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Master Thesis

Maternal predation risk affects offspring anti-predator behavior in the predatory mite *Phytoseiulus persimilis*

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Acknowledgments

Contents

1 Introduction

Predatory mites of the family Phytoseiidae Berlese, 1916 are frequently part of the natural enemy complex of herbivorous mites and small insects in natural and agricultural ecosystems. Accordingly, predatory mites are widely used study objects in various scientific disciplines and are important in natural and biological pest control all over the world (e.g. McMurtry 1985; van de Vrie 1985; McMurtry & Croft 1997).

Predation risk is a strong selective force shaping prey morphology, life history and behavior (e.g. Lima & Dill 1990; Lima 1998). Antipredator behaviors are performed to increase prey survival but are always traded-off against other activities such as feeding, mating or egg production. Therefore, every antipredator behavior bears also fitness costs (Lima & Dill 1990). During life, most prey individuals are threatened and get in contact with multiple predator species. On these grounds it is likely that also different predators competing for one and the same prey can face each other. Predation among species sharing and competing for the same resources is called intraguild predation (IGP; Polis et al. 1989). IGP differs from classical predation in that IG predators may not only obtain nutrients but at the same time eliminate a potential predator of themselves or their offspring and competitor for prey and other resources. IGP is extremely common among phytoseiid mites and usually mutual and life stage-specific. Smaller and younger individuals are usually preyed upon by larger and older ones, whereas adult females are relatively invulnerable to IGP (e.g. Schausberger & Croft 2000ab). Eggs are relatively well protected from IGP. Larvae are the most vulnerable IG prey because of being little mobile – they have only three pairs of legs – and thus often fall victim to larger individuals. Larvae may themselves reduce the risk of being killed (Walzer & Schausberger 2013), but predominantly or additionally their mothers commonly try to avoid or reduce IGP on their offspring via various strategies such as selective egg placement (Walzer et al. 2006) and/or killing potential future offspring predators (Walzer & Schausberger 2009, 2011). Mothers may also prepare the embryos in a way that helps them coping with IGP risk after birth but this has never been tested in predatory mites. For example, mother sticklebacks may enhance the transfer of information about the intensity and presence of such risks to their offspring or influence the nutritional or hormonal status and thereby influence their development and behavior (e.g. Giesing et al. 2011). Such effects are generally dubbed maternal effects, which are defined as environmental factors in the maternal

generation influencing the offspring phenotype (Mousseau & Fox 1998ab). Supposedly, offspring of a predatory mite mother experiencing IGP risk might be able to better react towards predation risk than offspring of a mother without such an experience. Accordingly, I hypothesized that predator-stressed mothers are able to prime their offspring to behave more optimally in risky IGP environments. Predation risk-mediated maternal effects are the main topic of my study.

1.1 Intraguild predation

Phytoseiid mites have five life stages, i.e. egg - larva – protonymph – deutonymph – adult (Sabelis 1985a). In general, at 25 °C and depending on species, food quality and quantity, it takes around six to ten days from egg to adulthood, and therefore generations overlap within and also between co-occurring predatory mite species (e.g. Croft et al. 1992). Predation does not only happen in classical prey-predator interactions, but also among various life stages between different predator species within a guild, then called intraguild predation (IGP). IGP is defined as predation among species sharing the same resources and widespread in the animal kingdom (e.g. Polis et al. 1989). IGP is also well-known to occur in predatory mites (e.g. Schausberger & Croft 2000ab). Phytoseiid mites can be classified as diet generalists and diet specialists (McMurtry & Croft 1997) with the former commonly being more fierce IG predators than the latter (Schausberger & Croft 2000b). The species used in my study as IG prey is the predatory mite *Phytoseiulus persimilis* Athias-Henriot, 1957 (fig. 1; table 1), which is classified as a type I specialist predator (highly specific on prey mites *Tetranychus* spp.). The species used in my study as IG predator is the predatory mite *Amblyseius andersoni* (Chant, 1957) (fig. 2; table 2), which is classified as a type III (wide range of foods) generalist predator of various mites and small insects (McMurtry & Croft 1997; Schausberger & Croft 2000ab). *A. andersoni* is known to be a strong and aggressive IG predator of co-occurring predatory mites such as *P. persimilis* (Walzer & Schausberger 2011). Compared with the predatory mite *A. andersoni*, the species *P. persimilis* is a weak IG predator and an often attacked IG prey.

1.2 Anti-predator behavior

Anti-predator behavior is any behavior of prey targeted at avoiding being killed (Lima & Dill 1990). Every anti-predator behavior can have on the one hand positive and on the other hand negative effects on evolutionary fitness. It is a classical trade-off between a decreased risk of being killed (positive), and costs paid in less energy available for other life activities such as feeding or laying eggs (negative; Lima 1998). Anti-predator strategies may involve changes in activity, use of refuges, counterattack, escape, aggregation etc. (Sih 1980; Lima & Dill 1990; Lima 1998). Additionally or alternatively to changing behavior, predation risk may also induce morphological changes in prey (e.g. Chivers et al. 2008). Due to the inherent costs of every anti-predator behavior prey should be able to distinguish between different levels of predation risk and adjust their behavior accordingly (Grostal & Dicke 2000; Dicke & Grostal 2001). This is called threat-sensitive predator avoidance hypothesis (Sih 1982; Helfman 1989). For example, a prey individual should be able to distinguish between a physically present predator and traces left by a predator, because the traces alone do not represent a direct risk of being killed (e.g. Lima & Dill 1990; Chivers et al. 1996). As explained in chapter *1.1*, in phytoseiid mites gravid females do not run the risk of being killed by IG predators, but their offspring, especially the larvae, are highly endangered. Therefore, under predation risk mothers should select a suitable place for oviposition, to present their offspring a safe place for embryonic and postembryonic development (Croft et al. 1996; Walzer et al. 2006; Walzer & Schausberger 2011). Moreover, mothers could prenatally prepare their offspring via nutritional and hormonal effects to better cope with predation risk after birth. Maternal effects influencing offspring anti-predator behaviors have been observed in various animals (Storm & Lima 2010; Coslovsky & Richner 2011) but have never been looked at in predatory mites.

1.3 Maternal effects

Maternal effects represent influences of a mother on her offspring, in which factors in the maternal environment are transferred to the filial generation, producing phenotypic but not genotypic changes in their offspring. Typical factors inducing maternal effects are food availability, social experiences and predation risk (Bernardo 1996; Mousseau & Fox 1998ab). Several studies showed that predation risk can trigger maternal effects on offspring

phenotypes. These effects can influence offspring antipredator behaviors (e.g. Storm & Lima 2010) or can induce predator robust morphologies in offspring (e.g. Downes & Shine 1999; McCormick 2006;) or can influence offspring development (e.g. Mousseau & Fox 1998ab). For example, in birds it has been shown that the maternal stress levels are higher when predators are present (Scheuerlein et al. 2001) and Coslovsky & Richner (2011) showed for the first time, without directly manipulating the hormonal balance, that predation risk may generate maternal effects in birds. Offspring from stressed mothers were smaller than those from unstressed mothers yet showed higher growth rates of the wings, and had longer ones at maturity. This might be an indirect result from changed hormone levels in mothers and due to compensatory growth in the filial generation. In my thesis, I hypothesized that *P. persimilis* mothers may change nutritional and/or hormonal egg provisioning under predation risk and thus induce phenotypic changes in offspring.

1.4 Study organisms

1.4.1 Predatory mite *Phytoseiulus persimilis*

The phytoseiid predatory mite *Phytoseiulus persimilis* Athias-Henriot, 1957 (fig. 1; table 1) was used as experimental animal in this study. *Phytoseiulus persimilis* has a sexual reproduction system. Females are diploid and males are haploid, but mating is obligate for oviposition. This is called pseudo-arrhenotoky and an extremely rare phenomenon in animals (Schulten 1985). General development is divided into five life-stages: egg – larva – protonymph – deutonymph – adult. Depending on temperature, humidity and food availability it takes around seven days from egg to adulthood at 25 °C. During ideal environmental conditions females are able to produce a maximum of five to six eggs per day at 25 °C, which results in an average lifetime reproduction of about 70 eggs per female (Sabelis 1985b).

Regarding predation on spider mites, phytoseiid mites can be categorized into lifestyle types (McMurtry & Croft 1997). *Phytoseiulus persimilis* is a type I specialist (i.e. highly specific on the mites *Tetranychus* spp.) and highly vulnerable to fall victim to IG predators (Walzer & Schausberger 2011) such as *Amblyseius andersoni*. In that respect, *P. persimilis* is a well-suited species to test for maternal effects in IGP scenarios.

Figure 1: Predatory mite *Phytoseiulus persimilis*, adult female.

Table 1: Taxonomic classification of the predatory mite *Phytoseiulus persimilis* Athias-Henriot, 1957 (following McMurtry & Croft 1997)

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

1.4.2 Predatory mite *Amblyseius andersoni*

The predatory mite *Amblyseius andersoni* (Chant, 1957) (fig. 2; table 2) is a type III (wide range of foods) generalist predator of various mites, small insects and plant-derived substances such as pollen (McMurtry & Croft 1997). *Amblyseius andersoni* is a strong IG predator of co-occurring predatory mites such as *P. persimilis* (Walzer & Schausberger, 2011). In choice experiments, *P. persimilis* preferred and deposited more eggs in patches

without than with cues from the IG predator *A. andersoni*. Oviposition behavior and site choice of *P. persimilis* can also be influenced by experience through direct exposure to cues of the IG predator *A. andersoni* (Walzer & Schausberger, 2012). Accordingly, in my experiments *A. andersoni* was used as IG predator to create predator-stressed mothers and -experienced offspring of *P. persimilis*.

Figure 2: Predatory mite *Amblyseius andersoni*, adult female. (© evergreengrowers.com)

Table 2: Taxonomic classification of the predatory mite *Amblyseius andersoni* (Chant, 1957). (following McMurtry & Croft 1997)

Kingdom	Animalia
Phylum	Arthropoda
Subphylum	Chelicerata
Class	Arachnida
Subclass	Acari
Superorder	Parasitiformes
Order	Mesostigmata
Family	Phytoseiidae
Genus	*Amblyseius*
Species	*Amblyseius andersoni*

2 Materials and methods

Two experiments were conducted to investigate whether in the predatory mite *P. persimilis* maternally experienced predation risk induces transgenerational behavioral effects in their offspring, as protonymphs or adult females, or not. In both experiments *Tetranychus urticae* Koch, 1836 (Acari: Tetranychidae; fig. 3) was used as extraguild prey and the predatory mite *A. andersoni* was used as IG predator of *P. persimilis*. In both experiments, the experimental individuals were observed under a stereomicroscope Nikon SMZ800 equipped with a light source (Volpi Intralux 6000-1).
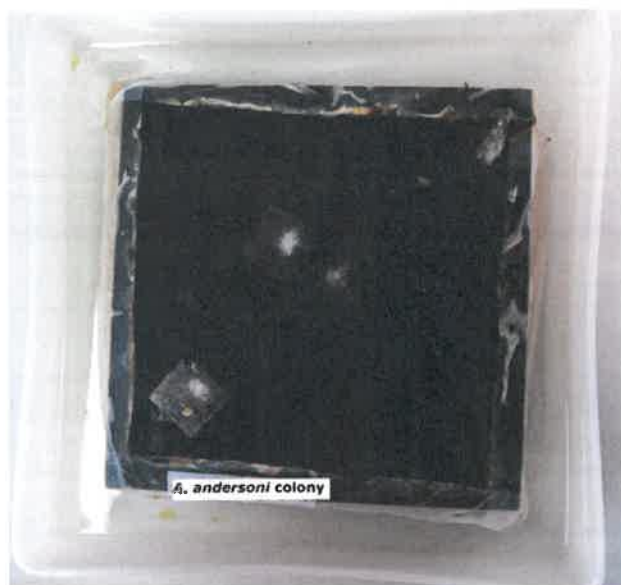

Figure 3: Spider mite *Tetranychus urticae*, adult female.

2.1 Rearing of predatory mites

Phytoseiulus persimilis and *A. andersoni* were reared in the laboratory using separate acrylic arenas. The laboratory populations were founded by specimens collected in Sicily (Walzer & Schausberger 2011), where both species are sympatric (De Moraes et al. 2004). Each rearing arena consisted of an acrylic plate (200 x 200 mm) placed on top of a water-saturated foam cube in a plastic box half-filled with tap water. Wet tissue paper was wrapped around the edges to establish a border between the acrylic plate and the surrounding water, and to prevent the predatory mites from escaping. For *A. andersoni,* cotton wool fibres under coverslips

served as shelters and oviposition sites for the predatory mites, and the prey spider mites were brushed from infested bean leaves onto the arena (fig. 4).

Figure 4: Rearing arena for *Amblyseius andersoni*. Arena in plastic box half-filled with water functioning as water source and barrier to avoid escaping. Cotton wool fibres under coverslips served as shelters and oviposition sites for the predatory mites.
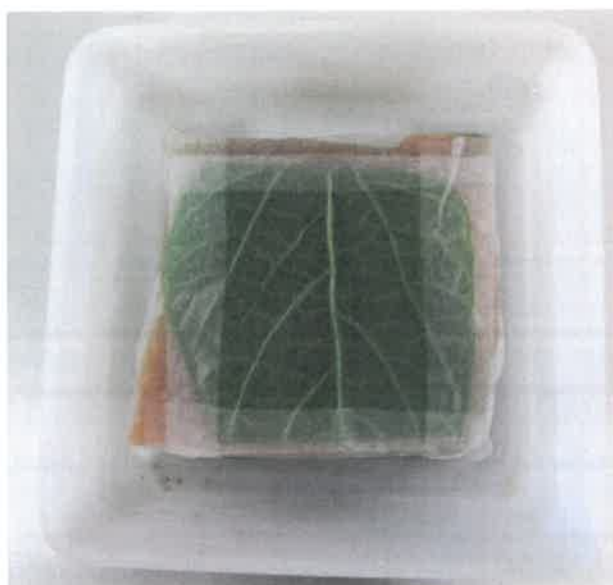
For *P. persimilis*, spider mite-infested bean leaves were piled up on the arena (fig. 5). As a precaution against contamination by other mites or unwanted insects, the plastic boxes containing the sponges and arenas were placed in a larger plastic box (44.5 x 34 x 9 cm) half-filled with tap water containing dishwashing detergent. Both predators were fed every two days with *T. urticae*, reared on whole bean plants, by adding spider mite-infested bean leaves (for *P. persimilis*) or brushing the spider mites directly from leaves or, using the so called "Mite Brushing Machine" (BioQuip 2836M), first on a glass plate and afterwards onto the predatory mite arenas (for *A. andersoni*). All rearing units were kept under the same conditions (25 ± 1 °C, 60 ± 5% RH, 16:8 h L:D) in a climate chamber.

Figure 5: Rearing arena for *Phytoseiulus persimilis*. Arena in plastic tray half-filled with water functioning as water source and barrier to avoid escaping. Spider mite-infested bean leaves were piled up to feed the predators.
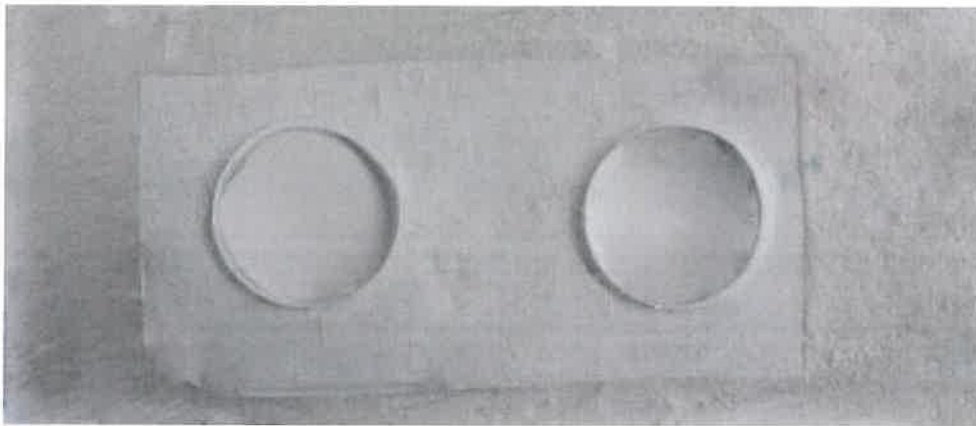
2.2 Experiments

To test for maternal effects, in both experiments *P. persimilis* mothers experiencing predation risk (subsequently called "stressed") or not (subsequently called "unstressed"), giving rise to the experimental individuals that were themselves either experienced with predators (subsequently called "predator-experienced") or not (subsequently called "predator-naïve") were needed. To generate stressed and unstressed mothers, detached bean leaf arenas were used. Each bean leaf arena (50 x 50 mm) consisted of a trifoliate bean leaf placed upside down on a water-saturated foam cube in a plastic box half-filled with tap water (fig. 6). Wet tissue paper was wrapped around the edges of the leaves to establish a border between the bean leaf and the water, and prevent the predatory mites and their prey from escaping.

Figure 6: Standardized detached trifoliate bean leaf arena for generating stressed and unstressed *P. persimilis* mothers. Arena in plastic tray half-filled with water functioning as water source and barrier to avoid escaping.

2.2.1 Generating stressed and unstressed mothers

Groups of 10 adult *P. persimilis* females, randomly taken from the general rearing arenas, were placed on bean leaf arenas for 72 h and provided with a pre-defined number of *T. urticae* as prey. The number of *T. urticae* was determined in pilot experiments and should represent enough prey for optimal oviposition and at the same time warrant frequent encounters between *P. persimilis* and *A. andersoni* (if present). For generating stressed *P. persimilis* females, two adult *A. andersoni* were added to establish a stressful IGP environment. Unstressed *P. persimilis* females were held on arenas without *A. andersoni*. After 72 h, stressed and unstressed adult *P. persimilis* females were placed singly for 12 h in an empty acrylic cage (Schausberger 1997) to deposit eggs giving rise to experimental individuals (fig. 7). The clean and empty acrylic cages were used to present a predator free environment. No cues and waste products of the intraguild predator were present inside the cages. This was necessary to obtain eggs without any external chemical cues from the predator and thereby warrant that, until hatching, offspring were only influenced by their mothers and not by cues in the egg environment.

Figure 7: Acrylic cages used for oviposition by adult *P. persimilis* females

2.2.2 Generating predator-naïve and -experienced offspring

To generate predator-experienced and –naïve offspring, eggs from unstressed and stressed *P. persimilis* females were taken out from the acrylic cages and placed in groups of ten on a new separate spider mite-infested bean leaf arena, either with – to generate experienced *P. persimilis* offspring – or without – to generate naïve *P. persimilis* offspring – two adult *A. andersoni* females. For experiment 1, the *P. persimilis* individuals were left on the arenas until reaching the late protonymphal stage; for experiment 2, they were left until adulthood. For experiment 2, the *A. andersoni* females were removed from the arena two to three h before starting the experiment to give the experimental *P. persimilis* females a rest before being used in the experiment. In both experiments, maternal stress (yes/no) and offspring predator experience (yes/no) resulted in four treatment groups of experimental individuals: (1) naïve offspring from unstressed mothers, (2) naïve offspring from stressed mothers, (3) experienced offspring from unstressed mothers and (4) experienced offspring from stressed mothers.

2.2.3 Experiment 1: behavior of offspring in the protonymphal stage

In experiment 1, acrylic choice cages were used (fig. 8). Each choice cage consisted of two large cavities, connected with each other and a small cavity by a T-shaped corridor, closed at the bottom by a mesh and on the upper side by a microscope slide (Schausberger & Hoffmann 2008). Each experimental protonymph was offered a choice between two sites, one with and one without predator cues. Choice cages were prepared one day before the actual experiment

took place. In each of the two large cavities, 20 eggs of *T. urticae* were placed using a moistened brush. The corridor was blocked by an inert plastic piece and on one site one single adult *A. andersoni* female was introduced and allowed to feed and leave metabolic waste products and, possibly, chemical footprints for 16 h. After removing the *A. andersoni* female, the number of *T. urticae* eggs was adjusted again to 20, the blocking plastic piece was removed and the cages ready for use in the experiment. To start the choice experiment, single late (~1 to 1.5 days after molting) protonymphs from the four different treatment groups were released in the small bottom cavity of the "T"-shaped corridor and thus given the choice between a site with only *T. urticae* eggs or a site with *T. urticae* eggs and cues of their intraguild predator, an *A. andersoni* female. The position of the protonymph was checked ten times, right immediately after release and then every 20 min for three hours in total. In addition to the position (in cavity with or without cues or somewhere else, considered the neutral zone) also their activity (moving/stationary/feeding) was observed. Each choice unit and each experimental protonymph were used only once. For each treatment at least 25 individuals were tested.

Figure 8: Acrylic cage used for choice experiments with protonymphs. One large cavity contained cues of an *A. andersoni* female and both large cavities contained 20 eggs of *T. urticae* each. The *P. persimilis* protonymph was released in the small cavity at the bottom end of the T-shaped corridor.
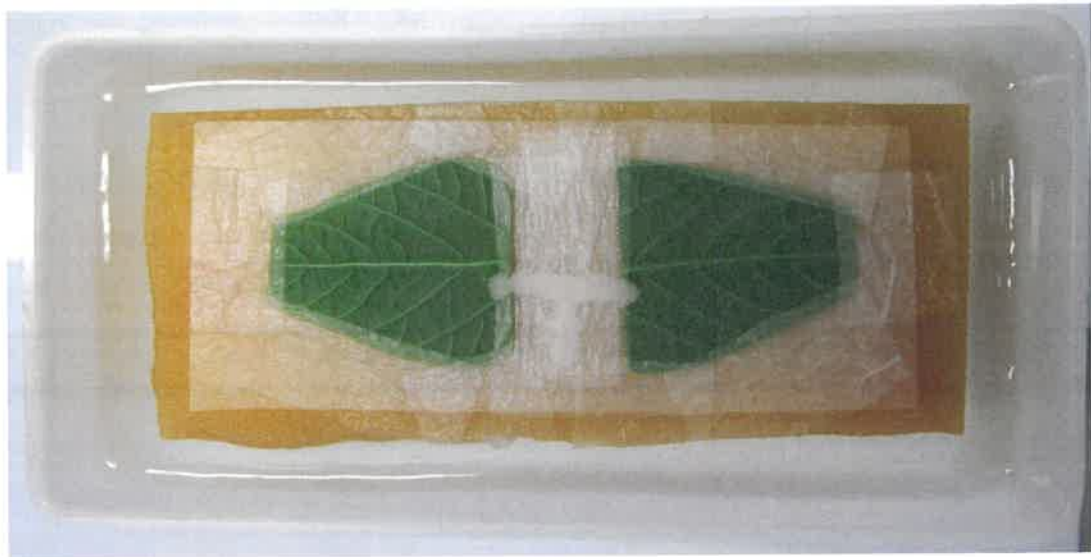
2.2.4 Experiment 2: behavior of offspring in the adult female stage

In experiment 2, single mated *P. persimilis* females, which were offspring from stressed or unstressed mothers, and which were themselves either experienced or not with the IG predator *A. andersoni,* were subjected to choice experiments using binary leaf arrangements (fig. 9).

Each leaf choice unit consisted of two detached bean leaves connected by a T-shaped wax bridge (Walzer et al. 2006). Each leaf of the choice unit was equipped with 60 eggs and 20 juveniles of *T. urticae*. This combination of eggs and mobile prey was chosen because of the specific prey stage preference of the predatory mites (Blackwood et al. 2001; Vanas et al. 2006). One leaf harbored additionally traces and eggs of the intraguild predator *A. andersoni*. To create a choice unit, 50 h before the experiment took place, two similarly sized trifoliate bean leaves were placed upside down on a rectangular, filter paper-covered, water-saturated foam cube inside a plastic box (150 x 100 mm) half-filled with tap water. Wet tissue paper was wrapped around the edges to establish a border between the leaves and the water, to prevent the predatory mites and their prey from escaping. One of the two leaves was equipped with adult spider mite females for 20 h to produce eggs. After 20 h the spider mite females were removed, their eggs adjusted to 60 and 20 juveniles added using a fine brush. Afterwards, two adult *A. andersoni* females were introduced and allowed to feed, leave traces (metabolic waste products, chemical footprints) and produce eggs for 24 h. Subsequently, the *A. andersoni* females were removed and the number of *T. urticae* eggs and juveniles were adjusted to 60 eggs and 20 juveniles. At this time also the second leaf was equipped with 60 eggs and 20 juveniles of *T. urticae* using a fine brush and the two leaves were connected by a T-shaped wax bridge (Walzer et al. 2006). The bridge was created by dripping hot wax from a non-fragrant candle onto the filter paper in between the leaves.

After another 6 h, the experiment was started by releasing single gravid (judged by visual inspection) *P. persimilis* females from the four different treatment groups at the bottom end of the T-shaped wax bridge and thus giving them a choice between a prey patch with only *T. urticae* eggs/juveniles or a prey patch with *T. urticae* eggs/juveniles and cues of *A. andersoni*. The position of the *P. persimilis* female was checked eight times: immediately after release and then every 30 minutes for three h, and then again after 24 h. In addition to the position of the female (on leaf with or without *A. andersoni* cues or in neutral zone, i.e. on the bridge), her activity (stationary, moving or feeding) as well as the location of and number of eggs produced were observed. Each choice unit and each experimental individual were used only once. For each treatment at least 25 individuals were tested.

Figure 9: Choice unit consisting of two bean leaves connected with a T-shaped wax bridge. One site contained cues of *A. andersoni* females and both sites contained 60 eggs and 20 juveniles of *T. urticae*. The *P. persimilis* females were released at the bottom end of the T-shaped wax bridge.

To check for the influence of the dissimilarity in generating the two spider mite patches of a choice unit - the bean leaf with cues of *A. andersoni* females was one day older and the 60 *T. urticae* eggs were naturally deposited (and thus contained also webbing and traces left by the adult *T. urticae* females) as compared to the leaf without predator cues, where the *T. urticae* eggs were manually added – an additional control choice experiment had to be run. To this end, naïve *P. persimilis* females derived from unstressed mothers were subjected to a choice situation between two spider mite patches created as described above but without adding any *A. andersoni*. One spider mite patch was thus older and more strongly webbed than the other one. The results of this control choice experiment were used to adjust the oviposition and site preference data of the four treatment groups before statistical analysis and thus allowed pinpointing the observed effects to the presence/absence of predator cues.

2.3 Statistical analyses

All statistical analyses were carried out using SPSS 18.0.1 (SPSS, Chicago, II, U.S.A.).

In experiment 1, the influence of maternal stress and larval predator experience on site choice and activity of the protonymphs (moving or stationary) was analyzed by means of generalized

linear models (GLM; binomial distribution, logit link). Before analysis the repeated observations were aggregated into one value for each individual.
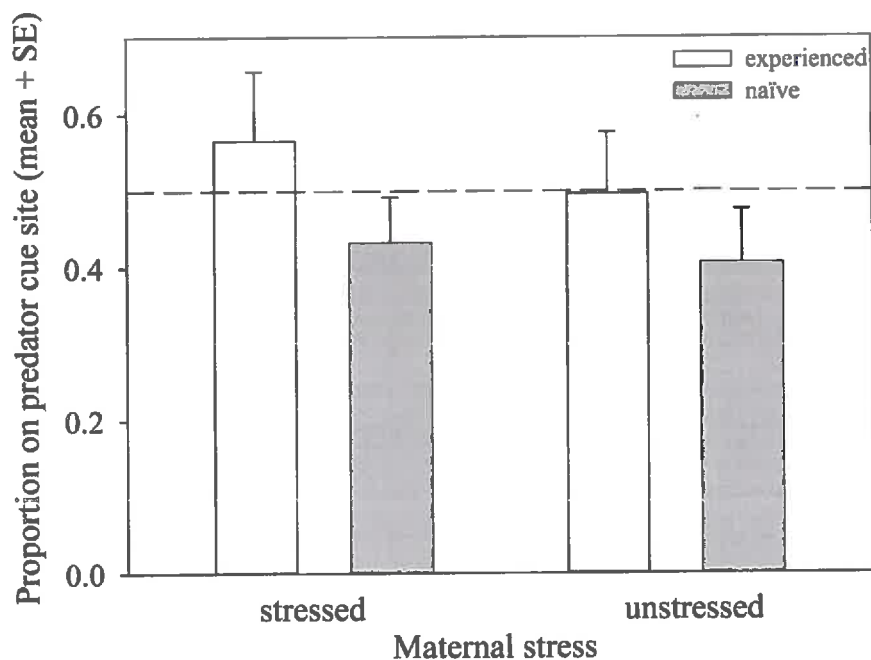
In experiment 2, after data adjustment, paired T-tests were used to compare the number of eggs deposited by *P. persimilis* within 24 h between prey patches with and without cues of *A. andersoni* within each of the four treatment groups. Additionally, binomial tests were used to compare the oviposition bias (more eggs laid on site with or without predator cues) within each of the four treatment groups. To analyze the influence of maternal stress, predator experience and site of first egg on the time of the first egg laid univariate analysis of variance (ANOVA) was conducted. Similarly, an ANOVA was used to analyze the influence of maternal stress and predator experience on the oviposition difference (eggs on leaf without predator cues minus eggs on leaf with predator cues). A generalized linear model (GLM; Poisson distribution with log link) was used to analyze the influence of maternal stress and predator experience on the total number of eggs laid by the females (both leaves combined). To analyze the activity (moving/stationary) of the females as influenced by maternal stress and predator experience, generalized estimating equations (GEE; binomial distribution with logit link; autocorrelation structure between observations) were used. A generalized linear model (GLM; binomial distribution with logit link) was used to analyze the influence of maternal stress and predator experience on feeding site preference (number of observations on site with or without predator cues). GEE (binomial distribution with logit link; autocorrelation structure between observations) was used to analyze the influence of maternal stress and predator experience on the residence preference (on leaf with or without predator cues) of the adult females over time.

3 Results

3.1 Experiment 1: behavior of offspring in the protonymphal stage
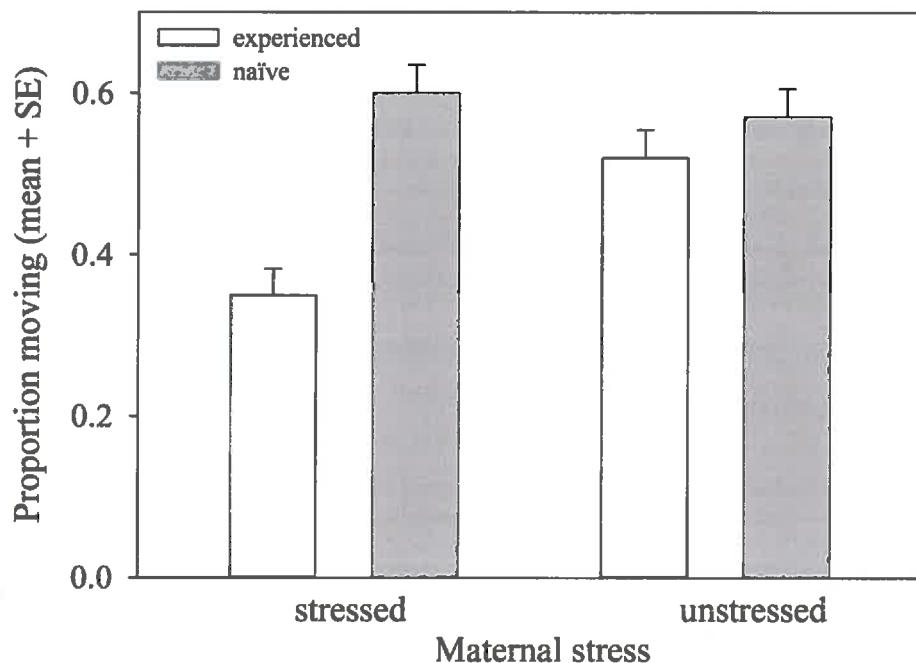
3.1.1 Site choice

Both maternal stress and intraguild predator-experience as main factors and their interaction influenced the site choice of *P. persimilis* protonymphs (fig. 10). Protonymphs from stressed mothers and predator-experienced protonymphs were more frequently observed on the predator cue side than protonymphs from unstressed mothers and predator-naïve protonymphs, respectively (GLM: maternal stress: Wald χ^2_1 = 4.290, P = 0.038; predator experience: Wald χ^2_1 = 10.168, P = 0.001). The significant interaction (maternal stress*predator experience: Wald χ^2_1 = 4.367, P = 0.037) indicates that the difference between protonymphs from stressed and unstressed mothers was more pronounced in predator-experienced than –naïve protonymphs (fig. 10).

Figure 10: Site preference of predator-naïve and -experienced protonymphs originating from unstressed and stressed mothers given a choice between two sites, one with and one without cues of the IG predator *A. andersoni*. The broken horizontal line represents random residence.

3.1.2 Activity

Both maternal stress (GLM: Wald $\chi^2_1 = 3.782$, P = 0.05) and predator experience (Wald $\chi^2_1 = 19.453$, P < 0.001) as main factors had an influence on the activity (moving/stationary) of the protonymphs (fig. 11). The lower activity of experienced than naïve protonymphs was more pronounced in stressed than unstressed mother, as indicated by the significant interaction (Wald $\chi^2_1 = 8.209$, P = 0.004).
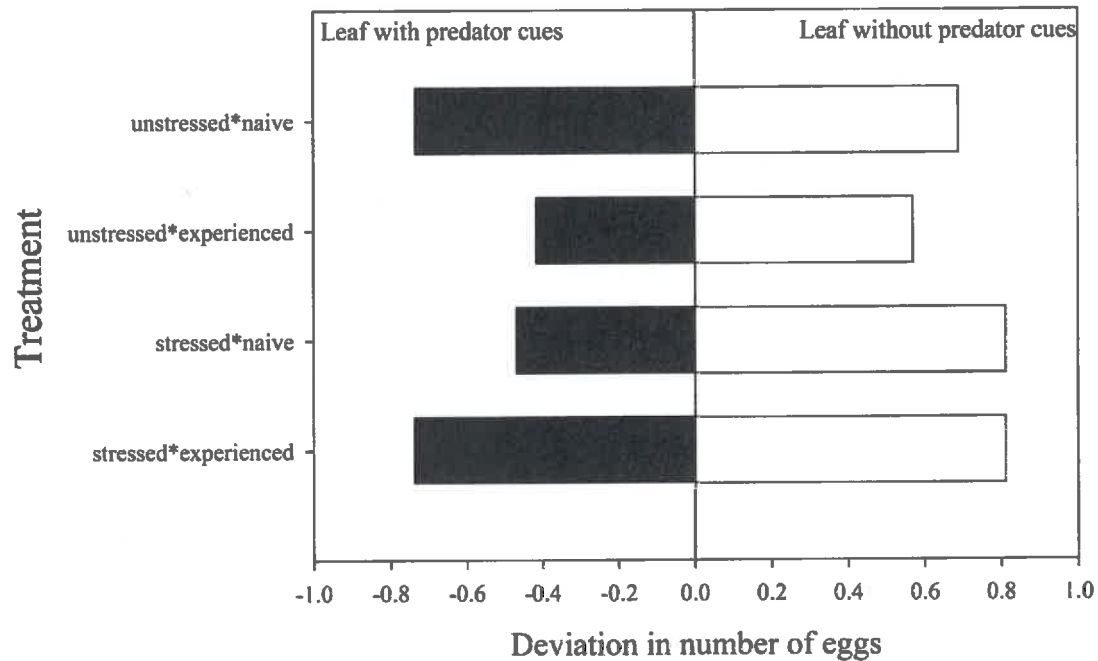

Figure 11: Activity (moving or stationary) of predator-naïve and -experienced protonymphs originating from unstressed or stressed mothers given a choice between two sites, one with and one without cues of the IG predator *A. andersoni*.

3.2 Experiment 2: behavior of offspring in the adult female stage

3.2.1 Oviposition behavior

Separate paired T-tests showed an oviposition site preference in all four treatment groups (fig. 12; table 3). The predatory mite females deposited their eggs preferentially on bean leaves without IGP cues. This preference was only marginally significant in predator-experienced females originating from unstressed mothers.
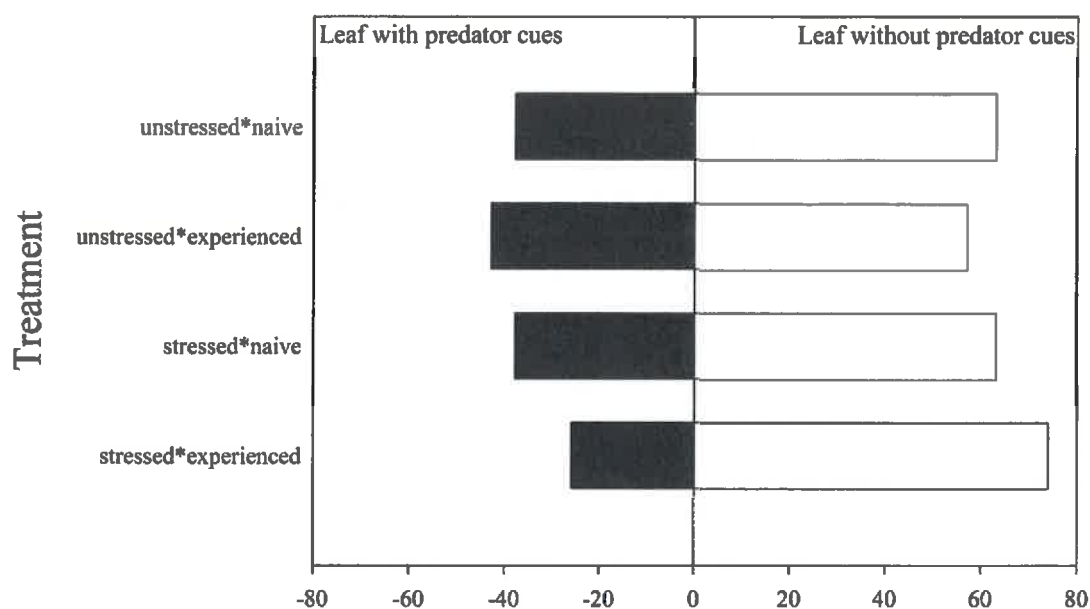
Figure 12: Deviation in the number of eggs laid by *P. persimilis* on two connected leaves, one with and one without predator cues, from control (i.e. two connected leaves both without predator cues).

Table 3: Paired T-tests for the number of eggs deposited by *P. persimilis* females within 24 hours on two connected prey patches, one with and one without cues of *A. andersoni,* within each of the four treatment groups.

Maternal stress	Predator experience	df	P
yes	yes	25	**0.011**
yes	no	25	**0.042**
no	yes	24	0.084
no	no	24	**0.021**

Two-tailed binomial tests for oviposition bias (more eggs) in sites with or without predator cues within each of the four treatment groups showed only a significant effect in predator-experienced females originating from stressed mothers ($N = 23$, $P = 0.035$; all other treatments: $P > 0.300$; fig.13).

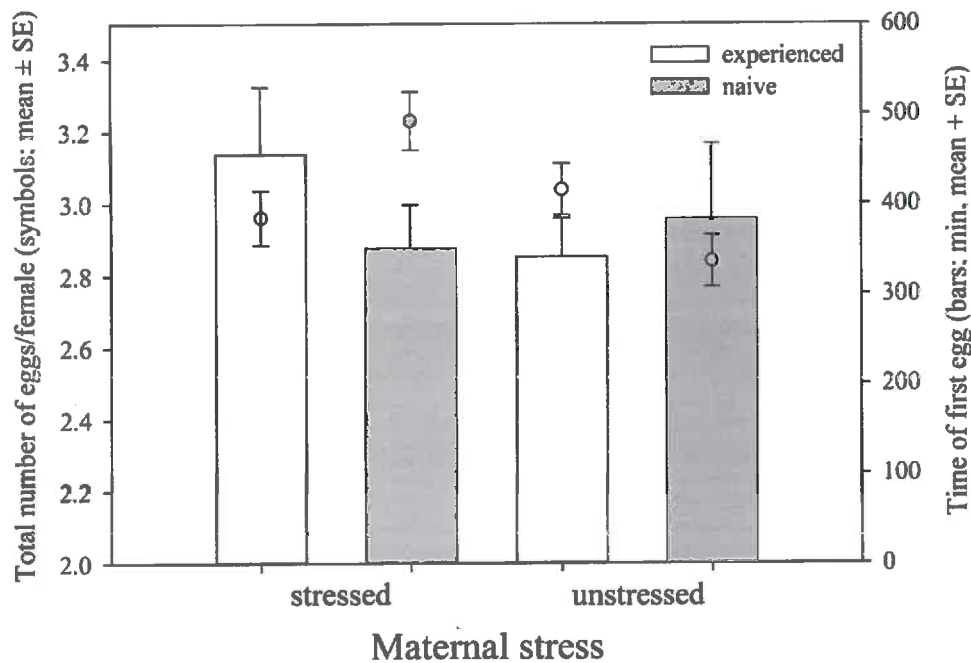Percentage oviposition bias on side with or without predator cues

Figure 13: Oviposition bias on side with or without predator cues of predator-naïve and -experienced *P. persimilis* females originating from unstressed or stressed mothers placed on two connected bean leaves, one with and one without IG predator cues.

Neither maternal stress (ANOVA: $F_{1,98}$ = 0.135, P = 0.714), predator experience ($F_{1,98}$ = 0.022, P = 0.881) as main factors nor their interaction ($F_{1,98}$ = 0.386, P = 0.536) had an influence on the difference between eggs deposited on the leaf without predator cues minus those on the leaf with predator cues (fig. 14). Similarly, total oviposition of the predatory mites within 24 h was neither affected by maternal stress nor predator experience (GLM: maternal stress: Wald χ^2_1 = 0.203, P = 0.653; predator experience: Wald χ^2_1 = 0.007, P = 0.934) nor their interaction (maternal stress*predator experience: Wald χ^2_1 = 0.461, P = 0.497) (fig. 15).
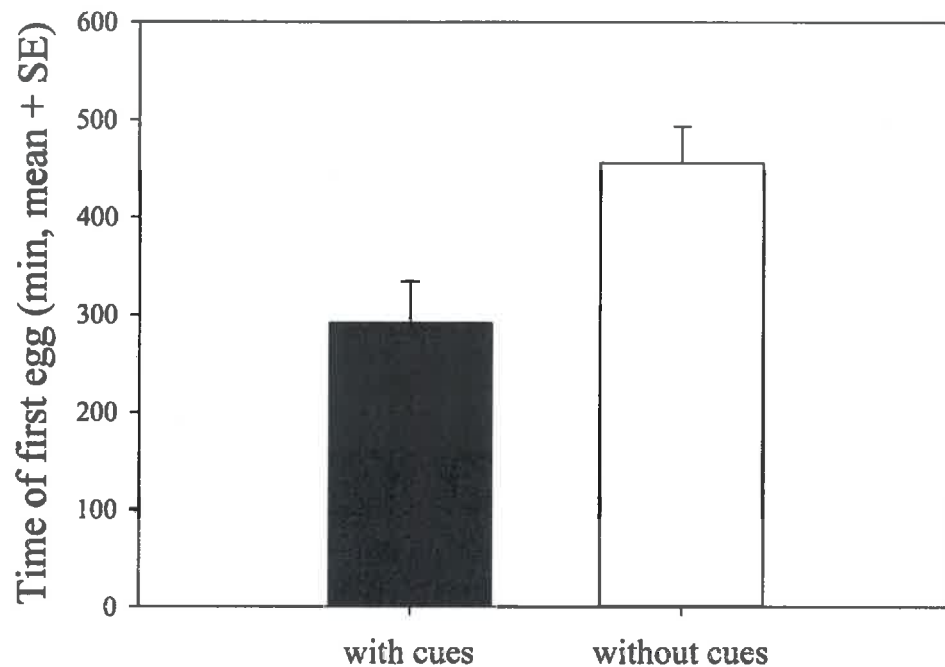
Figure 14: Difference in the number of eggs laid by predator-naïve and -experienced *P. persimilis* originating from unstressed or stressed mothers on the leaf without IG predator cues minus those laid on the leaf with IG predator cues.

Figure 15: Time of the first egg laid and total oviposition of predator-naïve and -experienced *P. persimilis* originating from unstressed or stressed mothers in the choice situation of two connected bean leaves, one with and one without IG predator cues.

The time of the first egg laid was neither affected by maternal stress, nor predator experience nor their interaction (fig 15; table 4). However, the predatory mite females generally deposited their first egg earlier on the site with than without predator cues (fig. 16; table 4).

Figure 16: Point in time when *P. persimilis* females laid their first egg when given a choice between two sites, one with and one without cues of the IG predator *A. andersoni*.

Table 4: Results of ANOVA for time of the first egg laid by *P. persimilis* females given the choice between two prey patches, one with and one without cues of *A. andersoni*.

Source	df	F	P
Maternal stress	1	0.119	0.731
Predator experience	1	0.341	0.561
Maternal stress*predator experience	1	0.900	0.346
First egg site (maternal stress)	1	0.154	0.696
First egg site (predator experience)	1	1.535	0.219
First egg site	1	5.831	**0.018**

3.2.2 Activity

Activity (moving or stationary inclusive feeding) of adult *P. persimilis* females was not affected by maternal stress and predator experience and either factor nested in time (GEE;

table 5). Females of all four treatment groups reduced their activity within the first hour and then stayed on a relatively low activity level for the rest of the experiment (fig. 17).
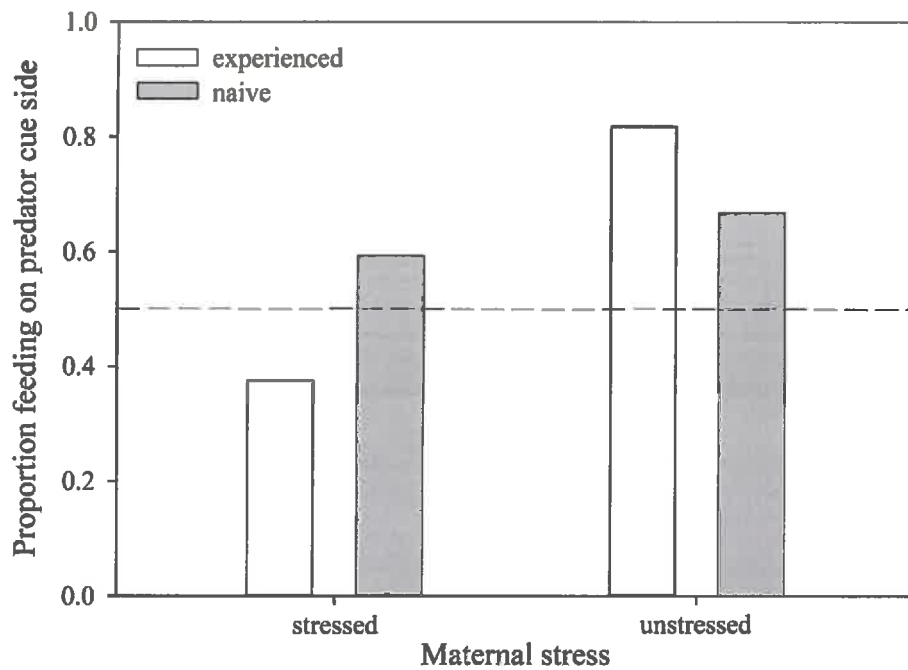
Table 5: Results of GEE for the effects of maternal stress and predator experience on the activity of the predatory mite females over time.

Source	Wald χ^2	df	P
Maternal stress	0.036	1	0.849
Predator experience	1.644	1	0.200
Maternal stress*predator experience	0.191	1	0.662
Time (maternal stress)	0.168	1	0.682
Time (predator experience)	0.001	1	0.980

Figure 17: Activity of predator-naïve and -experienced *P. persimilis* females originating from unstressed or stressed mothers given a choice between two connected bean leaves, one with and one without IG predator cues, over time.

Maternal stress (GLM: Wald $\chi^2_1 = 4.919$, P = 0.027) but not predator experience (Wald $\chi^2_1 = 0.024$, P = 0.876) and the interaction between maternal stress and predator experience (Wald $\chi^2_1 = 1.519$, P = 0.218) had an effect on the feeding site preference of adult *P. persimilis* females. Females emerging from unstressed mothers fed more often on the site with predator cues than females emerging from stressed mothers (fig. 18).
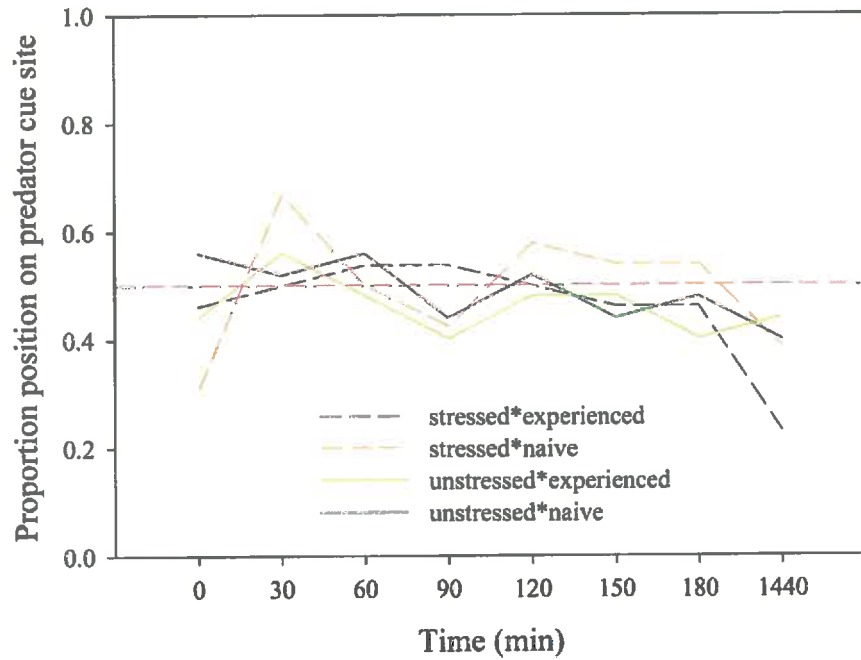
Figure 18: Feeding site preference of predator-naïve and -experienced *P. persimilis* females originating from unstressed or stressed mothers given a choice between two sites, one with and one without cues of the IG predator *A. andersoni*. The broken horizontal line depicts random choice of feeding site.

3.2.3 Residence preference

The pooled residence preference of the females was unaffected by maternal stress, predator experience and their interaction. However, residence preference of females from stressed and unstressed mothers developed differently over time (table 6). Females originating from unstressed mothers changed sites less often than females originating from stressed mothers (fig. 19).

Table 6: Results of GEE for the influence of maternal stress and predator experience on residence preference (site with or without predator cues) over time.

Source	Wald χ^2	df	P
Maternal stress	0.004	1	0.949
Predator experience	0.740	1	0.785
Maternal stress*predator experience	0.040	1	0.841
Time (maternal stress)	5.119	1	**0.024**
Time (predator experience)	0.001	1	0.981

Figure 19: Residence preference of predator-naïve and -experienced *P. persimilis* females originating from unstressed or stressed mothers given the choice between two connected bean leaves, one with and one without IG predator cues, over time. The broken horizontal line represents random residence.

4 Discussion

My study suggests that *P. persimilis* mothers experiencing IGP risk during internal egg formation influence their offspring through maternal effects. These maternal effects were more pronounced in protonymphal than adult female offspring and partly interacted with individual experience of IGP risk by the offspring. In the first experiment, the site choice and activity of *P. persimilis* protonymphs was affected by maternal stress and IGP experience. Protonymphs from stressed mothers and predator-experienced protonymphs were more frequently observed on the predator cue side than protonymphs from unstressed mothers and predator-naïve protonymphs. Experienced protonymphs originating from stressed mothers were less active than naïve protonymphs from stressed mothers while predator experience did not affect activity of protonymphs from unstressed mothers. In the second experiment, the time of the first egg laid and oviposition preference by *P. persimilis* females was affected by predator traces. The females of all four treatment groups laid their first egg earlier on the site with than without IGP traces and deposited their eggs preferentially on the site without IGP cues. The oviposition bias for the predator-cue free site was most pronounced in predator-experienced females from stressed mothers. Also the feeding site preference was affected by maternal stress. Females from stressed mothers fed more often on the site without predator cues than did females from unstressed mothers. Activity (moving or stationary inclusive feeding) of adult females was not affected by maternal stress and/or predator experience. In contrast, maternal stress influenced the time-dependent residence preference of females. Females emerging from unstressed mothers changed sites less often than females from stressed mothers. However, in the end they preferred to stay in the patch without predator cues.

Maternal stress and IGP experience had an influence on the site choice and activity of *P. persimilis* protonymphs. Protonymphs originating from stressed mothers acted bolder towards predator cues and were less active than naïve protonymphs and predator-experienced protonymphs originating from unstressed mothers. Previous studies showed that *P. persimilis* is a highly vulnerable IG prey in the larval stage and weak IG predator as adult females, whereas *A. andersoni* are little vulnerable IG prey as larvae and strong IG predators as adult females (Walzer & Schausberger 2011, 2013). *P. persimilis* protonymphs are less at risk to fall victim to IGP. In the first experiment, during the learning phase the larvae and early

protonymphs were exposed to high predation risk (physical presence of predator females and their traces) whereas in the choice situation later protonymphs were exposed to sites with and without predator traces, but always without a physically present predator. Since the predator-experienced protonymphs acted bolder towards predator traces than the naïve ones did, my experiment suggests that learning allowed the protonymphs to distinguish the risks posed by a physically present predator plus their traces versus the predator traces alone, which do not represent an immediate risk (Lima & Dill 1990; Walzer & Schausberger 2011, 2013; Hackl & Schausberger 2014). Since every anti-predator behavior is a tradeoff against other activities such as foraging or reproduction, misjudging the risks associated with a given predator or their cues may have negative consequences for the prey individual. Thus, prey individuals are expected to be threat-sensitive in predator avoidance (Sih 1982; Helfman 1989). In my experiment, predator-experienced protonymphs from stressed mothers adjusted their behavior accordingly and, under these circumstances, saved energy by being less restless and responding less fearful to predator traces alone. They had more time left for feeding and did not waste energy and time in avoiding traces not indicating immediate predation risk. Thus, a likely explanation for the observed behavioral changes is adjusted risk assessment, as shown for various animals including mites (Jachner 2001; Epp 2013; Hackl & Schausberger 2014). For example, Jachner (2001) documented for the roach *Rutilus rutilus,* Epp (2013) for the salamander *Eurycea nana* and Hackl & Schausberger (2014) for the spider mite *Tetranychus urticae* an attenuated response to alarm and/or predator cues by predator-experienced than - naïve individuals. These authors argued that the attenuated response was due to adjusted risk assessment or habituation.

The time of the first egg laid by *P. persimilis* females was affected by predator traces. Females of all treatments laid their first egg earlier on the site with than without IGP traces, but overall they deposited their eggs preferentially on the site without IGP cues. Considering that information processing and accurate decision-making takes time (Chittka et al. 2009) it thus seems that females that deposited their first egg quickly on the site with predator traces were those females that inappropriately processed the information provided by these traces. Maternal stress had an effect on the feeding site preference of *P. persimilis* females. Females from stressed mothers fed more often on the site without predator cues than did females from unstressed mothers, and this was especially true when the females were additionally predator-experienced. This observation coincides with an oviposition bias for the predator-cue free side, which was most pronounced in predator-experienced females from stressed mothers.

IGP risk for larvae is largely influenced and determined by the oviposition site preference of the mothers (Walzer et al. 2006; Walzer & Schausberger 2011, 2012). Because larvae have only six legs and are less mobile than the eight-legged nymphs and adults (Schausberger & Croft 1999), selective egg placement is a highly important strategy to increase the survival chances of offspring. Similar to my study, Walzer & Schausberger (2011) showed that *P. persimilis* avoids placing eggs in environments with cues of the IG predator *A. andersoni*. Total oviposition within 24 h was not affected by maternal stress or predator experience and showed no differences between the four treatment groups. Similarly, activity (moving or stationary inclusive feeding) of *P. persimilis* females was not affected by maternal stress and/or IGP experience. Time-dependent residence preference of females was influenced by maternal stress. Females emerging from unstressed mothers changed sites less often than females from stressed mothers. Frequent changes between leaves may reflect repeated information sampling, to check whether the risk in the surroundings changed or not, but needs further scrutiny by video-taping and -analysis.

Learning is a ubiquitous, tremendously important phenomenon across the animal kingdom, allowing an individual to appropriately adjust its behavior in changing environments (e.g. Papaj & Lewis 1993). Learning may affect every important life activity (e.g. foraging, mating, anti-predator behavior, etc.), and this has always fitness costs, but little is known about maternal effects, and here particularly maternal predation risk, on offspring learning ability in any animal. One of the few pertinent examples is the study by Roche et al. (2012), who showed for threespined sticklebacks (*Gasterosteus aculeatus*) that an ecologically relevant stressor (in this case a typical natural predator: the Northern pike) can induce negative effects on offspring learning. Offspring of predator-exposed mothers were less well able to improve in finding the food reward after training than were offspring of unexposed mothers (Roche et al. 2012). In my experiments, maternal stress during egg production interacted in some of the measured characteristics with individual learning by offspring, i.e. experiencing predators during development. In the first experiment, experienced protonymphs from stressed mothers were the least active and acted the boldest towards predator cues. A possible explanation is that protonymphs from stressed mothers had improved learning abilities because they were better able to discriminate the immediate risk associated with physical predator presence and their traces from the latent risk posed by predator traces alone, which are never directly fatal. Hackl & Schausberger (2014) observed a similar phenomenon in spider mites. In the second experiment, first oviposition occurred the latest in experienced females originating from

stressed mothers. Since information processing and decision-making takes time (Chittka et al. 2009), it could be that the experienced individuals from stressed mothers were the most selective ones. Selective egg placement is highly important for the fitness of the mother and her offspring because, if the decision is taken right, it increases the survival chances of offspring (see also Walzer & Schausberger 2011).

5 Conclusions

Predation risk-mediated maternal effects observed in my study were more pronounced in protonymphal than adult female offspring. It is plausible that maternal effects act the strongest early in life and weaken in the course of ontogeny due to the increasing and cumulating influence of individual experiences. Based on the fact that every anti-predator behavior bears costs in form of fitness loss, the attenuated response of experienced protonymphs from stressed mothers to predator traces alone may increase their fitness. A strong response was not necessary because no predator was physically present and no immediate risk existed. Moreover, since protonymphs are generally less endangered of being killed, the attenuated response to predator traces saved energy by being less restless and allowing spending more time feeding. Thus, all in all, my study suggests that *P. persimilis* mothers experiencing IGP risk may influence their offspring to behave more optimally in risky IGP environments. However, further comprehensive research is needed to find out whether the attenuated response of the protonymphs indeed only occurred because of the changes in risk level (coming from an immediate to a latent risk environment) or whether it would occur similarly under high immediate risk. In the latter case the maternal effects causing the behavioral change in the protonymphs would have to be considered non-adaptive because the protonymphs would then be considered less sensitive to predator cues. Maternal effects compromising the sensitivity of offspring to predator cues have recently been demonstrated for sticklebacks (McGhee et al. 2012). Future research should also quantify the fitness costs and benefits for offspring under predation risk, as influenced by maternal effects. Questions concerning the life-long consequences of maternally induced effects on offspring and the mother herself need to be addressed. My study provides first hints on whether and to which extent maternally induced behavioral effects can be balanced and/or superimposed by individual experience but studies scrutinizing the interactions between maternal stress and individual experience on other behaviors such as mating or foraging are lacking. Overall, my study is the first example for the existence of maternal effects in predatory mites in an (intraguild-) predation scenario and hence represents an important starting point and stimulus for exciting future research.

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List of figures

List of tables

Summary

Predation risk is a strong selective force shaping prey morphology, life history and behavior. Anti-predator behaviors may be innate, learned or both but little is known about the transgenerational behavioral effects of maternally experienced predation risk. In my thesis, I examined intraguild predation (IGP) risk-induced maternal effects on offspring anti-predator behavior, including learning, in the predatory mite *Phytoseiulus persimilis*. I reared predatory mite mothers on spider mites under risky and benign conditions (presence or absence of the IG predator *Amblyseius andersoni*) and assessed whether maternal stress during egg production affects the anti-predator behavior, including larval learning ability, of their offspring. Protonymphs and adult females originating from stressed or unstressed mothers, and having been exposed to predation risk during development or not, were subjected to choice situations with and without predator cues (traces of *A. andersoni*). The maternal effects observed in my study were more pronounced in protonymphal than adult female offspring. Predator-experienced protonymphs originating from stressed mothers were less active and acted bolder towards predator cues than naïve protonymphs and predator-experienced protonymphs originating from unstressed mothers. The attenuated response of the protonymphs to predator traces alone can ultimately be explained by the fact that every anti-predator behavior bears costs in terms of fitness loss. A strong response was not necessary because no predator was physically present and no immediate risk existed. Adult female offspring generally avoided oviposition on leaves harboring cues of *A. andersoni* but were subtly affected in oviposition timing and site choice by maternal stress and/or predator experience during development. Experienced females originating from stressed mothers deposited their first egg later and more strongly avoided oviposition on leaves with predator cues stronger than other females. Based on the fact that information processing and decision-making takes time, it thus seems that the experienced individuals from stressed mothers were the most selective ones. Accurate and selective egg placement is highly important for maternal and offspring fitness because, if the decision is taken right, it increases the offspring survival chances. Overall, my study suggests that *P. persimilis* mothers experiencing IGP risk may prime their offspring to behave more optimally in risky IGP environments.

Zusammenfassung

Prädationsrisiko ist eine starke Selektionskraft, die sich mannigfaltig auf die Morphologie, den Lebenszyklus und/oder das Verhalten von Beutetieren auswirken kann. Anti-Prädationsverhalten kann angeboren, erlernt oder ein Produkt von beidem sein. Sehr wenig ist über generationsübergreifende Beeinflussung des Anti-Prädationsverhaltens bekannt, d.h. wie sich z.B. mütterliche Erfahrungen mit Prädationsrisiko auf die Nachkommen auswirken. In meiner Studie habe ich die Frage untersucht, ob mütterliche Effekte einen Einfluss auf das Anti-Prädationsverhalten der Nachkommen, inklusive Lernen, in der Raubmilbe *Phytoseiulus persimilis* haben. Raubmilbenmütter wurden in Präsenz oder Absenz des Intragilden-Räubers *Amblyseius andersoni* aufgezogen, um herauszufinden, ob Stress während der Eiproduktion einen Einfluss auf das Anti-Prädationsverhalten der Nachkommen, inklusiver ihrer Lernfähigkeit, hat. Protonymphen und adulte Weibchen, die von gestressten oder nicht-gestressten Müttern abstammten, wurden ihrerseits während der Juvenilentwicklung Prädationsrisiko ausgesetzt oder nicht. Danach wurde das Verhalten der Tiere in binären Wahlversuchen beobachtet, wobei Plätze mit und ohne Spuren des Intragilden-Räubers *A. andersoni* angeboten wurden. Mütterliche Effekte waren stärker bei den Protonymphen als bei den adulten Weibchen zu beobachten. Prädator-erfahrene Protonymphen von gestressten Müttern waren weniger aktiv und reagierten wagemutiger gegenüber Räuberspuren, als naive Protonymphen und Prädator-erfahrene Protonymphen von ungestressten Müttern. Diese abgeschwächte Reaktion auf Räuberspuren, die ja keine direkte Gefahr darstellen, bringt wahrscheinlich Fitnessvorteile, da jedes übersteigerte Anti-Prädationsverhalten übermässige Fitnesskosten verursacht. Die adulten Weibchen haben es generell vermieden ihre Eier an Plätzen mit Räuberspuren abzulegen, waren aber subtil in der zeitlichen und räumlichen Ovipositionsabfolge durch mütterliche Effekte und individuelle Räuberfahrung beeinflusst. Erfahrene, von gestressten Müttern abstammende Weibchen legten ihr erstes Ei später und waren insgesamt selektiver in der Wahl der Eiablageplätze als die anderen Weibchen. Akkurate Informationsverarbeitung und Entscheidungsfindung benötigt Zeit und besonders selektive Wahl des Eiablageplatzes hat positiven Einfluss auf die evolutionäre Fitness der Mutter und ihrer Nachkommen, weil es deren Überlebenschancen erhöht. Insgesamt liefert meine Studie Hinweise darauf, dass Weibchen der Raubmilbe *P. persimilis*, die einer Intragilden-Umgebung ausgesetzt waren, ihre Nachkommen so programmieren können, dass sich diese optimaler bei Prädationsrisiko verhalten.

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