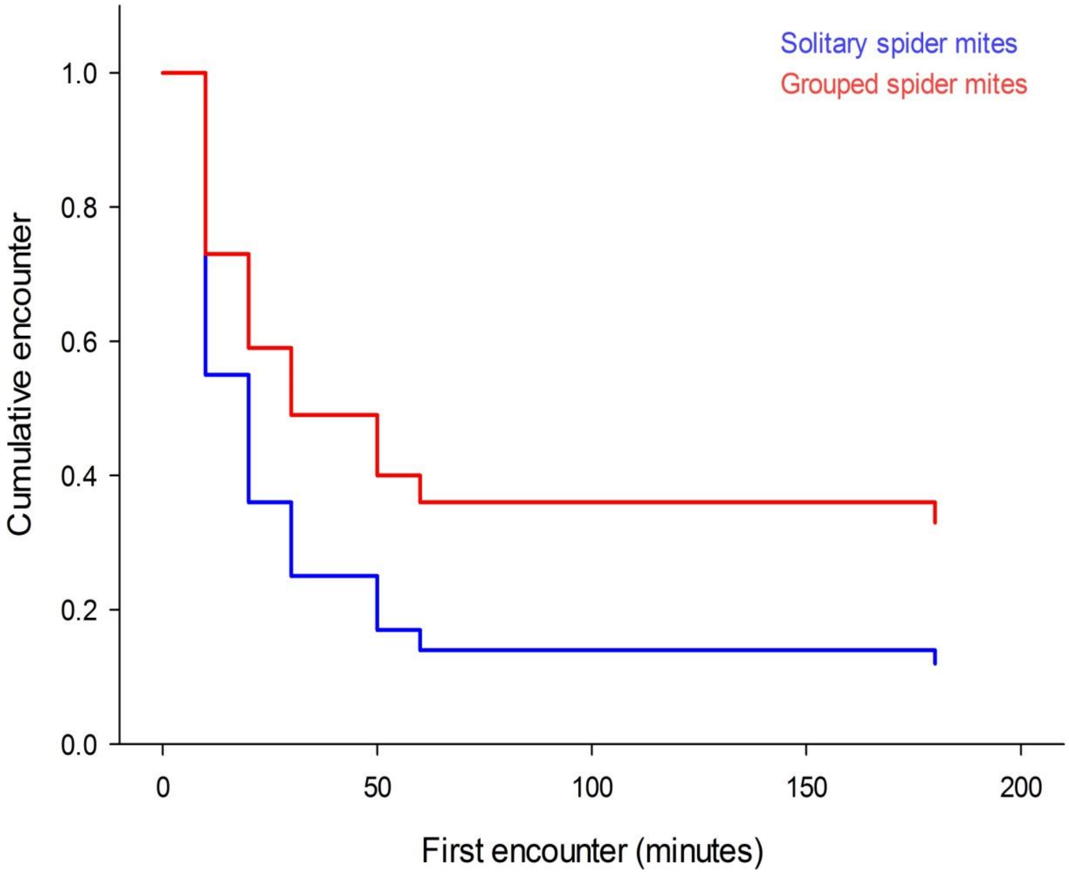

Figure 3.9: Cumulative first encounters between predator and prey over time.

3.2.2 First attack

Grouped spider mite females were significantly later attacked by the predatory mite females than solitary spider mite females (Cox Regression: Wald $\chi_1^2 = 7.681$, $P = 0.006$). Therefore, the survival likelihood of grouped spider mite females was much higher than that of solitary spider mite females (Fig. 4).

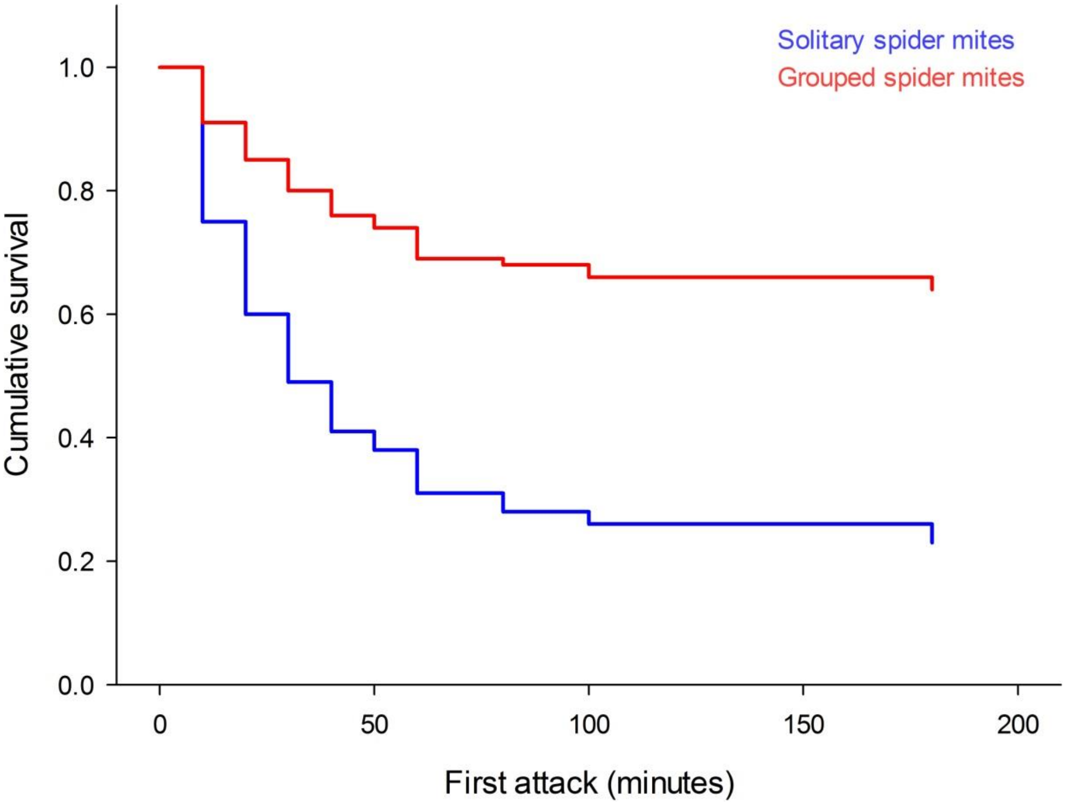

Figure 3.10: Cumulative survival of spider mite females over time.

3.2.3 Killed spider mites

The predators killed in total more solitary than grouped *T. urticae* females in the course of the experiment (GLM: Wald $\chi_1^2 = 9.585$; $P = 0.002$). Approximately three times more solitary than grouped spider mites were killed (Fig. 3.11).

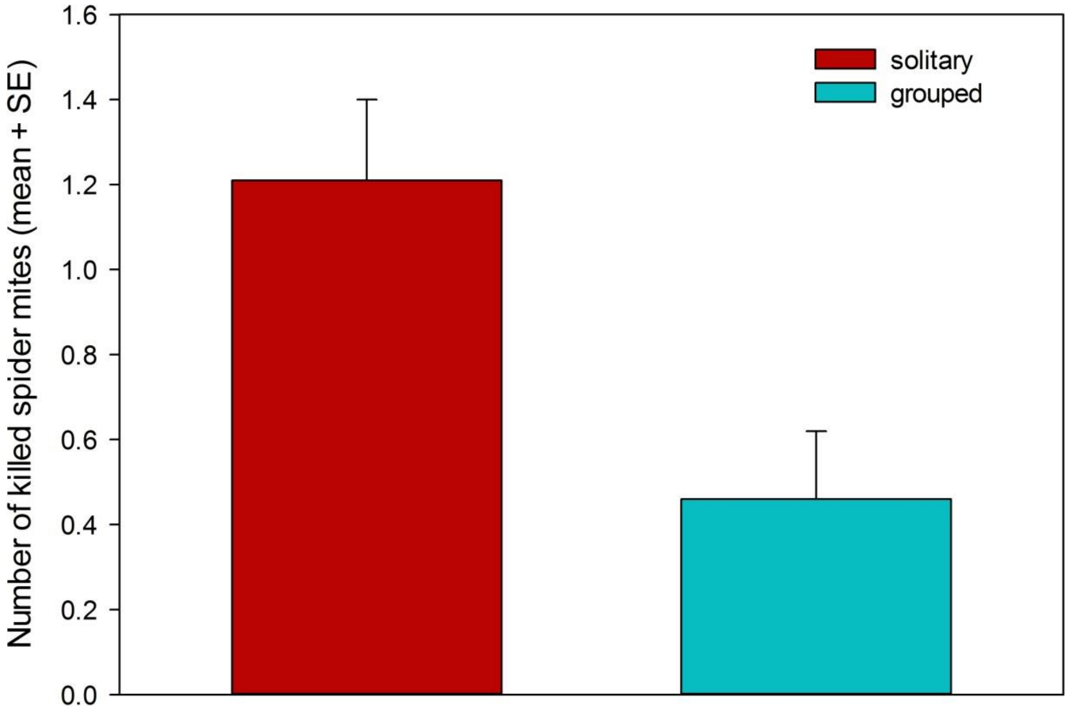

Figure 3.11: Mean number of spider mites (out of 4) killed by the predators per leaf disc during the experiment.

Attack of a grouped spider mite female by a predatory mite did not increase the risk of the other individuals of that group to be attacked, as compared to solitary spider mites. On leaf discs where at least one spider mite was attacked by the predatory mite, the total number of spider mites that were killed in the course of the experiment was the same in both solitary and grouped spider mites (GLM: Wald $\chi_1^2 = 0.138$; $P = 0.710$) (Fig. 3.12).

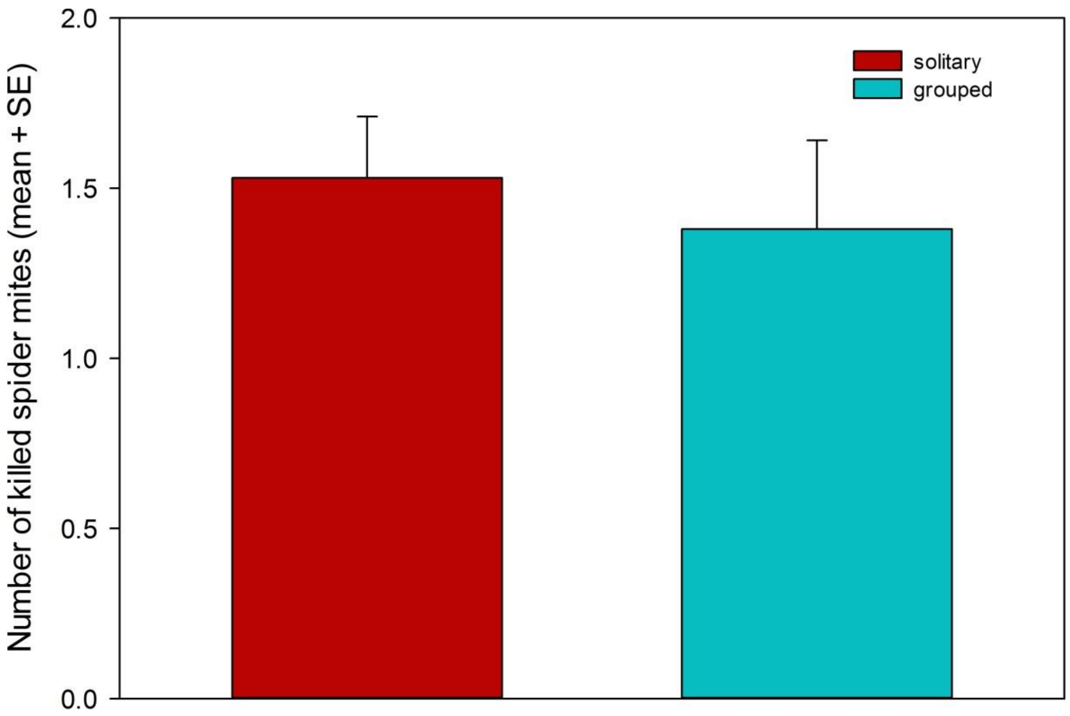

Figure 3.12: Mean number of spider mites killed (out of 4) during the experiment, including only those leaf discs where at least one spider mite was killed.

4 Discussion

Predation risk strongly shapes the behavior of prey organisms, which evolve strategies targeted at avoiding or minimizing predation. These so called anti-predator behaviors are widespread across animal taxa. To form groups or to increase aggregation is one of the strategies to decrease the risk of predation (Beauchamp 2014). For example, Wrona and Dixon (1991) describe the formation of groups by pupae of the stream-dwelling trichopteran *Rhyacophila vao* to avoid predation risk by the planarian predator *Polycelis coronate*. As immobile pupae without any defense mechanisms, they benefit from the dilution effect and a possible delayed encounter with their predators when they are aggregated. This effect is called attack abatement, originally described by Turner and Pitcher (1986). Attack abatement is the combination of two effects. One is the dilution effect: An individual member of a group is less likely attacked when surrounded by conspecifics that could be attacked instead. The other effect is the avoidance effect: Although being more conspicuous, a group of aggregated prey is often, but not always (see for example Low 2008), less likely encountered by visually hunting predators as the same number of single scattered individuals. Ioannou et al. (2011) tested the avoidance effect with three-spined sticklebacks searching for dead chironomid larvae, and found out, that formations of aggregations decrease the likelihood of being encountered by predators, which use primarily visual cues for hunting.

In my study, I wanted to explore if adult females of the two-spotted spider mite *Tetranychus urticae* respond to the presence of cues of the specialist predatory mite *Phytoseiulus persimilis* with tighter aggregation. The second aim was to find out if such an anti-predator behavior leads to a higher survival chance of the prey individuals. In detail, I scrutinized if the specialized spider mite predator *P. persimilis*, which primarily uses volatile and tactile chemosensory cues for locating its prey, encounters an aggregation of spider mites later than solitarily sitting, i.e. scattered, spider mites. Aggregation as an anti-predator behavior has been widely studied across animal taxa (Larsson 1986; Spieler 2003; Creel and Winnie 2005; Frommen et al. 2009), but is poorly investigated in spider mites (Yano 2012). Yano (2012) examined cooperative web sharing and group-living as an anti-predator strategy in two closely related spider mite species, *Tetranychus urticae* and *T. kanzawai*. He found out that the complicated webs effectively protected the spider mites against the generalist predatory mite *Euseius sojaensis*, which has difficulties moving in the web. Further, he observed that living in larger groups diluted predation, because of the denser webbing, and that the spider mites stayed closer together when a predator was physically present. Yano (2012) concluded that the degree of aggregation is facultative in spider mites, and that living in groups, because of the dense webs, can be an effective defense against generalist predators. The anti-predator function of aggregation itself, in absence of webbing, has not yet been scrutinized.

Studies with other animals were mainly concerned with the effects of aggregation behavior on visually hunting predators (Spieler 2003, Travis and Palmer 2005, Ioannou et al. 2011). In contrast, studies on predators using chemosensory cues are extremely scarce. Johannesen et al. (2014) recently provided an example for the effects of prey aggregation on predators, sticklebacks, which use both visual and olfactory cues for hunting. However, to the best of my knowledge, for predators hunting prey by exclusively using chemosensory cues, like the predatory mite *P. persimilis*, the relationship between aggregation behavior of a certain prey species and its benefits or disadvantages for survival of prey has not yet been rigorously experimentally examined (Beauchamp, 2014).

Experiment 1: Aggregation of spider mites

Aggregation

The first experiment clearly revealed that *Tetranychus urticae* females become more tightly aggregated in presence of predatory mite cues. Spider mite females on leaf discs with predatory mite cues aggregated more tightly than spider mite females on leaf discs without such cues. These results imply that the spider mites are able to perceive chemosensory cues left by *P. persimilis* on the surface, which corroborates previous studies by, for example, Grostal and Dicke (2000), Skaloudova et al. (2006) and Fernandez-Ferrari and Schausberger (2013). The aggregation level of the spider mites did not differ between the three predation risk levels created with *P. persimilis* traces, *P. persimilis* traces plus two *P. persimilis* eggs, and *P. persimilis* traces plus 5 *P. persimilis* eggs. Hence, aggregation by the spider mites was not threat-sensitive.

Spider mites are principally group-living animals (Helle and Sabelis 1985a; Yano 2012) and benefit from Allee effects through their webs and the presence of conspecifics (Astudillo Fernandez et al. 2012a). However, tighter aggregation in the presence of predators or its cues is clearly an anti-predator response (Yano 2012). The distances between the spider mite females in the treatments with predatory mite cues increased after 1 h and 2.5 h, respectively. These results suggest that, albeit the spider mites do respond to predation risk with a tighter aggregation, the level of aggregation is not constant, and the distances between the females increase again after some time. This could indicate that either the predator traces vanished and became less repellent to the spider mites over time, or the spider mites adjusted their behavior by learning that the traces of *P. persimilis* alone do not represent a risk, because they suffered no consequences. Similarly, Le Goff et al. (2012) observed that aged spider mite silk is less attractive to conspecifics than fresh silk and suggested that the chemical cues present on the silk might become oxidized or degraded, or that volatile components must have vanished.

Activity and presence on leaf

Spider mites perceiving chemosensory traces of predatory mites (Grostal and Dicke 1999) commonly try to get away from this dangerous area and are thus more active compared to spider mites not perceiving such traces. Higher activity of spider mites in presence than absence of predatory mite cues was shown before by, for example, Skaloudova et al. (2006), and Fernandez-Ferrari and Schausberger (2013). Also Hackl and Schausberger (2014) observed a higher activity in predator-naive than -experienced spider mites under predation risk. Similarly, in my experiments, the three treatments with predatory mite cues, representing different risk levels, revealed a higher activity of the spider mites, compared to the control treatment without predatory mite cues, but the activity levels did not differ between the three risk levels. Likewise, Fernandez-Ferrari and Schausberger (2013) did not observe a different activity of the spider mites on leaves with predatory mite cues plus eggs than on leaves with only predatory mite cues. In my experiment, the spider mites reduced their activity gradually after 1 h and 1.5 h, respectively. The reduction in activity could be due to learning, similar to the increase of the inter-individual distances over time. The spider mites became used to the predatory mite cues, because they did not suffer any consequences from the presence of cues and thus reduced their activity. Madsen and Boertmann (2008) observed that pink-footed geese *Anser brachyrhynchus* gradually adjusted their behavior towards wind farms that were previously avoided, because perceived as being dangerous. The geese kept a greater distance to new wind farms, but then constantly decreased the distances. After behavioral adjustment to the new conditions, the geese were observed foraging between the wind turbines. An alternative or additional possible explanation for the reduction of the activity of the spider mites on the leaf discs with predator cues over time can be that the aging predatory mite traces lost their repellent effect on the spider mites. Barnes et al. (2002) studied the effect of the age of chemical predator cues on the anti-predator behavior in wolf spiders. Contrary to the spider mites, which increased their activity in predation risk scenarios, the smaller wolf spider *Pardosa milvina* decreased its activity in presence of the larger wolf spider *Hogna helluo*. It moved significantly less in the treatments with chemical predator cues compared to the control treatment without cues. It exhibited a significantly stronger anti-predator behavior to 1 h old, fresh silk and excreta of its predator or associated cues than to one or five day old cues. After 24 h, the spider mites on the control leaf discs without predatory mite cues were even more active than the ones on the leaves with predator cues. Probably the mites on the control leaf discs started to search for a new feeding site due to the circumstance that the quality of the leaf disc suffered from the loss of water and nutrients. It could be that the spider mites perceiving predation risk, which were more active in the first 3.5 h of the experiment, had to feed more afterwards to regain energy. Skaloudova et al. (2006)

observed a nonsignificant higher plant damage on the leaves with spider mites under predation risk scenarios and concluded that this could be due to the higher activity and the higher energy needs of the spider mites. The active mites spent less time resting, feeding and ovipositing, due to the perceived risk, which can be interpreted as the costs resulting from this anti-predator behavior.

The number of spider mites present on the leaf discs throughout the experiment did not differ between treatments. Predation risk did not lead to a higher escape rate into the water barrier surrounding the leaf disc. In all treatments, the number of mites was constantly high until 3.5 h but strongly decreased after 24 h. A possible reason for the latter observation is that the quality of the leaf disc decreased after one day due to the loss of nutrients. Probably, with increasing age of the leaf disc, some spider mite females started searching for new feeding sites, followed by others (Yano 2008), and finally got stuck and drowned in the water barrier.

Oviposition

The number of eggs laid by the spider mite females after 3.5 and 24 h, respectively, was slightly, but not significantly, lower in the treatments with predatory mite cues than on control discs. Also egg aggregation after 3.5 h was slightly, but not significantly, tighter on the leaf discs with predatory mite cues than on the discs without cues. After 24 h, the egg aggregation did not differ among treatments. Fernandez-Ferrari and Schausberger (2013), as well as Hackl and Schausberger (2014) observed that spider mites laid their first egg significantly later in presence of *P. persimilis* cues, which could be due to egg retention under predation risk. The ability to retain eggs under predation risk was shown for predatory mites by Monserrat et al. (2007). They found out that the predatory mite *Neoseiulus cucumeris* delayed oviposition under predation risk of its intraguild predator *Iphiseius degenerans*, which feeds on the juvenile stages of its prey but not on eggs and adults. Proximately, under predation risk *N. cucumeris* retained its eggs because, after hatching, these individuals developed more quickly to adult. In the experiments of Montserrat et al. (2007), the predators were physically present throughout the experiment, so the predation risk lasted until the end of the experiment. This was not the case in my experiment. Egg retention under predation risk could be an explanation for the slightly lower number of eggs produced in the treatments with predatory mite cues. Under predation risk, the spider mites could have started later with oviposition, but after 3.5 h the differences were not significant anymore. In the course of the experiment, the predator cues could have partially vanished or the spider mites got used to the predatory mite cues. These results are similar to those of Grostal and Dicke (1999), who observed that the number of eggs laid by spider mite females within 24 h did not differ significantly between leaf discs with and without *P. persimilis* cues.

The aggregation of the eggs was slightly but not significantly tighter in the treatments with predatory mite cues after 3.5 h and did not differ after 24 h. The females themselves did aggregate under predation risk, but they did not aggregate their eggs more. Since the whole leaf disc was exposed to predatory mite cues, there was no safe site to lay their eggs. Spider mite females, which have the choice to lay their eggs in sites with and without predatory mite cues, avoid laying their eggs in the site with predatory mite cues (Grostal and Dicke, 1999). In my experiments, the reason for the small difference after 3.5 h and no difference after 24 h in egg aggregation could also be the small size of the leaf disc, offering no safe possibilities. After 24 h, nearly all virtual leaf sectors contained spider mite eggs.

Experiment 2: Survival chances in dependence of aggregation

In the second experiment, solitary spider mites were significantly earlier encountered and attacked by *P. persimilis* than the grouped spider mites. As a consequence, the survival chance of grouped spider mites was much higher than that of solitary spider mites. Moreover, during the observation time, in total more solitary than grouped spider mites were killed. Detection of the group of spider mites and attack of one individual of the group did not increase the risk for the other individuals of that group to be attacked, as compared to solitary spider mites. On leaf discs where at least one spider mite was attacked, the total number of killed spider mites was approximately the same in both treatments.

The combined benefits of the dilution effect and the avoidance effect, dubbed attack abatement (Turner and Pitcher 1986), are based on the predators' prey searching and capturing strategies. Predators can be visual, mechanosensory and/or chemosensory oriented hunters (Sternthal 1974; Brock-Fenton and Fullard 1981; Clark 2004; Anjum et al. 2006) and their sensory modalities and search strategies decisively determine the anti-predator behavior of their prey. For example, prey of visually hunting predators would benefit from being cryptic and hiding. For prey of predators using tactile and auditory cues for hunting, low activity would be the best. For all of them, tighter aggregation, escaping or active defense mechanisms would be possible strategies. Predatory mites are blind, but light-sensitive, and mainly use volatile and tactile chemosensory cues to locate and recognize their prey. Spider mites clearly benefited from tighter aggregation as an anti-predator response against predatory mites, by reducing the possibility of being encountered, that is, the avoidance effect, and dilution (Turner and Pitcher 1986). Moreover, under natural settings, where the mites are not fixed to the surface, as in my experiment, but movable, the predator:prey body size ratio has relevance for the survival chances after detection of the group. Gravid *P. persimilis* females have approximately the same size as adult spider mite females. The time of attacking and feeding on a prey of the same size can take a few to several minutes for a predatory mite. This time may be used by surrounding spider mites to escape. Surrounding individuals can also benefit from the satiation effect, when the predators hunger is satisfied for a while until it starts to search for prey again. The predator is satiated after consuming one prey of approximately the same size and some time will pass until starting hunting again. When the prey is much smaller than the predator, the handling time per individual prey item is lower and the consumption rate increases (Parrish 1991; Riipi et al. 2001).

Johannesen et al. (2014) tested the effect of prey aggregation on predator detection with chironomid larvae as prey and three-spined sticklebacks as predators in laboratory and field conditions, representing differences in visual cue availability. Three-spined sticklebacks primarily use visual but also olfactory cues and lateral line detection to locate their prey. Johannesen et al. (2014) used dead chironomid larvae and turbid water conditions or feeding stations to reduce the importance of visual cues and to increase the importance of olfactory cues for prey detection. In the laboratory, they compared the time of detection by the fish predator with aggregated and dispersed prey under clear and turbid water conditions. They found out that in turbid water the predators detect aggregated prey later than dispersed prey. In contrast, in clear water, they detect aggregated prey earlier than dispersed prey. Therefore, the survival of subsequent prey consumed by the predator after the first encounter of one prey individual was, in turbid water, lower for aggregated than for dispersed prey. The field experiments were conducted in water rock pools with feeding stations where visual detection of prey was hardly possible, whereas olfactory cues could be transmitted. Three aggregation levels (aggregated, semi-dispersed, dispersed) were created; each of them with the same number of prey distributed over one, half or all of the feeding stations. Johannesen et al. (2014) observed that dispersed prey was found and consumed significantly earlier than semi-dispersed and dispersed prey. The data from the field experiment of Johannesen et al. (2014) can be compared to my results, where aggregated spider mites were encountered and attacked later than scattered spider mites. Comparing the laboratory experiment of Johannesen et al. (2014) with the results of my experiment, they found out that in turbid water, where visual cues are strongly reduced, aggregated prey is found later, likewise to my results. However, different from my results, after detecting the group of chironomid larvae, individual larvae of this group were attacked and consumed with a higher likelihood than dispersed larvae, which survived longer. In my experiments, individuals of the grouped spider mites survived longer than scattered individuals. Even after attacking one individual of the group, the other spider mites of the group were not at higher risk to be killed than solitary spider mites. The differences between the sticklebacks of Johannesen et al. (2014) and the predatory mites in my experiments are likely due to differences in the used sensory modalities and search strategies of the different predator species. Three-spined sticklebacks are normally visual hunters and use olfactory cues and lateral line detection only in addition, whereas *P. persimilis* is a blind hunter exclusively using olfaction and tactile chemical cues to detect and recognize its prey. Thus, after group detection the sticklebacks probably used visual cues or a combination of visual and olfactory cues to locate other larvae of the group, which was not possible for *P. persimilis*.

5 Conclusions

Altogether, I observed that spider mites do aggregate under latent predation risk, posed by cues, but physical absence, of the predatory mite *P. persimilis*. Tighter aggregation is adaptive because this anti-predator behavior increased the survival chances of the spider mites. Previous studies showed that spider mites are more active (Fernandez-Ferrari and Schausberger 2013; Skaloudova et al. 2006) and delay oviposition (Hackl and Schausberger 2014) under predation risk. The benefits of tighter aggregation are later detection by the predators (see also Johannesen et al. 2014 for sticklebacks) and a higher likelihood to survive after detection by the predator due to the dilution effect (Wrona and Dixon 1991), together dubbed attack abatement (Turner and Pitcher 1986).

Several studies were concerned with the function of the webs of the spider mites in protection against predators (Oku et al. 2003; Lemos et al. 2010; Yano 2012). My study was concerned with the aggregation behavior of spider mites and the effects on predation in absence of webbing. As predatory mites such as *P. persimilis* use the spider mite webs to locate their prey colonies, and specialist predators are well able to cope with the dense webs (Shimoda et al. 2009; Yano and Osakabe 2009), future work could investigate the effects of spider mite aggregation on specialist predatory mites in presence of webbing.

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Abstract

Predation has a strong influence on prey morphology, life history and/or behavior. In response to predation, prey organisms commonly evolve special anti-predator behaviors to minimize predation risk. Living in groups can dilute the risk of predation between the individual members of the group. The formation of an aggregation can avoid an early encounter by a predator. Modifying the level of aggregation is a widespread phenomenon in group-living animals. My study was concerned with the aggregation behavior of the two-spotted spider mite *Tetranychus urticae* and the effects on predation in absence of webbing. I tested this anti-predator behavior in two laboratory experiments. My aim was finding out if adult spider mite females respond with tighter aggregation to the cues of the predatory mite *Phytoseiulus persimilis.* I created four different risk levels on leaf discs, with *P. persimilis* traces, *P. persimilis* traces plus two *P. persimilis* eggs, *P. persimilis* traces plus five *P. persimilis* eggs and also control leaf discs without predatory mite cues. The distances between the spider mite females and between their eggs, the oviposition rate and the activity level of the females were examined over time. My second aim was finding out if spider mites under predation risk benefit of tighter aggregation in enhanced survival chances. I surveyed the encounter and attack risk of solitary and grouped spider mites over time by allowing a starved *P. persimilis* female to locate spider mite females fixed on leaf discs. My study reveals that the two-spotted spider mite *T. urticae* aggregates more tightly under predation risk of the predatory mite *Phytoseiulus persimilis*. The aggregation level of the spider mites did not differ between the three predation risk levels. There was no difference in the oviposition rate and in the aggregation level of the eggs between the treatments with and without predatory mite cues. A further anti-predator behavior of the spider mites was a higher activity under predation risk. The spider mites benefited from tighter aggregation in a higher survival chance due to delayed detection and attack by the predatory mite and the dilution effect. The encounter and attack of one group member did not increase the risk for the other individuals of that group to be attacked as compared to solitary spider mites.

Zusammenfassung

Prädation übt einen starken Einfluss auf Morphologie, Lebenszyklus und/oder Verhalten der Beuteorganismen aus. Als Reaktion auf den Prädationsdruck entwickeln Beuteorganismen üblicherweise spezielle Anti-Prädationsverhaltensweisen um das Prädationsrisiko zu minimieren. Das Leben in Gruppen kann das Risiko eines einzelnen Individuums erbeutet zu werden zwischen den einzelnen Mitgliedern der Gruppe aufteilen. Gruppenbildung ermöglicht es ein frühzeitiges Auffinden durch den Räuber zu vermeiden. Den Grad der Aggregation zu modifizieren, ist ein weit verbreitetes Phänomen bei in Gruppen lebenden Tieren. Meine Studie beschäftigt sich mit dem Aggregationsverhalten der Gemeinen Spinnmilbe *Tetranychus urticae* und den Auswirkungen auf die Prädation in Abwesenheit der Spinnmilben-Gespinste. Es wurden zwei Laborexperimente durchgeführt, um dieses Anti-Prädationsverhalten zu untersuchen. Mein Ziel war es, herauszufinden, ob erwachsene Spinnmilbenweibchen mit einer stärkeren Aggregation auf Spuren der Raubmilbe *Phytoseiulus persimilis* reagieren. Es wurden vier verschiedene Risikostufen auf Blattscheiben kreiert - *P. persimilis* Spuren, *P. persimilis* Spuren plus zwei *P. persimilis* Eier, *P. persimilis* Spuren plus fünf *P. persimilis* Eier und, als Kontrolle, Blattscheiben ohne Raubmilbenspuren. Die Distanzen zwischen den Spinnmilbenweibchen, ebenso wie zwischen den Spinnmilbeneiern wurden gemessen und die Eiablagerate und zeitliche Aktivität der Spinnmilben wurden erhoben. Mein zweites Ziel war es, herauszufinden, ob Spinnmilben unter Prädationsrisiko von einer stärkeren Aggregation durch verbesserte Überlebenschancen profitieren. Untersucht wurde das zeitliche Auffinden, sowie die Attackrate und -zeit von einzeln und gruppiert platzierten Spinnmilbenweibchen, die auf Blattscheiben fixiert wurden, durch ein *P. persimilis* Weibchen. Meine Studie zeigt, dass sich die Spinnmilbe *T. urticae* bei Prädationsrisiko durch die Raubmilbe *P. persimilis* dichter in Gruppen zusammenschließt. Als weiteres Anti-Prädationsverhalten der Spinnmilben trat eine erhöhte Aktivität unter Prädationsrisiko auf. Die Aggregationsdichte der Spinmilbenweibchen unterschied sich nicht zwischen den drei untersuchten Levels des Prädationsrisikos. Auch in der Anzahl und Aggregationsdichte der Eier gab es keinen Unterschied zwischen Spinnmilbenweibchen auf Blättern mit und ohne Raubmilbenspuren. Spinnmilben profitieren von einer dichteren Aggregation durch erhöhte Überlebenschancen, da es zu einem späteren Auffinden und Attackieren durch die Raubmilben und einem Verdünnungseffekt zwischen den Gruppenmitgliedern kommt. Das Finden und Attackieren eines Gruppenmitgliedes erhöhte nicht das Risiko für die anderen Gruppenmitglieder ebenfalls attackiert zu werden, im Vergleich zu einzeln platzierten Spinnmilben.

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Curriculum vitae

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