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Sex-specific parental intraguild predation risk affects offspring personality in predatory mites

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1. INTRODUCTION

Animal personalities are characterized by within-individual consistency and consistent among-individual variation in behaviour across time and contexts (Biro and Stamps 2008). Animal personality studies have traditionally mainly focused on vertebrate animals, even though 98% of all animal species are invertebrate animals (Kralj-Fišer and Schuett, 2014). In the last decade, quite a few studies showed that also insects (e.g., Tremmel and Müller, 2012; Jandt et al., 2014; Golab et al., 2021), spiders (e.g., Chang et al., 2014; Liedtke et al., 2015) and mites (e.g., Schausberger et al., 2024; Schausberger and Nguyen, 2025) have personality. Apart from, or in addition to, the genetic makeup, the personality of an individual can be formed and influenced by the environmental conditions experienced by themselves and/or by their parents, with the latter being called parental effects (Reddon, 2011). Some examples of environmental stress conditions are cannibalism, intraguild predation (IGP) and/or competition for food. IGP is defined by consumers that are potential resource competitors killing and eating each other, and it is a functionally complex relationship (Polis et al., 1989; Polis and Holt, 1992). Environmental factors can have long-lasting impacts on shaping the personality of an individual, especially when they are experienced in early life (Langenhof and Komdeur, 2018), or when they are experienced by the parents and effects are transferred to offspring. Such parental or transgenerational effects also play an important role in shaping an individual`s personality (Reddon, 2011). In this master thesis, I investigated whether the early life experience of parents affects the offspring' personality in predatory mites *Phytoseiulus persimilis*, and if so, whether this effect is mediated by the mother (maternal effect), the father (paternal effect) or by both parents (parental effect).

1.1 Animal Personality

Animal personality describes the consistency of individual behaviour and consistent variability among individuals over time and contexts (e.g., Biro and Stamps, 2008). Typical behavioural traits used to characterise animal personalities are sociability, exploration, boldness, activity, and aggressiveness (Figure 1), which have been accordingly used to evaluate personality in many animal species (Réale et al., 2007;

Biro and Stamps, 2008), including predatory mites of the family Phytoseiidae (Acari, Mesostigmata) (Schausberger et al., 2024).

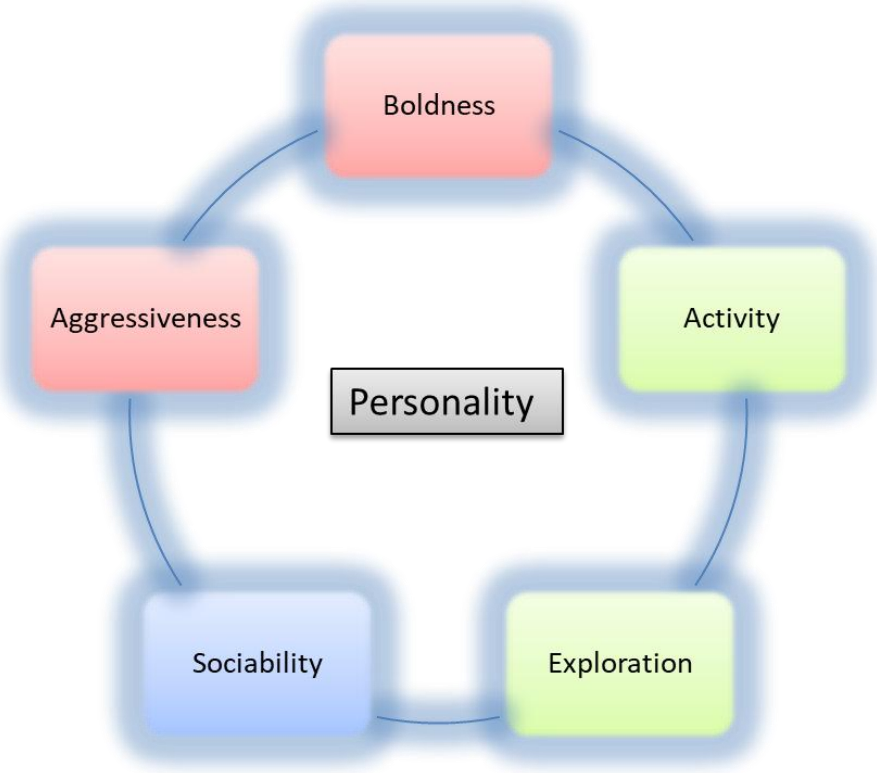

Figure 1. Five canonical behavioural dimensions of animal personality (Réale et al., 2007).

Several pathways may mediate personality, including the genetic makeup and environmental effects experienced by the individuals themselves (Langenhof and Komdeur, 2018) as well as transgenerational influences (Reddon, 2011). Regarding environmental effects, diet, social interactions, or predation risk can critically shape an individual's personality (Figure 2). The associated behavioural shifts are typically seen as an individual's adaptive behavioural response (Réale et al., 2010). As an example of a diet effect, Southern field cricket (*Gryllus bimaculatus*) males became more active during mating and more aggressive when they previously fed a high-protein diet (Han and Dingemanse, 2017).

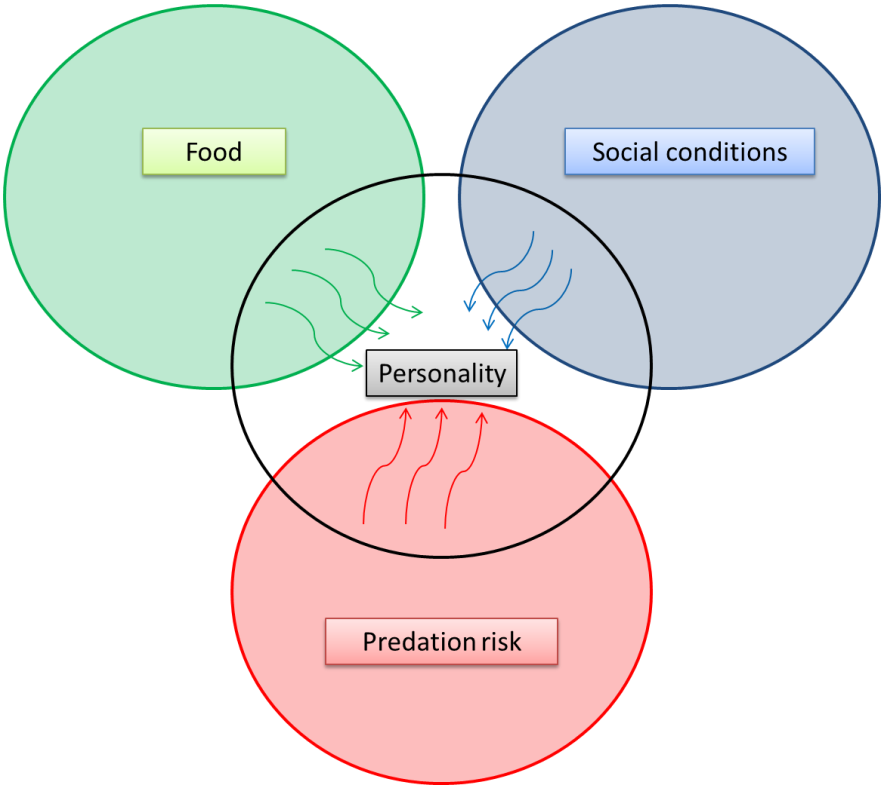

Figure 2. Major environmental contexts affecting animal personality.

Predation risk is one of the most critical environmental factors affecting survival and reproductive success (e.g., Lima and Dill, 1990; Ferrari et al., 2009). Exposure to predators or their cues can increase boldness or shyness in prey species (Lima and Dill, 1990). For instance, wild zebrafish, *Danio rerio*, from populations from a high-predation risk stream habitat were on average more aggressive and bolder than those from low-predation risk habitat populations (Roy and Bhat, 2018). Similarly, Trinidadian guppies (*Poecilia reticulata*) showed higher boldness and exploration behaviour when they came from high-predation risk environments, compared to others from low-predation risk areas, which can be interpreted as an adaptive response (Brown et al., 2005). Environmental factors, if experienced in very early life stages, can cause persistent and even life-long behavioural changes in individuals (Langenhof and Komdeur, 2018). In consequence, they can also influence offspring behaviour via transgenerational effects (Reddon, 2011; Yin et al., 2019).

1.2 Early Life Experiences

Early life experiences are some of the most critical factors shaping behavioural trajectories, including animal personality formation and phenotypes of adults (Langenhof and Komdeur, 2018). Traumatic experiences at an early age, such as exposure to predation risk, have the potential to permanently impact an individual's personality (Langenhof and Komdeur, 2018). Boldness, activity and aggressiveness are typical personality traits influenced by early-life predation risk experience, and are often part of a behavioural syndrome (Schausberger et al., 2024). For instance, adult clonal Amazon mollies (*Poecilia formosa*) individuals became less active during feeding trials when they had been exposed to predation risk in their early life stage (Scherer et al., 2024). By contrast, adult predatory mites *Phytoseiulus persimilis* showed increased aggressiveness and boldness when they had experienced predation risk during the larval and protonymphal stages (Schausberger et al., 2024). Also, adult *P. persimilis* females became less sociable and avoided being close to other females when they had been socially isolated in their early life (Schausberger and Nguyen, 2025).

1.3 Intraguild Predation (IGP)

Intraguild predation (IGP) is defined as the killing and eating among predators from the same guild (Polis and Holt, 1992). A guild comprises all species and individuals that exploit joint resources in a similar way and may thus engage in exploitation competition (Polis et al., 1989). IGP is a functionally complex relationship between two predator species or individuals, because it is a combination of predation and competition (Polis et al., 1989; Han and Salman, 2024). In many IGP relationships, there is a minimum of two or three species: an IG-Predator, an IG-Prey, and a shared prey species or other shared food for both predators (Figure 3; Arim and Marquet, 2004). This complex relationship can be observed in different ecosystems and in many organisms, such as in terrestrial, fresh water and marine ecosystems, in vertebrates as well as invertebrates (Sharif and Mohd, 2022). For instance, cape fur seals (*Arctocephalus pusillus*) can kill blue sharks (*Prionace glauca*) (Fallows et al., 2015) or salticid spiders (*Hyllus brevitarsus*) can predate large orb weaver spiders (*Nephila senegalensis*) (Gilman, 2016). Humans also have IGP interactions as IG-

Predators, for example, when consuming tuna fish and their shared prey, sardines (Lucas and Maisonhaute, 2019).

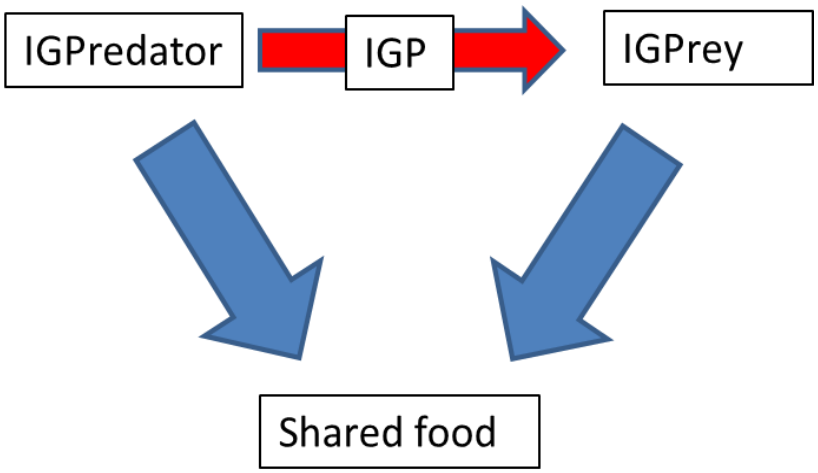

Figure 3. Scheme of Intraguild Predation (IGP).

IGP does not occur randomly; several factors influence its occurrence and intensity, such as the population densities of IG-Predators, IG-Prey, and extraguild prey (Figure 4) (Lucas and Maisonhaute, 2019). Often, IGP can be mutual or two-sided, and the IG-Prey can kill the early life stages of the IG-Predators. IGP can be symmetrical, when both predators equally eat each other, or asymmetrical, when one predator more likely or more often eats the other one. When comparing the body sizes of mutual IG-Predators, the larger animal typically kills the smaller one.

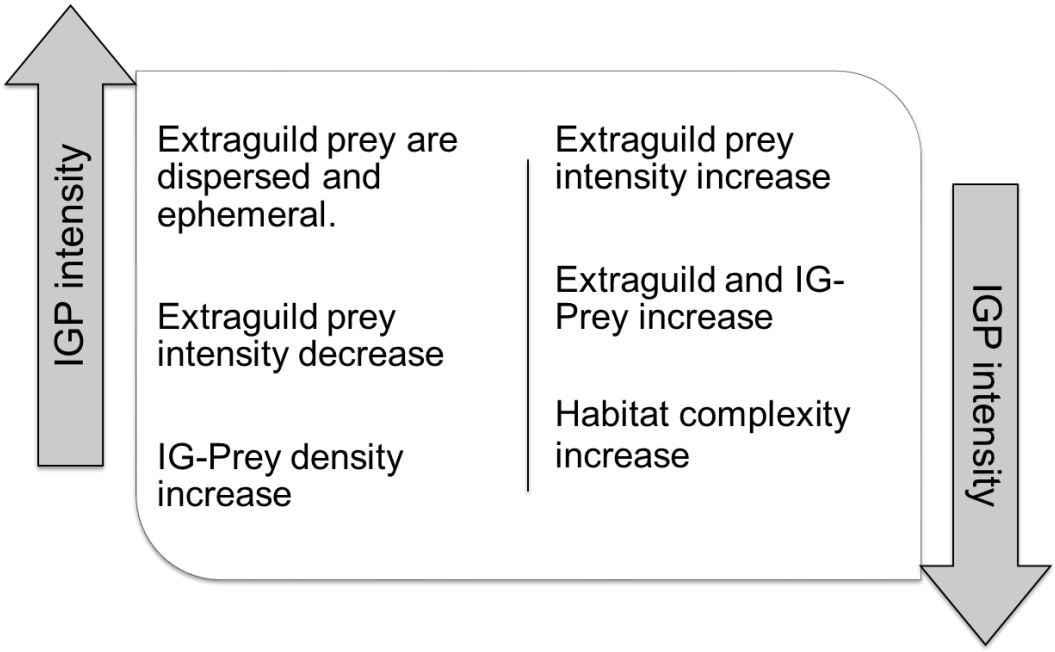

Figure 4. Typical factors influencing IGP intensity (Lucas and Maisonhaute, 2019).

IGP plays a critical role in biodiversity and population dynamics. IGP can benefit the IG-Predator population by eliminating or reducing the potential predation and competition risk for the IG-Predators themselves or their offspring (Palomares and Caro, 1999). It impacts IG-Prey populations, such as reducing, or even extinction of, the IG-Prey population in shared habitats (Lucas and Maisonhaute, 2019).

1.3.1 Phytoseiid IGP

Some species of the family Phytoseidae are highly important natural enemies of herbivores and widely used as biological control agents in agriculture and horticulture (Helle and Sabelis, 1985; McMurtry and Croft, 1997). They can predate important pests like two-spotted spider mites (TSSM) *Tetranychus urticae* and thrips (Helle and Sabelis, 1985). Some predatory mite species are diet specialists and feed on just one specific food type, like *Phytoseiulus persimilis* feeding on tetranychid spider mites, but most species have more generalized feeding habits; they can feed on more than one prey species or plant-derived food such as pollen (McMurtry and Croft, 1997). IGP commonly occurs in the family Phytoseiidae, and especially generalist species often kill other specialist members of the same family (Schausberger and Croft, 2000). A previous study reported that *Amblyseius andersoni* and *Neoseiulus californicus* are IG-Predators of *P. persimilis*, and among these species, *A. andersoni* is the strongest IG-Predator; meanwhile, *P. persimilis* is the weakest IG-Predator and most vulnerable IG-Prey (Figure 5; Walzer and Schausberger, 2011). The larval stage of *P. persimilis* is the smallest and least mobile stage, making them the most vulnarable life stage against IG-Predators (Walzer and Schausberger, 2011).

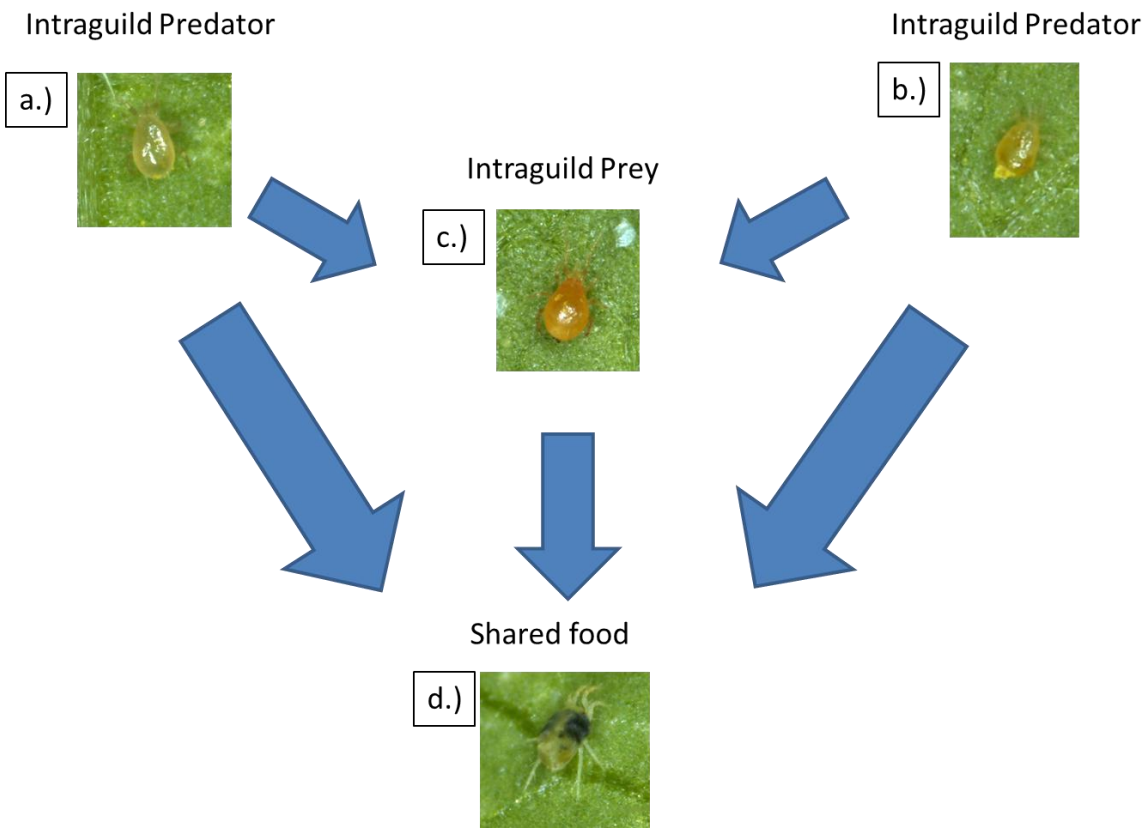

Figure 5. Scheme of phytoseiid IGP as used in my study, with *P. persimilis* being the target species: a.) intraguild predator *A. andersoni*, b.) intraguild predator *N. californicus* c.) intraguild prey *P. persimilis* and d.) shared food (= extraguild prey) *T. urticae* (© Mustafa Altintas).

1.4 Parental Effects

Parental effects are a type of transgenerational effects, i.e. non-genetic environmental influences passed from ancestral generations to offspring and causing phenotypic but not genotypic changes (Bonduriansky and Day, 2009), can influence the offspring in several ways across animal and plant species (Yin et al., 2019). Parents can affect their offspring' personality maternally, paternally, or both together (Reddon, 2011). Traumatic stress often modifies behaviour, and its impact can be transmitted to the next generations even if the individuals of these generations are no longer exposed to the same traumatic stress (Figure 6; Jawaid et al., 2018; Yin et al., 2019).

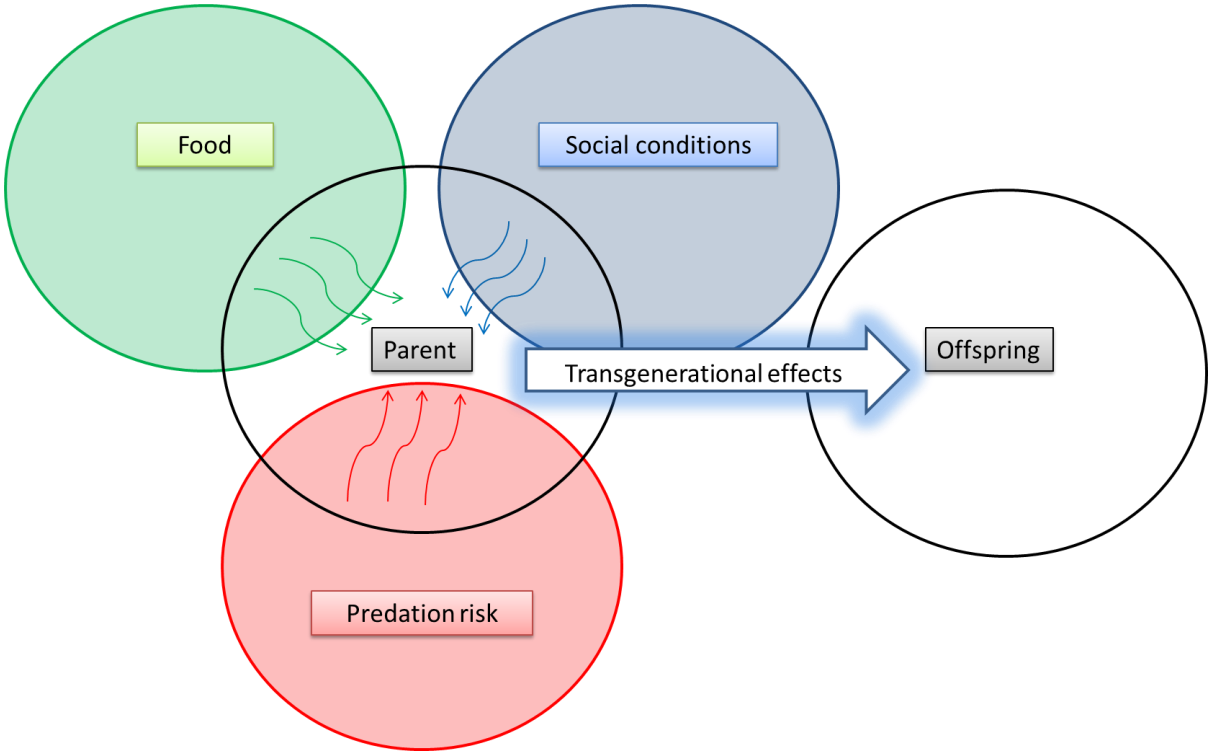

Figure 6. The scheme of transgenerational effects on offspring.

Arthropods, including the embryos inside eggs, can respond to risks in several ways to increase their survival rates. Parents can adjust the egg phenotype or composition, embryos inside eggs can react to environmental challenges, or egg-associated microbes (symbionts) can modify later-expressed phenotypes (Hilker et al., 2023). Also, some arthropods like *P. persimilis* can change their oviposition preferences, kill the potential predators of their offspring or postpone/reduce oviposition when there is predation risk, as a defence mechanism to minimise risk (Walzer and Schausberger, 2011). Strikingly, there is no study on whether these parental behavioural shifts to IGP risk impact the offspring' personality. Besides such prenatal parental influences, prenatal learning can also influence offspring behaviour. For instance, the diet preference of juvenile *Neoseiulus californicus* can be influenced by the maternal diet through chemosensory experiences of embryos inside the egg (Peralta Quesada and Schausberger, 2012).

1.5 Aims of the Study

This study aims to understand (i) whether the parental early-life experiences of the predatory mite *Phytoseiulus persimilis* influence the behaviour and personality of their offspring and, if so, (ii) to determine, which parent affects the offspring' behaviour and personality. Previous studies with *P. persimilis* showed that early-life IGP risk experiences influence the personality along the shy/bold axis (Schausberger et al., 2024). Still, no further research exists about whether early-life experiences transfer to the next generations and induce personality changes in offspring. In this study, I examined parental early-life IGP risk experience effects on the expression of personalities in boldness, exploration and sociability of plant-inhabiting predatory mites *P. persimilis*. *P. persimilis* is an ideal organism to test these research questions because of its short life cycle, being a specialist predator of spider mites, living in groups, and often being intraguild prey of other phytoseid mites. *Amblyseius andersoni* and *N. californicus* were used as IG-Predators, because they are known to be strong IG-Predators of *P. persimilis* (Walzer and Schausberger 2011), and all three predatory mite species co-occur in the Mediterranean basin (De Moraes et al., 2004; Schausberger et al., 2024).

2. MATERIALS AND METHODS

2.1 Study Organisms

2.1.1 Predatory Mite *Phytoseiulus persimilis*

Phytoseiulus persimilis was used as the target experimental species (Figure 7). *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseidae; Table 1) is one of the most effective predatory mites in biological control.

Table 1. Taxonomy of *Phytoseiulus persimilis* (https://www.uniprot.org/taxonomy/44414).

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

P. persimilis was first time described by Athias-Henriot in 1957 from Algerian plant samples (Sekeroglu and Kazak, 1993). It is a biological control agent against *Tetranychus urticae* in arable and horticultural crops, greenhouse crops, and widely used as a model animal in laboratory studies in behaviour, ecology and evolution (Tiftikci et al., 2020). *P. persimilis* feeds only on tetranychid mites, and is dubbed as a Type-I specialist predator by McMurtry and Croft (1997) (Fathipour et al., 2019).

Figure 7. Adult *P. persimilis* female attacking a spider mite female (©Peter Schausberger)

This predatory mite species has been introduced in many parts of the world, exists worldwide between the latitudes 60°S and 60°N (Figure 8). An estimated 21.67% of the world's land area is climatically suitable for the release and use of *P. persimilis* (Li et al., 2024).

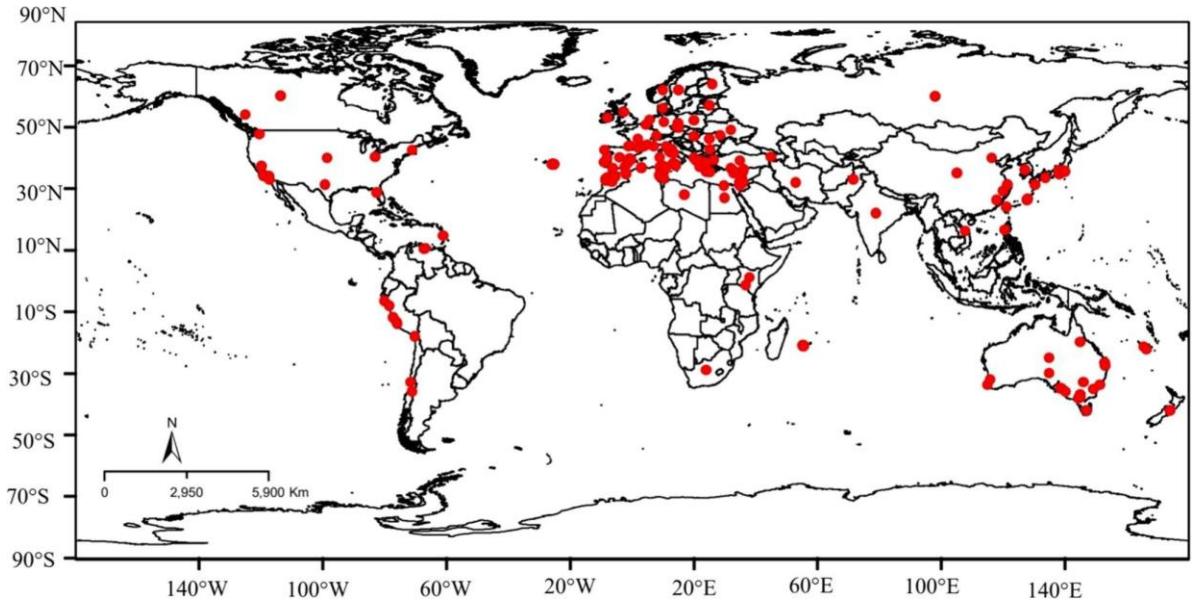

Figure 8. The occurrence reports of *P. persimilis* worldwide (Li et al., 2024, https://scijournals.onlinelibrary.wiley.com/cms/asset/76aaeca9-d0de-4d9e-b9f4-3a33428c7b78/ps8196-fig-0001-m.jpg).

The optimal development of *P. persimilis* is between 15 °C and 27 °C and a relative humidity of 60 to 90% (Le Hesran et al., 2019). *P. persimilis* is very sensitive to low humidity and cold; it requires a minimum of 55% humidity for egg hatch, and 10.6 °C is the minimum threshold for its developmental progress (Li et al., 2024).*Phytoseiulus persimilis* has five life stages, like all other phytoseiid mites (Fathipour and Maleknia, 2016): egg, larva, protonymph, deutonymph, and adult (Figure 9).

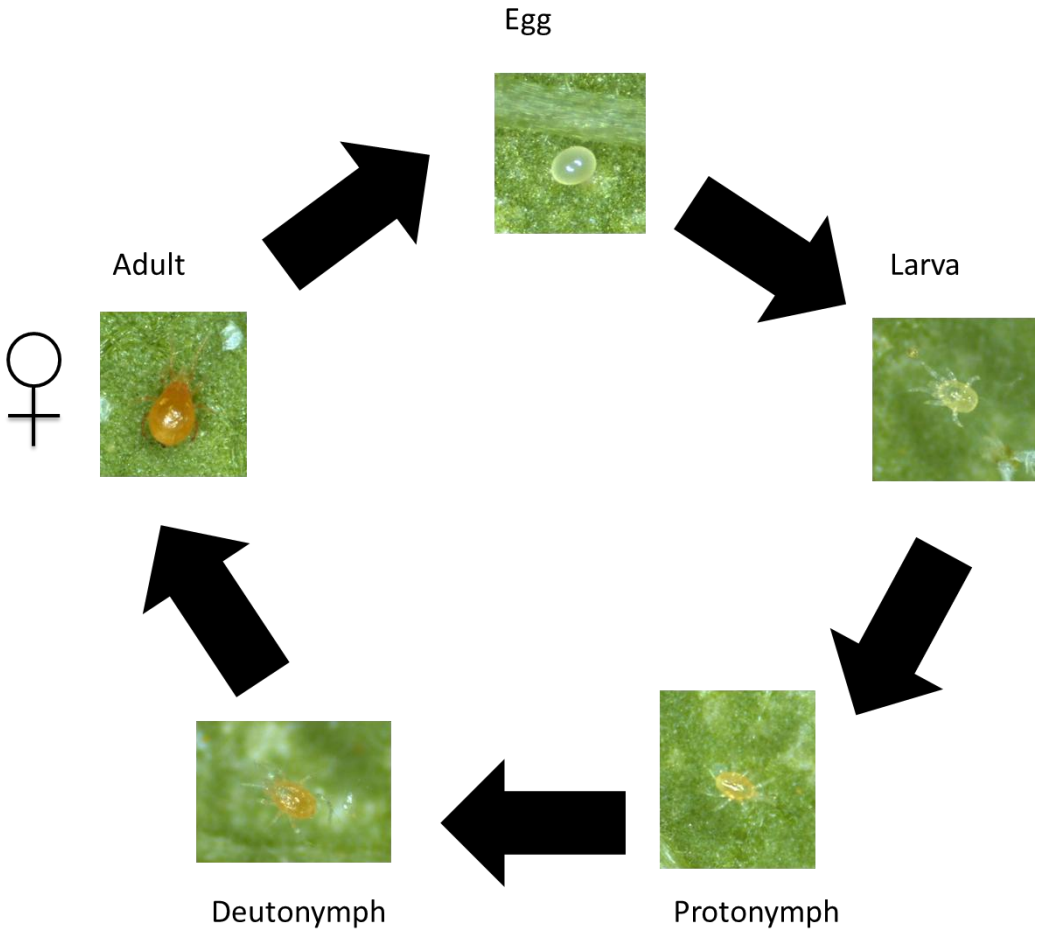

Figure 9. The life cycle of a *Phytoseiulus persimilis* female (© Mustafa Altintas).

Under optimal conditions (25 °C, >60% RH), its development takes around five to six days from egg to adult. The larvae do not eat, but after reaching the protonymphal stage, they start feeding on tetranychid prey. One adult female can predate daily up to 20 to 30 spider mite eggs, 10 to 20 juveniles, or 3 to 5 adult spider mite females (Fathipour and Maleknia, 2016). *P. persimilis* mites start mating right after the last moult of the deutonymphal stage, and females can lay up to 5 eggs daily at 25 °C and 98% relative humidity (Stankevych et al., 2021). They lay eggs mainly on the

underside of leaves, typically on trichomes (leaf hairs) and inside the spider mite webbing. Their eggs differ from spherical spider mite eggs, by having an oval shape, larger size and pale pink colour (Stankevych et al., 2021). Depending on the temperature, the egg stage takes 1 to 2 days, and six-legged larvae hatch from the egg. After the first moulting, they turn into eight-legged protonymphs, and moulting occurs between each stage. Like most phytoseiid mites, *P. persimilis* also engage in IGP and cannibalism but less so than *Amblyseius andersoni* and *Neoseiulus californicus* (Walzer and Schausberger, 2011; Schausberger et al., 2024).

2.1.2 Predatory Mite *Amblyseius andersoni*

Amblyseius andersoni was used as IG predator*. Amblyseius andersoni* Chant (Acari: Phytoseidae; Table 2) is a type-III generalist predatory mite (McMurtry and Croft, 1997).

Table 2. Taxonomy of *Amblyseius andersoni* (https://www.uniprot.org/taxonomy/714357).

Kingdom	Animalia
Phylum	Arthropoda
Subphylum	Chelicerata
Class	Arachnida
Subclass	Acari
Superorder	Parasitiformes
Order	Mesostigmata
Superfamily	Phytoseioidea
Family	Phytoseiidae
Genus	Amblyseius
Species	*Amblyseius andersoni* Chant, 1957

It can be used as a biocontrol agent against phytophagous mites (Figure 10) in greenhouses, orchards and vineyards (Puchalska et al., 2021). *A. andersoni* can feed on pollen and plant juices when there is no prey available, making them highly

versatile in biological control (Duso and Pasini, 2003). Many generalist phytoseiid mites can also predate small insects like thrips, coccids and/or whiteflies (Lorenzon et al., 2012).

Figure 10. *Amblyseius andersoni* female predating *Tetranychus urticae* (© Mustafa Altintas).

A. andersoni is commonly found in apple orchards, especially in Europe, but it also occurs in China (Li et al., 2019) and North America (De Moraes et al., 2004). It can well reproduce between 17 and 35 °C and goes into diapause during winter time; egg production increases with temperature, and most eggs are produced at 25 °C (Li et al., 2019). The ability to survive and reproduce at temperatures between 30 to 35 °C makes them important predators in hot conditions (Li et al., 2019). They have the strongest propensity to cannibalism and IGP among the three phytoseiid species, *P. persimilis*, *N. californicus* and *A. andersoni* (Walzer and Schausberger, 2011). *A. andersoni* also has five life stages: egg, larva, protonymph, deutonymph, and adult, the same as *P. persimilis* (Figure 9).

2.1.3 Predatory Mite *Neoseiulus californicus*

Neoseiulus californicus was used as IG predator. *Neoseiulus californicus* McGregor (Acari: Phytoseidae; Table 3) is a type-II selective predator of tetranychid mites (McMurtry and Croft, 1997). It also has characteristics of a type-III predator and prefers tetranychid mites as prey but can also feed on other mites and thrips or pollen when no tetranychid food is available (Fathipour and Maleknia, 2016). This species is successfully used as a biocontrol agent against spider mites in field and greenhouse crops (Walzer et al., 2007).

Table 3. Taxonomy of *Neoseiulus californicus* (https://www.uniprot.org/taxonomy/84382).

Kingdom	Animalia
Phylum	Arthropoda
Subphylum	Chelicerata
Class	Arachnida
Subclass	Acari
Superorder	Parasitiformes
Order	Mesostigmata
Superfamily	Phytoseioidea
Family	Phytoseiidae
Genus	Neoseiulus
Species	*Neoseiulus californicus* McGregor, 1954

N. californicus is widely distributed in Asia, Europe, Africa, North America and South America (Wang et al., 2021; Figure 11). It naturally occurs in California, South America, North Africa and the Mediterranean basin, which indicates that this species has the potential to adapt to arid conditions better than other phytoseiid predators (Walzer et al., 2007). It can reproduce well between 15 to 35 °C (Gotoh et al., 2004), but most eggs are laid at 25 °C (Nguyen and Amono, 2010).

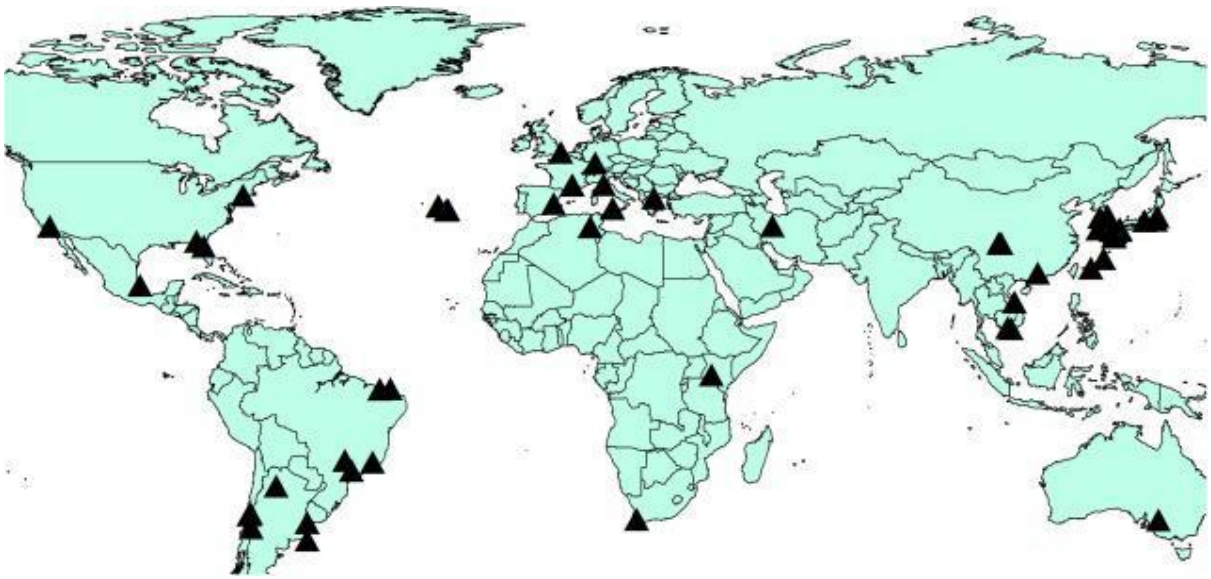

Figure 11. Global occurrence of *N. californicus* (Wang et al., 2021, https://ars.els-cdn.com/content/image/1-s2.0-S2351989421002833-gr1.jpg).

N. californicus has the same life cycle as the previously described phytoseiid predators (Figure 9).

2.1.4 Prey Mite *Tetranychus urticae*

The two-spotted spider mite (TSSM) *Tetranychus urticae* (Koch) (Acari: Prostigmata: Tetranychidae; Table 4) is a significant herbivorous pest in agriculture and horticulture, with more than 1000 host plant species described (Han et al., 2024).

Table 4. Taxonomy of *Tetranychus urticae* (https://www.uniprot.org/taxonomy/32264).

Kingdom	Animalia
Phylum	Arthropoda
Subphylum	Chelicerata
Class	Arachnida
Subclass	Acari
Superorder	Acariformes
Order	Trombidiformes
Suborder	Prostigmata
Superfamily	Tetranychoidea
Family	Tetranychidae
Genus	Tetranychus
Species	*Tetranychus urticae* Koch, 1836

The typical black spots on both sides of the body represent digestive cells (Bensoussan et al., 2018) and are the reason why they are called two-spotted (Figure 12). They also have one pair of eyes on the front part of the body. Spider mites reproduce well between 15 to 35 °C, but the optimum temperature is about 30 °C (Praslicka and Huszar, 2004). From egg to adult, it takes about 6.5 days at 35 °C and about 7.5 days at 30 °C; when the temperature decreases to 15 °C, it takes around 16 days (Praslicka and Huszar, 2004). Fecundity also increases with temperature until 30 °C, but decreases again at temperatures >30 °C. They have the same life stages described for *P. persimilis* above (Figure 9), with the exception that they enter so called chrysalis stages before each moulting event.

Figure 12. Adult *T. urticae* female and an egg (© Peter Schausberger).

T. urticae occurs worldwide in open field and greenhouse crops and has the potential to cause enormous economic damage (Figure 13; Al-Zahrani et al., 2023).

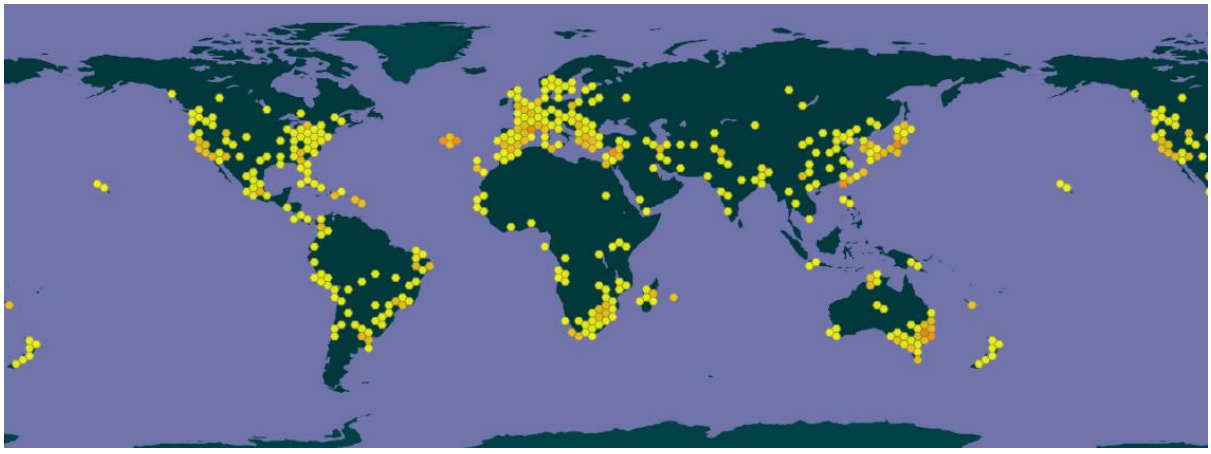

Figure 13. Global distribution of *T. urticae* (https://www.gbif.org/species/2130185).

Tetranychus spp. can produce dense silk webs to construct nest-like structures (Figure 13). One potential function of this complicated web structure is an anti-

predator defence system (Shimoda et al., 2010). They feed on the contents of parenchyma cells, especially on the abaxial side of the leaves, but the damage is also visible on the upper surface of the leaves, with whitish or cream-coloured punctuations first, which then turn into darker brown spots (Figure 14; Al-Shammery and Al-Khalaf, 2022). In this study, all life stages of *T. urticae* were used as prey.

Figure 14. The leaf damage caused by *T. urticae* and the web structure on a bean plant (© Mustafa Altintas).

2.2 Rearing

2.2.1 Predatory Mite Rearing

The founder specimens of the laboratory population of *P. persimilis* were collected from eggplants (*Solanum melongena*) in Palermo, Sicily. In the laboratory, *P. persimilis* was reared in heaps of *T. urticae*-infested bean leaves. The infested leaves were placed on an acrylic platform (14.0 x 14.0 x 0.2 cm) on a water-soaked sponge block (14 x 14 x 5 cm) surrounded by tap water inside a plastic box (20 x 20

x 6 cm). Fresh spider mite-infested leaves were placed twice weekly on top of old ones to feed the predators. Each rearing unit was placed in a plastic tray (40 x 30 x 8 cm) and covered by a cubic acrylic case with a mesh-covered ventilation hole (10 cm Ø) on top, to avoid contamination by other organisms and prevent predator escaping (Figure 15).

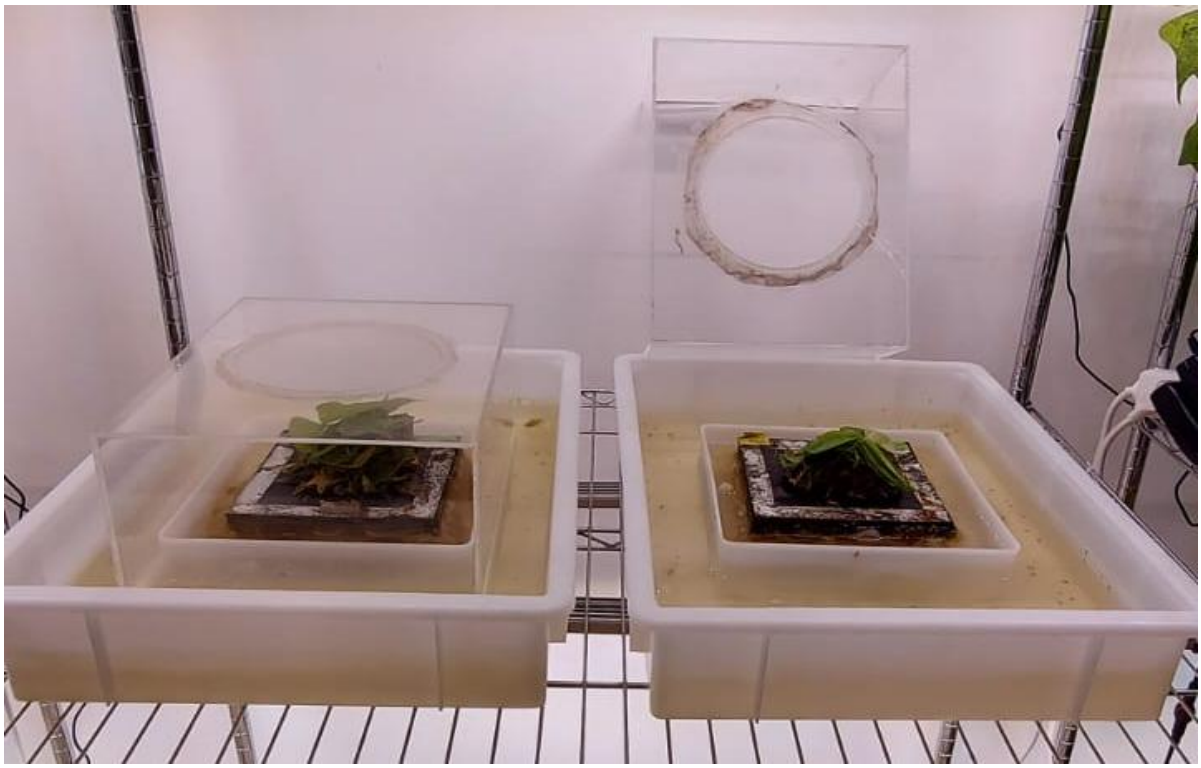

Figure 15. *P. persimilis* rearing in heaps of detached bean leaves (© Mustafa Altintas).

Amblyseius andersoni (founder specimens obtained from Biobest, BE) and *Neoseiulus californicus* (founder specimens obtained from Koppert, NL) were reared on platforms that were similarly constructed as those described above for *P. persimilis* but without leaves (Figure 16). Two-spotted spider mites were brushed from infested bean leaves twice weekly on the platforms to feed the predators. Also, cattail pollen, *Typha angustifolia* (Nutrimite^{TM}), was dusted onto the platform twice weekly. All laboratory populations of predatory mites were kept in the same room at 23 ± 1 °C, 50 to 60% RH, and 16h light, 8h dark conditions.

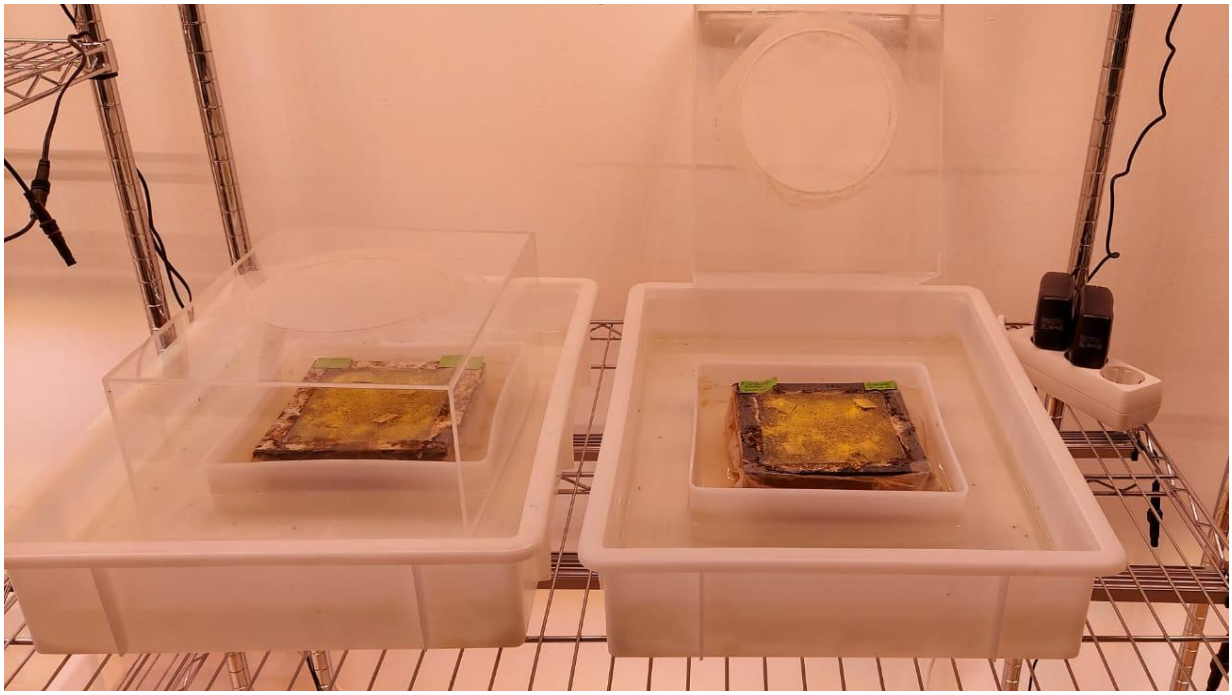

Figure 16. *A. andersoni* rearing (© Mustafa Altintas).

2.2.2 Spider Mite Rearing

The founder specimens of the laboratory population of *T. urticae* (green form) were collected on common bean plants, *Phaseolus vulgaris* in a greenhouse in Vienna. In the laboratory, the spider mites were reared on whole common bean plants *Phaseolus vulgaris* L. (var. Maxi) at 23 ± 1 °C and 16h light 8h dark conditions (Figure 17).

Figure 17. Spider mite population on common bean plants (© Mustafa Altintas).

2.3 Experimental Procedure

2.3.1 Pre-Experimental Treatments

In the experiment, I used four types of individuals that emerged from parents that had been subjected to IGP risk during early development or not. All experimental animals had the same genetic background and differed only in the parental early-life IGP experiences. To generate the parental generation (F0) of the experimental animals, gravid female predators were randomly chosen from the rearing and placed in groups of 15 in large detached bean leaf arenas infested with spider mites. Each large detached bean leaf arena consisted of a primary leaf of common bean *Phaseolus vulgaris* (Maxi), placed abaxial side up on a moist filter paper on top of a water-soaked sponge cube (14 x 14 x 4 cm) inside a plastic box (20 x 20 x 6 cm) half-filled with tap water. Wet tissue paper was wrapped around the edges of the detached bean leaves to avoid that the predators escape from the arenas. Eggs laid

by the predators within the first 24 h were collected and transferred in groups of 15 to small detached bean leaf arenas. Each small leaf arena consisted of a trifoliate leaflet of common bean, which was placed with the abaxial side up on a moist filter paper on top of a small sponge cube (6 x 6 x 5 cm) inside a small plastic box (10 x 10 x 6 cm) (Figure 18).

Figure 18. IG predator risk arenas for the parental generation of *P. persimilis* (© Mustafa Altintas).

Before adding the predator eggs on the leaves, five gravid spider mite females were placed in the leaf arenas for three days and allowed to lay eggs; after three days, the spider mite females were removed, and some cattail pollen, *Typha angustifolia* was dusted on the leaf. When all eggs of *P. persimilis* had hatched, two gravid females of the IG-Predator *Amblyseius andersoni* were added in half of the arenas for two days, to expose the immature *P. persimilis* to IGP risk, and the other half of arenas was left

without IGP risk, i.e. without adding *A. andersoni* females. The arenas were checked daily for the survival and developmental progress of *P. persimilis*, from egg to the deutonymphal stage, which took six to seven days. When they reached the deutonymphal stage, the predatory mites were singly transferred to small fresh detached leaf arenas, constructed as described above, to avoid random mating. As soon as the isolated individuals became adult, their sex was determined and the predators grouped according to their treatment on separate small leaf arenas. Each adult female (F) that had experienced IGP risk in early life (+) or not (-) was paired with a male (M) that had experienced IGP risk (+) or not (-), resulting in four parental treatments (F+M+, F+M-, F-M+, F-M-) (Figure 19). Eggs laid within 24 h by the females of the four treatments were collected and transferred in four groups of 10 eggs each, grouped according to the four parental treatments, into four fresh spider-mite infested detached bean leaflet arenas. Offspring (F1) of the four parental treatments (F+M+, F+M-, F-M+, F-M-) were separately reared on these leaf arenas, all with surplus spider mites but without IG-Predators, until they became adult and mated. Mated females and males of the F1 generation were used as experimental animals.

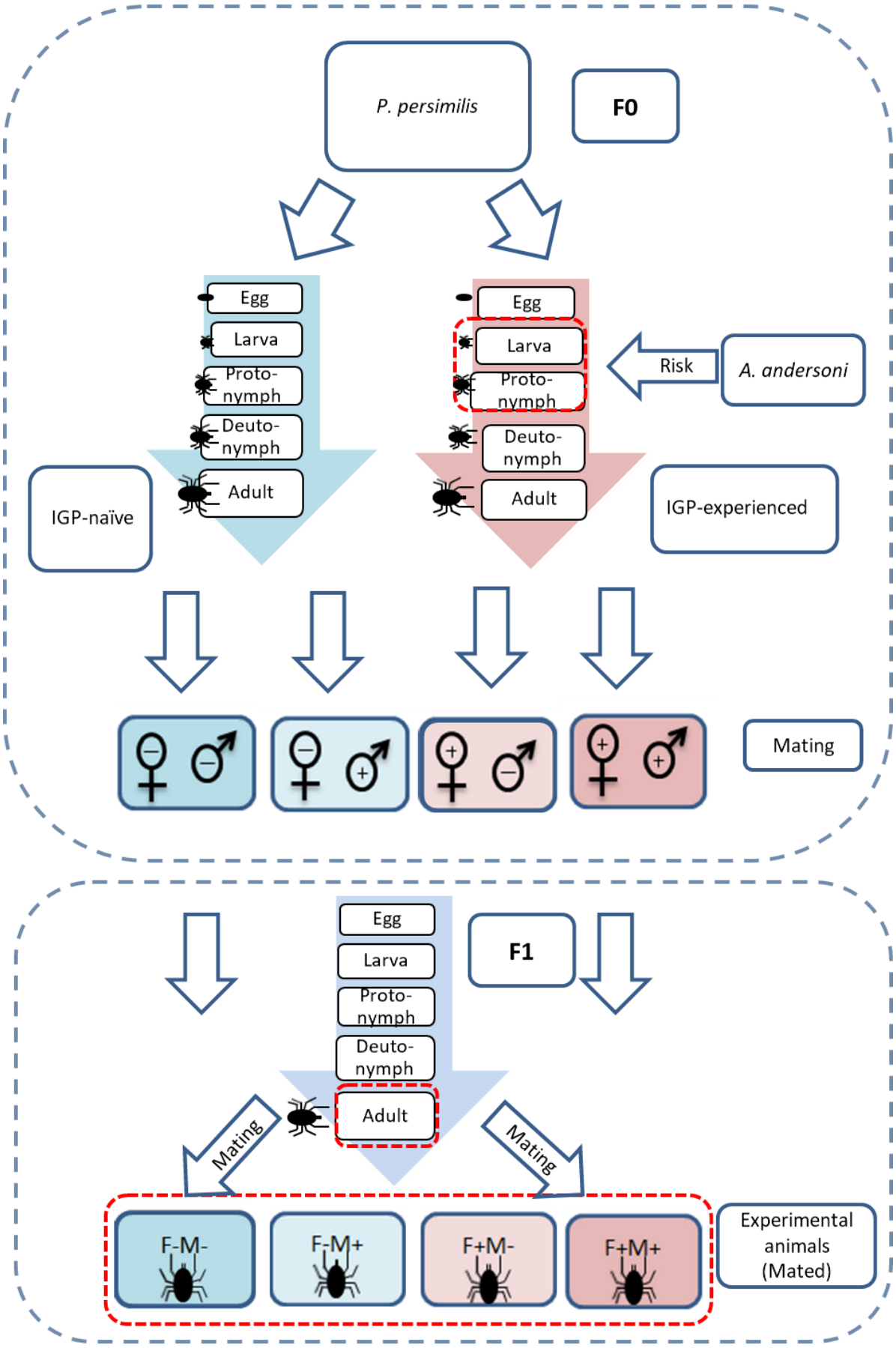

Figure 19. The scheme of the procedure of producing the experimental animals.

2.3.2 Personality Assays

The experiment aimed at assaying three of the five canonical personality traits, exploration, boldness and sociability (Réale et al., 2007). For the experiment, gravid females and adult males were singly transferred from the leaf arenas to acrylic cages containing spider mites, serving as the home cages of the predatory mites throughout the experiment. Each home cage consisted of a cylindrical cavity (15 mm ø) drilled into rectangular acrylic plates (80 x 35 x 3 mm), covered with fine mesh on the bottom for ventilation and with a microscope slide on top, secured in place with binder clips (Schausberger, 1997; Figure 20). Each cage was labelled with the unique code of the experimental individual inside. All experimental individuals were returned to their home cages between personality assays. Fresh spider mites were added to the cages as needed, approximately every two days. The home cages were stored in a climate chamber (Panasonic MLR-352H-PE) at 23 ± 1 °C, 60 ± 5% RH, and 16h light, and 8h dark between the personality assays.

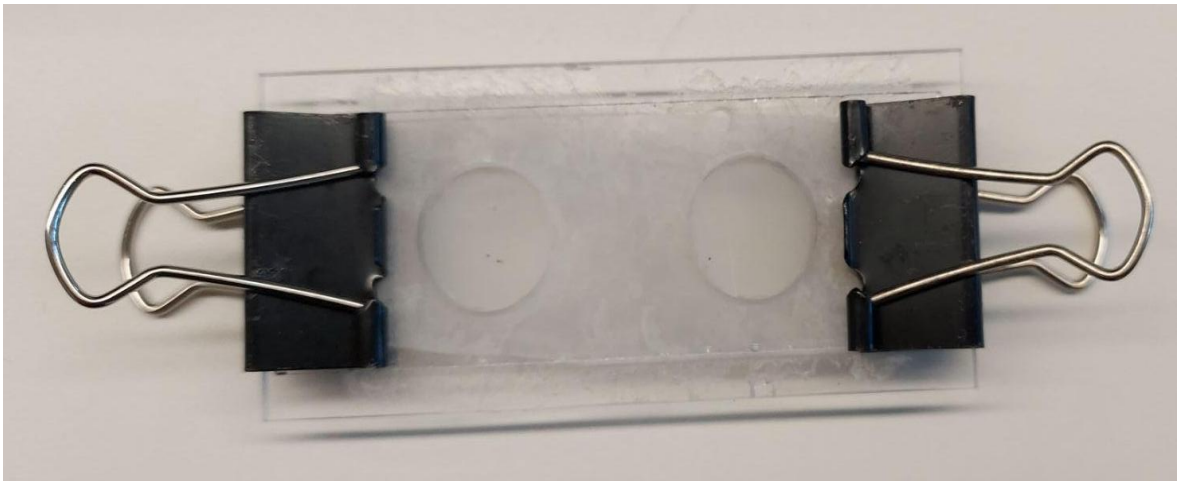

Figure 20. Home cages of the predatory mites (© Mustafa Altintas).

Personality assays were conducted over eight consecutive days, with one assay per day. On the first two days, always one of the two exploration assays was conducted followed by the other exploration assay. On the remaining six days, the three boldness assays and the three sociability assays were performed, with the order of sociability and boldness randomized within each group. Single exploration, boldness,

and sociability assays were never intermingled among traits but all assays of a given trait were conducted on consecutive days.

2.3.2.1 Exploration Assays

Each experimental animal was subjected to two exploration assays.

Assay 1. Explore a habitat with novel leaf infested by spider mites

The first exploration assay was conducted using a setup of two cylindrical cavities (15 mm ø) connected by a 2 mm-wide aisle, drilled into an acrylic plate (80 x 35 x 3 mm). Each acrylic plate was covered with fine mesh on the bottom for ventilation and a microscope slide on top, secured with a binder clip (Figure 21). Single *P. persimilis* individuals were placed into one cavity of the two-sided setup, containing five spider mite eggs. The aisle leading to the second cavity, which was equipped with a fragment from a cucumber leaf (1.1 cm disc) with five spider mite eggs, was blocked by a piece of a silicon tube for 5 min. After removing the silicon tube from the connecting aisle, the cage was continuously monitored to record the time elapsed until the experimental animal moved to the cavity with the novel leaf fragment, for a maximum of four hours.

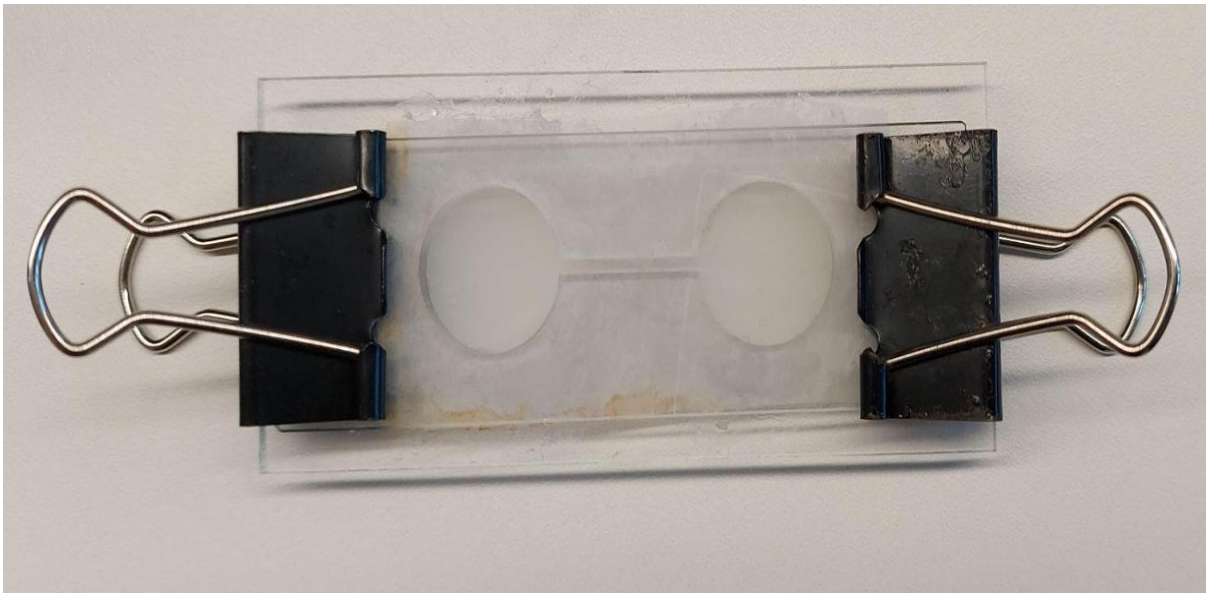

Figure 21. Two-sided cage (© Mustafa Altintas).

Assay 2. Explore a habitat with novel food in interconnected leaf/plastic disc arrangement

The second exploration assay was conducted using an arrangement of a leaf disc connected to a plastic disc (Figure 22). Each experimental *P. persimilis* individual was released on the bean leaf disc (1.4 cm), which was connected to a plastic disc (1.4 cm) by a wax bridge (Figure 22). There were five spider mite eggs each on the leaf disc and the plastic disc. Upon release of *P. persimilis* on the leaf disc, the wax bridge was blocked with a strip of moist tissue paper for 5 minutes. After removing the blockage from the wax bridge, the time elapsed until the *P. persimilis* individual moved onto the bridge and started to explore the plastic disc was measured from videos shot by a digital microscope (Leica DMS 1000) for a maximum of 15 minutes for each replicate. Each two-discs arrangement and individual were used only once.

Figure 22. Leaf disc and plastic disc connected by a wax bridge (© Mustafa Altintas).

2.3.2.2 Boldness Assays

Each experimental animal was subjected to three boldness assays.

All three boldness assays were carried out using T-shaped acrylic choice arrangements (Figure 23). Each choice arrangement consisted of two large cylindrical cavities (15 mm ø) and one small cavity (5 mm ø) in the middle, drilled into 3 mm thick rectangular acrylic plates (80 x 35 x 3 mm), connected by a T-shaped aisle (2 mm wide). The choice arrangement was covered with fine mesh on the bottom for ventilation and a microscope slide on top, secured with binder clips (Figure 23; Schausberger and Hoffmann, 2008).

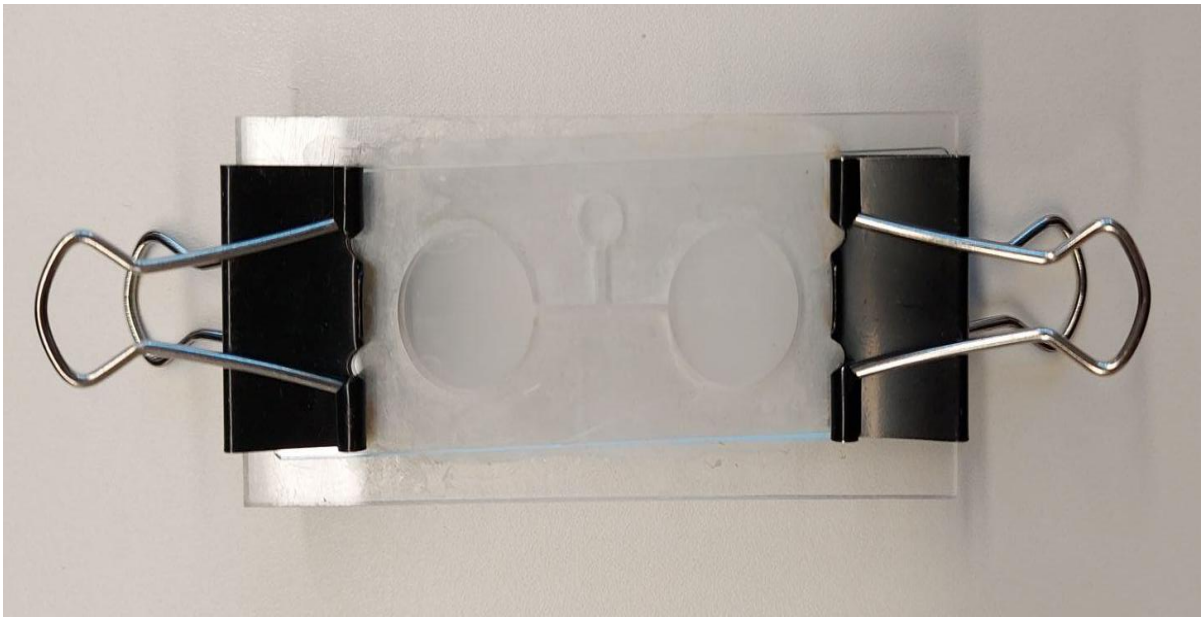

Figure 23. T-shaped choice arrangement (© Mustafa Altintas).

Assay 1. IGP risk posed by *A. andersoni*, without extra food

For testing the response of *P. persimilis* to IGP risk by *A. andersoni*, one *A. andersoni* female was caged in one cavity of the T-shaped choice cage for 12 h, while the connecting aisle between the two large cavities was blocked with a small piece of a silicon tube. The *A. andersoni* female produced IGP cues, by releasing traces (metabolic waste products and/or footprints) and laying eggs inside their cavity. After 12 h, the *A. andersoni* female, her eggs and the block between the cavities were removed, and the experimental *P. persimilis* individual was released

inside the small cavity located between the two large cavities. The first choice of the experimental animal and its position and activity (moving/stationary) were checked every 20 min for a total of 2 h. There was no food provided to the predators during the assay.

Assay 2. IGP risk posed by *N. californicus*, without extra food

The second boldness assay followed the same procedure described for assay 1 with *A. andersoni.* The only difference to assay 1 was using *N. californicus* instead of *A. andersoni*.

Assay 3. IGP risk posed by *N. californicus*, with spider mite prey

The third boldness assay followed the same procedure described for assay 1 with *A. andersoni* and assay 2 with *N. californicus*, with the only difference that 20 spider mite eggs were provided as prey inside each of the two large cavities of the choice cage.

2.3.2.3 Sociability Assays

Each experimental animal was subjected to three sociability assays.

Before starting the sociability assays, each experimental individual was marked with a blue, green, yellow, red or black water colour dot (Jolly Supertabs, Brevillier Urban & Sachs, AT) on their dorsal shield, to recognise their identity throughout the experiment.

Assay 1. Group joining tendency in T-shaped choice cage

The first sociability assay was conducted using T-shaped choice arrangements as described in the boldness assays (Figure 23). Two individuals from the same

treatment and same sex were jointly placed in the same cavity for five min, while the alley connecting to the other cavities was blocked by a piece of silicon tube. After five min, the block was removed, and the target individual was transferred to the small cavity in between the two large cavities. First large cavity choice by the target individual and the positions of both individuals were checked every 20 min for a total of 2 h.

Assay 2. Group joining after separation using leaf discs

The second sociability assay was conducted using an interconnected leaf disc arrangement (Figure 24). One large (2.3 cm Ø) and 3 or 4 small (each 1.2 cm Ø) leaf discs, punched out from common bean leaves, were placed on moist filter paper on top of a water-soaked sponge cube inside a plastic box (10 x 10 x 6 cm) half-filled with tap water. The small leaf discs were connected to the larger disc by wax bridges. There were five spider mite eggs on each small disc and twenty spider mite eggs on the large disc. To start the assay, all wax bridges were blocked by strips of moist tissue paper, and five predator individuals from the same treatment were placed together on the large leaf disc for five min (Figure 24).

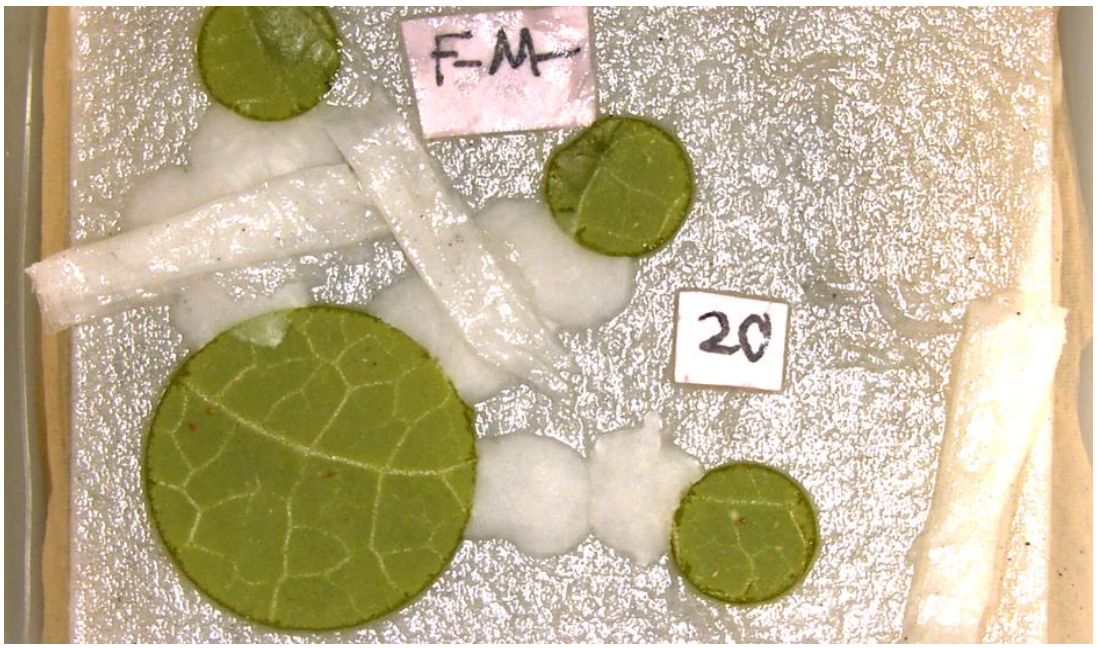

Figure 24. Second sociability (group joining) assay using interconnected leaf discs (© Mustafa Altintas).

After five min, one of the five individuals was transferred to a small leaf disc, the block on the wax bridge was removed and the whole arrangement was videotaped for 15 min using a digital microscope (Leica DMS 1000). From the videos, the time elapsed until the target individual re-joined the group on the large disc was measured. Each small disc and wax bridge was used only once to prevent any inadvertent influence possibly emanating from cues left by the previous predator.

Assay 3. Group joining after separation using a setup of two connected cages

The third sociability assay was conducted using two-sided cages (Figure 21). To start the assay, two individuals from the same treatment were placed together in one cavity of a two-sided acrylic cage (Figure 21), while the connecting aisle was blocked by a piece of silicon tube. After five minutes, the silicon tube was removed, one of the two individuals was transferred to the other cavity and the time elapsed until the two individuals came together again in one of the two cavities was checked for a maximum of six h.

2.4 Statistical Analyses

All statistical analyses were conducted using IBM SPSS Statistics 27.0.1.0. For analyses, I only used the data of the female experimental animals because of low replicate numbers of males.

To quantify boldness, the number of residences in the risky site and the benign no-risk site (without IGP risk) were used. For the exploration assays, the time-dependent data of the three assays were log-transformed before analysis. This was needed because of differing time periods in the two assays. To standardize the measures of the three sociability assays, I converted the data into a sociability index, ranging from 0 to 2, with 0 being the most sociable and 2 being the least sociable: in the first sociability assay, I averaged the scores of the two individuals of the seven observations (for each observation: 0 when both were together in a cavity, 1 for one in a cavity and the other in the middle of the setup, 2 when they were in opposite cavities); in the second assay, I used 0 when they re-joined within 1 min, 1 when

between 1 and 15 min, and 2 when they did not re-join; in the third assay, I used 0 when they re-joined within 120 min, 1 when between 120 and 360 min, and 2 when they did not re-join.

Separate generalised estimating equations (GEE) were used to analyse the effect of the early-life IGP experience by the mother and father on mean exploration (normal, identity link), boldness (Poisson, log link), activity during boldness (binomial, counts of events) and sociability (normal, identity link) across tests. A generalised linear model (GLM) was used to analyse the effect of parental sex and their early-life experience of IGP on the mean number of eggs produced in the home cages during the experiment (normal distribution, identity link). In each model, I started with the full model and removed the interaction if it was not significant.

To check if the experimental animals were repeatable in their behaviours over the two or three different contexts of the exploration, boldness and sociability assays, the intraclass correlation coefficients (ICC) were calculated.

3. RESULTS

3.1 Population Means

3.1.1 Exploration

The mean exploration times (log scale) ranged from a mean of 1.28 (F+M+ and F+M-) to a mean of 1.09 (F-M-) across treatments (Figure 25).

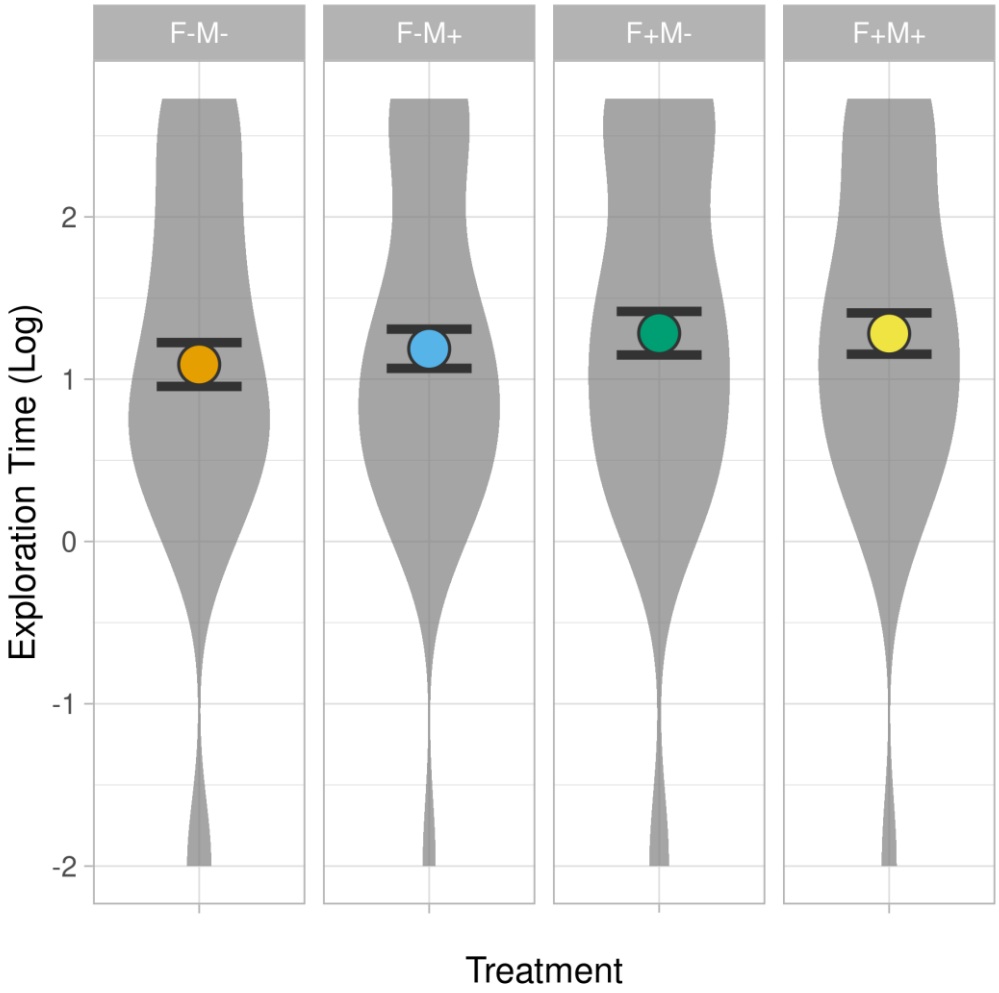

Figure 25. Exploration times (log scale) for each treatment. The grey areas show the distribution of data, the coloured circles are the means of each treatment and the error bars represent the standard errors of the means.

There was no significant influence of parental treatment (GEE; mother: Wald χ^2_2 =1.239, p = 0.266; father: Wald χ^2_2 = 0.139, p = 0.709) on the mean exploration propensity (Table 5).

Table 5. The GEE results of the exploration times.

Tests of Model Effects			
	Wald Chi-Square	df	Sig.
(Intercept)	351.410	1	.000
Maternal Treatment	1.239	1	.266
Paternal Treatment	.139	1	.709

3.1.2 Boldness

The mean number of residences in the risky site ranged from 1.7 (F-M-) to 1.3 (F+M+) across treatments (Figure 26).

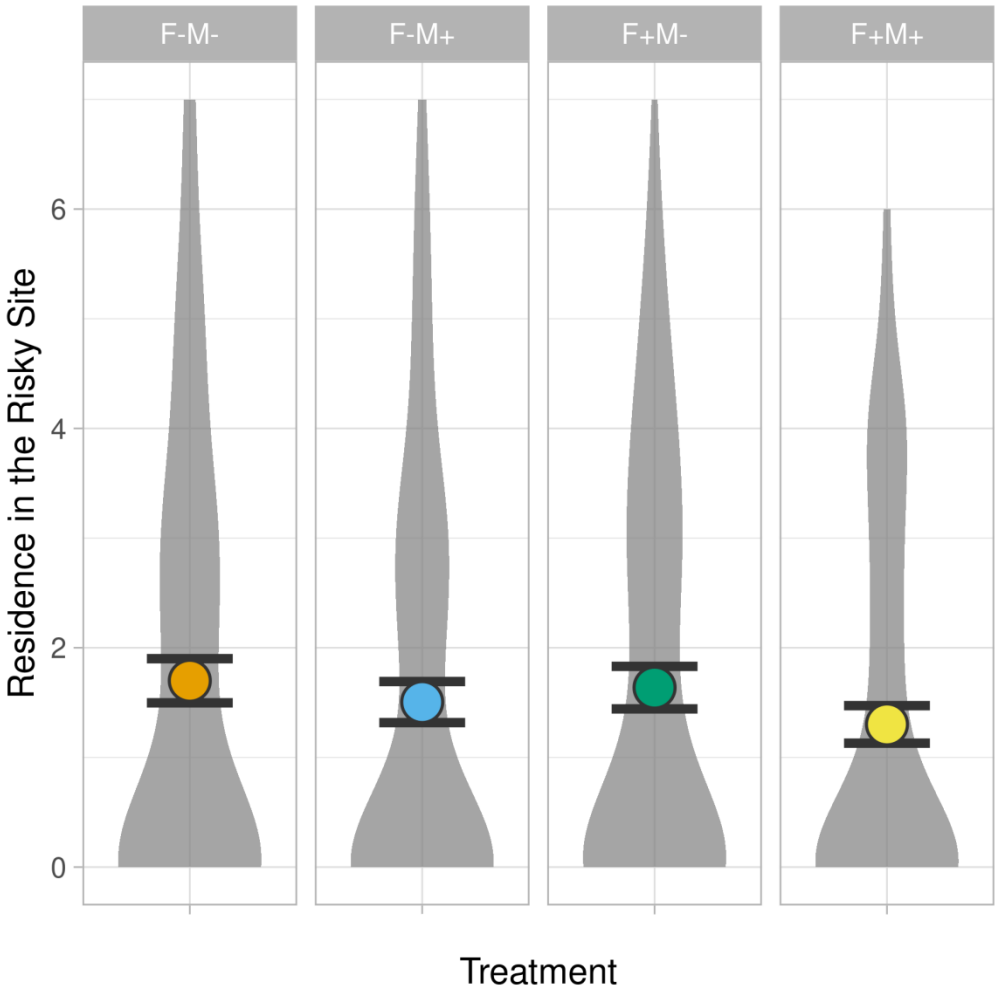

Figure 26. Residences in the risky site for each parental treatment. The grey areas show the distribution of data, the coloured circles are the means and the error bars represent the standard errors of the means.

By contrast, the residences in the no-risk site were between 3.49 (F+M-) and 3.23 (F-M-) (Figure 27).

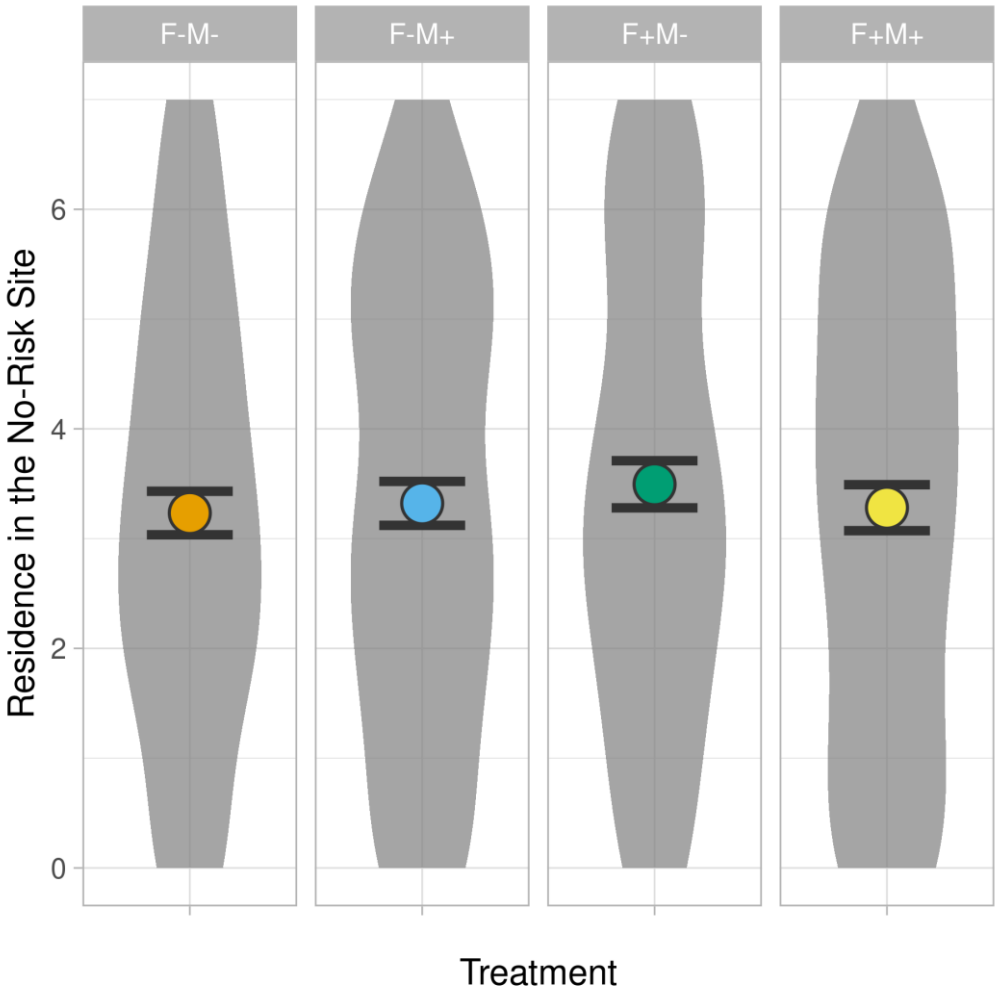

Figure 27. Residences in the no-risk site for each parental treatment. The grey areas show the distribution of data, the coloured circles are the means and the error bars represent the standard errors of the means.

During the boldness assays, the predatory mites' moving activity (number of observations out of 7 where the mites were active) in the T-cages varied between 5.12 (F+M-) and 4.8 (F+M+) (Figure 28).

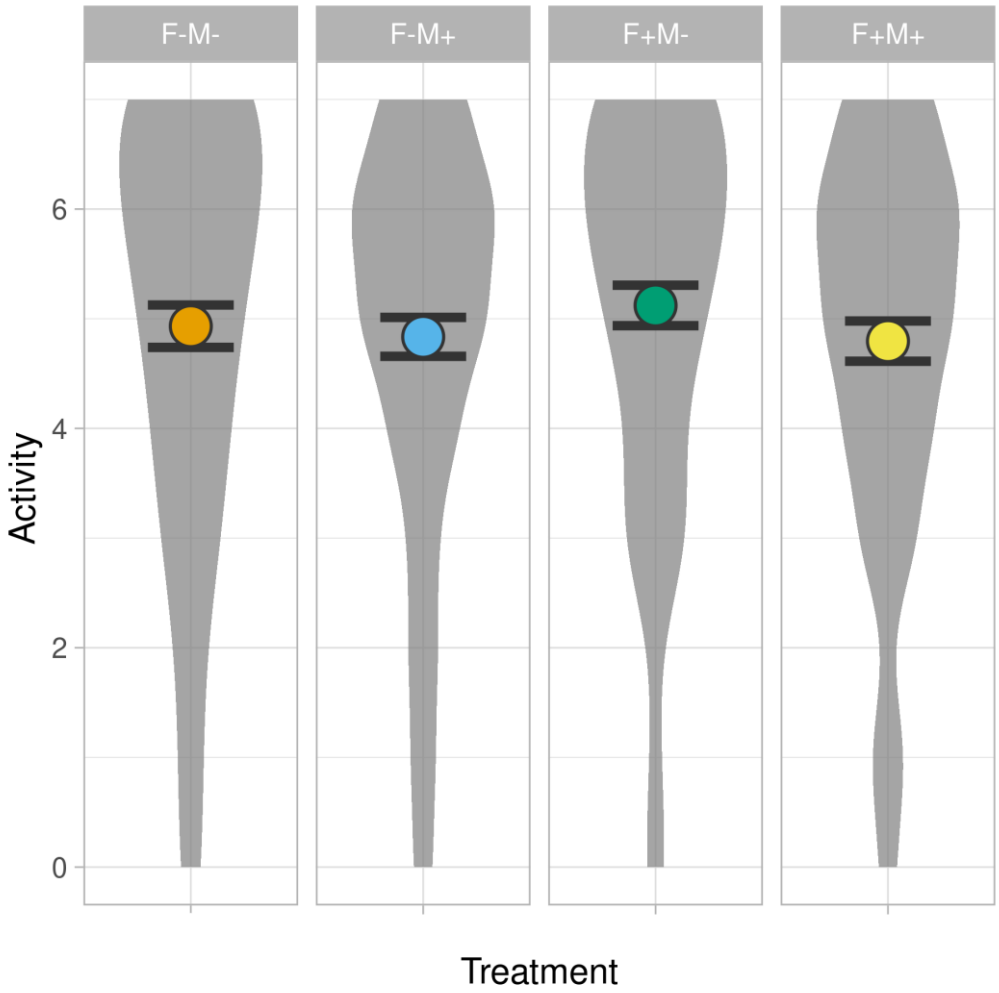

Figure 28. Activity during the boldness assays for each parental treatment. The grey areas show the distribution of data, the coloured circles are the means and the error bars represent the standard errors of the means.

There was a significant influence of paternal treatment on residence in the risky site, with offspring from IGP-experienced fathers being shyer than those from IGP-naïve fathers and offspring in the F+M+ treatment being the shyest. There was no maternal influence on offspring' residence in the risky site (GEE; mother: Wald χ^2_2 = 1.225 p = 0.268; father: Wald χ^2_2 = 4.661, p = 0.031) (Table 6). Residence in the no-risk site was not influenced by parental IGP experience (GEE; mother: Wald χ^2_2 = 0.359 p = 0.549; father: Wald χ^2_2 = 0.108, p = 0.742) (Table 7). Activity during the boldness assays was significantly influenced by maternal IGP experience, and marginally significantly influenced by paternal IGP experience (GEE; mother: Wald χ^2_2 = 3.981 p = 0.046; father: Wald χ^2_2 = 2.975, p = 0.086) (Table 8). Offspring from the F+M+ treatment were the least active (Figure 28).

Table 6. GEE results of residence in the risky site.

Tests of Model Effects			
	Wald Chi-Square	df	Sig.
(Intercept)	113.276	1	.000
Maternal Treatment	1.225	1	.268
Paternal Treatment	4.661	1	.031

Table 7. GEE results of residence in the no-risk site.

Tests of Model Effects			
	Wald Chi-Square	df	Sig.
(Intercept)	1997.376	1	.000
Maternal Treatment	.359	1	.549
Paternal Treatment	.108	1	.742

Table 8. GEE results of activity during the boldness assays.

Tests of Model Effects			
	Wald Chi-Square	df	Sig.
(Intercept)	680.427	1	.000
Maternal Treatment	3.981	1	0.046
Paternal Treatment	2.975	1	0.085

3.1.3 Sociability

The mean sociability scores ranged from 1.36 (F-M-) to 1.17 (F+M+) across parental treatments (Figure 29). There was a significant influence of maternal but not paternal IGP experience on offspring' sociability (GEE; mother: Wald $\chi^2_2 = 4.136$ $p = 0.042$; father: Wald $\chi^2_2 = 0.600$, $p = 0.439$), with offspring from F- mothers being less sociable than those from F+ mothers (Table 9).

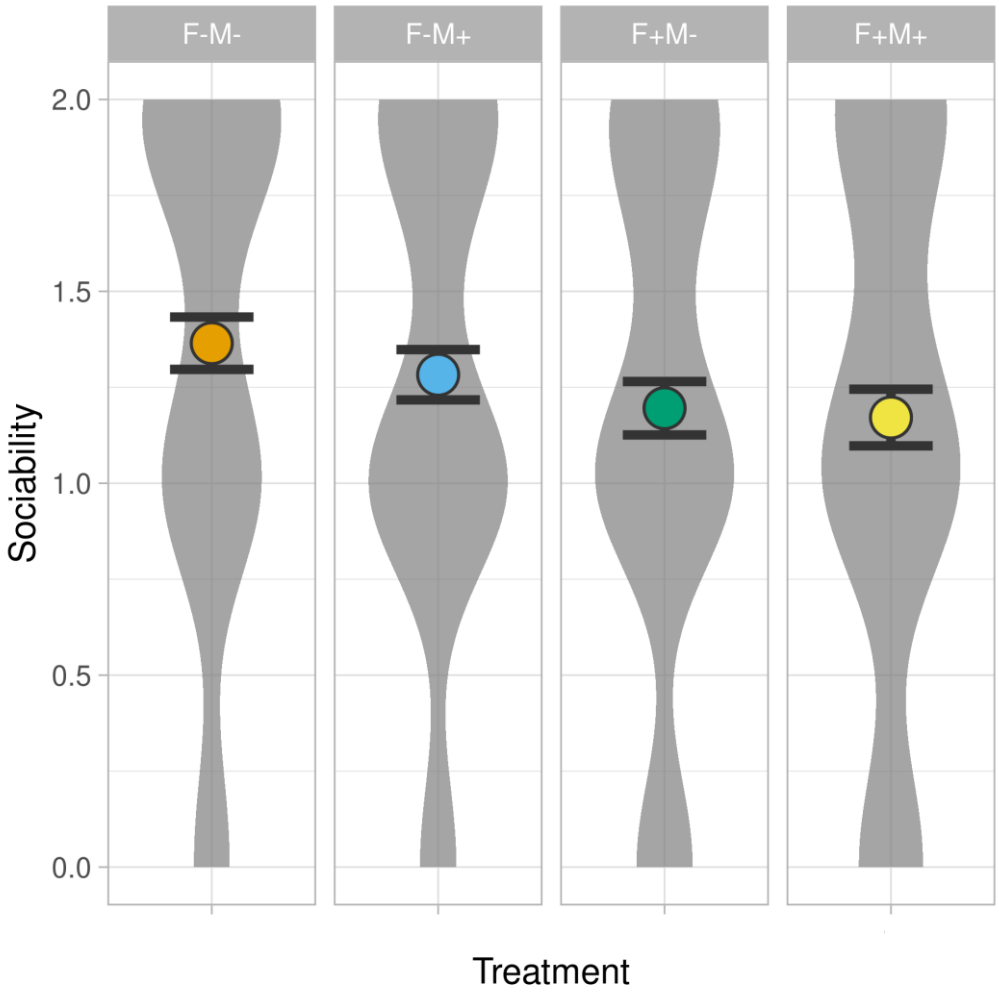

Figure 29. Sociability scores for each parental treatment (the lower the score the more sociable). The grey areas show the distribution of data, the coloured circles are the means and error bars represent the standard errors of the means.

Table 9. GEE results of the sociability scores.

Tests of Model Effects			
	Wald Chi-Square	df	Sig.
(Intercept)	1313.396	1	.000
Female Treatment	4.136	1	.042
Male Treatment	.600	1	.439

3.1.4 Mean Number of Eggs Produced in Home Cages

Across parental treatments, the females produced on average 2.82 (F+M+) to 1.79 (F+M-) eggs per day during the experiment (Figure 30). Maternal treatment had a strong effect on the number of eggs (GLM; Wald χ^2_2 = 6.994, p = 0.008), while

paternal treatment had a marginally significant effect (GLM; Wald χ^2_2 = 3.694, p = 0.055) (Table 10). Females in the F+M- treatment produced fewer eggs than females of the other three treatments; females of the F+M+ treatment produced the most eggs (Figure 30).

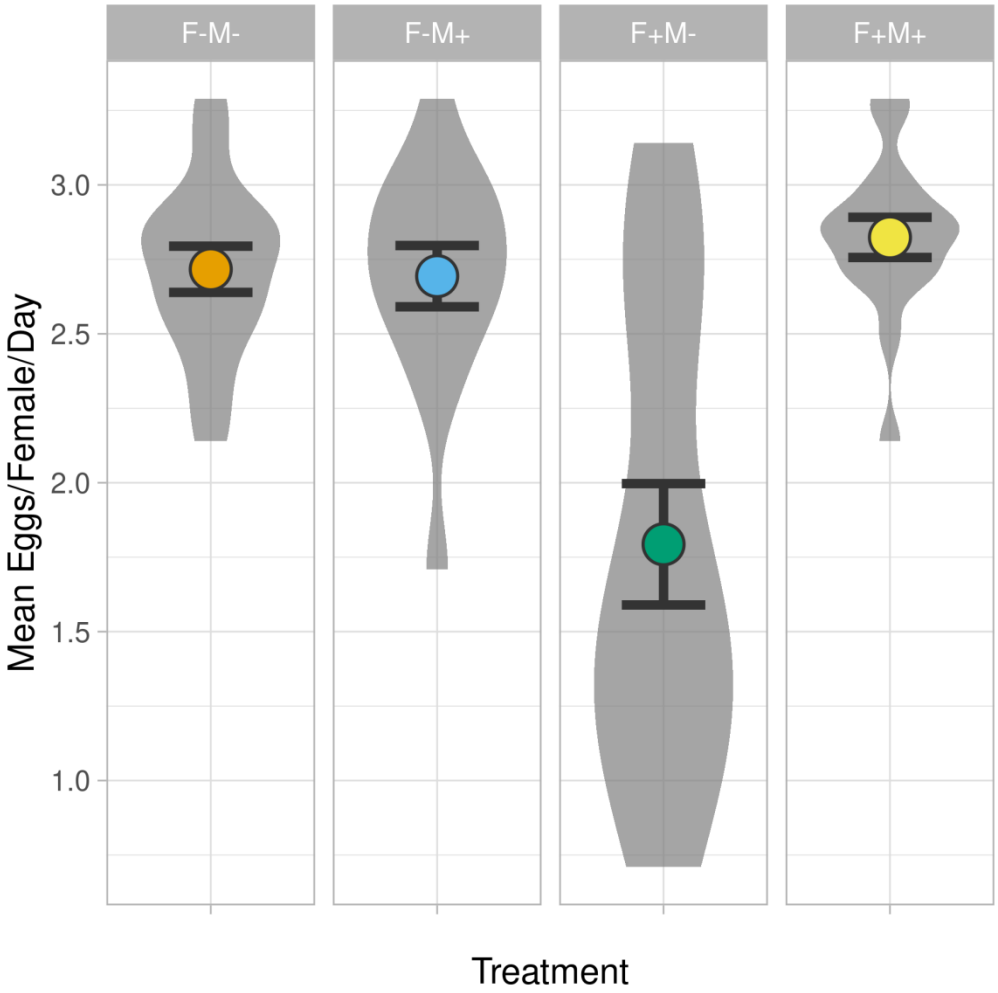

Figure 30. Number of eggs produced per day in home cages for each parental treatment. The grey areas show the distribution of data, the coloured circles are the means and error bars represent the standard errors of the means.

Table 10. GLM results of eggs produced in the home cages.

Tests of Model Effects			
	Wald Chi-Square	df	Sig.
(Intercept)	507.230	1	.000
Female Treatment	6.994	1	.008
Male Treatment	3.694	1	.055

3.2 Intraclass Correlation Coefficients (ICC)

Analyses of the intraclass correlation coefficients (ICC) for the data pooled across parental treatments indicate significant repeatability in boldness (residence in the no-risk site) and activity during the boldness assays (Table 11). Repeatability in exploration pooled across parental treatments was marginally significant.

Table 11. ICC scores and P values pooled across parental treatments. Significant ICCs (P≤0.05) are highlighted in red, marginally significant ICCs (0.05<P<0.1) are green.

	Pooled	
	ICC	P
Boldness(w)	0.098	0.240
Boldness(wo)	**0.359***	**0.001***
Activity	**0.501***	**<0.001***
Exploration	**0.199**	**0.088**
Sociability	0.149	0.157

When the data were split into the four parental treatments (Table 12), the offspring of both IGP-experienced parents were marginally repeatable in residence in both the risky and no-risk sites. Offspring of IGP-naive females mated with IGP-experienced or -naive males were significantly repeatable in residence in the no-risk site (Table 12). Regarding activity during the boldness assay, offspring of all treatments were repeatable except for the offspring of IGP-experienced females mated with IGP-naïve males (Table 12). Only the offspring of IGP-experienced parents were marginally repeatable in exploration but in neither parental treatment were the offspring repeatable in sociability (Table 12).

Table 12. ICC scores and P values when the data were split into four parental treatments. Significant ICCs (P≤0.05) are highlighted in red, marginally significant ICCs (0.05<P<0.1) are green.

	F+M+		F+M-		F-M+		F-M-	
	ICC	P	ICC	P	ICC	P	ICC	P
B(w)	**0.339**	**0.083**	-0.010	0.499	0.012	0.470	0.035	0.440
B(wo)	0.377	0.057	0.151	0.285	**0.381**	**0.047**	**0.486**	**0.011**
A	**0.761**	**<0.001**	-0.079	0.584	**0.392**	**0.039**	**0.577**	**0.001**
E	0.426	0.053	0.271	0.167	-0.321	0.806	0.331	0.116
S	0.282	0.144	-0.161	0.656	0.162	0.282	0.280	0.155

ICC analyses of the data split into maternal and paternal IGP experience did not reveal significant parental effects on residence in the risky site of the boldness assays. By contrast, the offspring of all parental treatments were significantly or marginally significantly (F+M+) repeatable in residence in the no-risk site. Moving activity during the boldness assays was significantly repeatable in all treatments. While IGP-experienced mothers produced offspring with significantly repeatable exploration propensity, IGP-naive fathers produced offspring with moderately repeatable propensity in exploration (Table 13).

Table 13. ICC scores and P values when data were split according to maternal or paternal IGP experience. Significant ICCs (P≤0.05) are highlighted in red, marginally significant ICCs (0.05<P<0.1) are green.

	F+		F-		M+		M-	
	ICC	P	ICC	P	ICC	P	ICC	P
B(w)	0.178	0.175	0.025	0.442	0.171	0.181	0.012	0.467
B(wo)	0.262	0.074	**0.434**	**0.003**	**0.380**	**0.010**	**0.341**	**0.022**
A	**0.508**	**<0.001**	**0.493**	**<0.001**	**0.591**	**<0.001**	**0.380**	**0.010**
E	**0.338**	**0.039**	0.031	0.446	0.096	0.332	0.316	0.051
S	0.115	0.289	0.151	0.232	0.238	0.111	0.066	0.376

4. DISCUSSION

Animal personality refers to consistent individual behavioural differences across time and contexts (Réale et al., 2007). These behaviours can be shaped by individual responses to environmental factors and/or can be inherited from parents, playing a critical role in adaptation (Stamps and Groothuis, 2010). Although environmental factors experienced at any stage or phase of life can impact personality, early-life experiences often have the most pronounced and long-lasting effects (Monaghan, 2008; Langenhof and Komdeur, 2018). While numerous studies have examined how environmental factors experienced during early life affect animal personality, the experiences made by previous generations, i.e. transgenerational effects, remain poorly understood.

This study investigated the effects of parental IGP experience on offspring' boldness, exploration, and sociability in the plant-inhabiting predatory mites *Phytoseiulus persimilis*. My study revealed complex significant parental effects on mean behavioural trait expression at the population and individual levels across traits and assays. At the individual level, ICC analyses suggest that parental early-life IGP experience affects offspring personality in boldness, activity and exploration but not sociability. Offspring were only marginally repeatable in residence in the risky site when both parents were IGP-experienced (F+M+), while exploration-related personality traits were influenced primarily by maternal experience. At the population level, the paternal IGP experience was significant for boldness, while maternal IGP experience was significant for activity, sociability and egg production. Also, paternal IGP experience had a moderately significant effect on mean activity and egg production. These findings highlight that transient early-life IGP experiences of parents can have lasting, transgenerational impacts on offspring personality trajectories.

4.1 Parental Effects on Offspring' Boldness

Parental effects, which are one type of transgenerational effects, can influence offspring phenotypes and behaviours in various ways. However, while several studies document parental effects on mean behavioural or life history trait expression, studies documenting changes in personality expression are scarce and

none exist for the influence of IGP risk. For example, in predatory mites *Amblydromalus limonicus*, exposure to simulated heatwave conditions resulted in F2 females being larger and developing more quickly, illustrating how parental environmental stress can shape offspring morphology and life history (Walzer et al., 2020). Poeciliid fish *Brachyrhaphis episcopi* from high- and low-predation environments exhibited parental effects on offspring' mean boldness, suggesting either a genetically and/or non-genetically heritable component of this trait (Brown et al., 2007). In the same study, when the offspring of both populations were repeatedly chased with a net, they showed an increase in boldness, which indicates that also personal environmental experiences can strongly influence this personality trait. One possible explanation for this pattern could be the high degree of behavioural plasticity, allowing offspring to rapidly adapt to current environmental conditions. Also, in a study on cichlids *Neolamprologus pulcher*, maternal stress influenced offspring antipredator behaviour through changes in the biochemistry of eggs, resulting in faster mean escape responses (Sharda et al., 2021). In their meta-analysis, Smith and Blumstein (2008) concluded that bolder individuals have higher reproductive success.

Besides fish and other animals, several studies documented that parental predation risk influences mean behaviour of offspring in mites. For instance, offspring of two-spotted spider mites *Tetranychus urticae* showed a maternal influence on their anti-predator behaviours (Freinschlag and Schausberger, 2016), especially during the early life of the offspring. The spider mites' antipredator behaviour then changed with their own predator experiences, which is analogous to the behavioural plasticity observed in fish mentioned above (Brown et al., 2007). Similarly, in the target animal of this study, *Phytoseiulus persimilis,* juvenile offspring (protonymphs) of IGP-experienced mothers changed the mean expression of predation risk-associated behaviours, such as in site choice and activity (Seiter and Schausberger, 2015).

My study detected a significant paternal influence on mean boldness, with offspring from parents that were both experienced with IGP risk being the shyest. Proximately, the paternal influences may be explained by IGP risk inducing changes in epigenetics, hormones, or seminal fluids, which in turn changed the fertilized egg and the behaviour of offspring hatching from these eggs. The paternal effects could have been mediated by a response of the females to the males in the parental generation and/or be induced independent of the female response to the mates

(Crean and Bonduriansky, 2014). Parental IGP experience had highly sophisticated effects on offspring' personality expression. Scrutiny of the ICCs revealed just one treatment, when both parents were IGP-experienced, where offspring showed marginally significant repeatable residence in the risky site . In contrast, parental IGP experiences had strong effects on repeatability in residence in the no-risk site, which is an indicator of being the farthest away from the risky site in my experiment. The finer resolution of the boldness data when measured as residence in the no-risk site is explainable by the much higher among-individual variability as compared to residence data in the risky site (many individuals did not move a single time to the risky site). Together, these results suggest that even though there is no significant maternal influence on mean behavioural trait expression, the early-life IGP experiences of mothers clearly contribute to the joint parental effects on offspring' personality expression. Also, the parental impacts on activity during the boldness assays were significant at both the individual and population level, and at the population level, it was mainly a maternal effect. The findings of parental IGP experience on offspring personality in boldness in my thesis are novel for any animal. Also, the results on paternal effects on mean boldness of offspring are highly original and novel because previous findings regarding parental predation risk effects on mean boldness expression did either not distinguish between maternal and paternal effects (Brown et al., 2007) or showed only maternal effects (e.g., Sharda et al., 2021; Freinschlag and Schausberger, 2016; Seiter and Schausberger, 2015) and most were not concerned with IGP. Overall, the findings suggest complex and long-lasting transgenerational early-life IGP experience effects on offspring boldness, which conforms to theoretical predictions (Dall et al., 2004).

4.2 Parental Effects on Offspring' Exploration

Exploratory behaviour is about the way individuals interact with and check out novel environmental features and seek resources, ultimately affecting survival and reproduction. Exploratory behaviour serves as a strategy to gather information about novel environments, allowing to find and explore food, shelter and mates, dispersing or avoiding predators (Réale et al., 2007). Fast or good explorers can explore novel environments more efficiently, which may be beneficial in unpredictable or

competitive environments, as it allows to discover novel resources and opportunities for reproduction. Exploration behaviour can vary between sexes across animal species. For example, one study reported that females showed greater exploration propensity than males in Long-Evans rats (McElroy and Howland, 2025), while another study in woodlice *Armadillidium vulgare* showed no exploration difference between the sexes (Cazentine et al., 2023). This personality trait can be influenced by parental experiences, as suggested by paternal effects on offspring exploration behaviour in zebrafish *Danio rerio* (Zajitschek et al., 2017). Exploration can reflect a trade-off between the benefits of acquiring new information and the potential costs of increased risk (Wolf et al., 2007). In my study, there was no significant parental influence on mean exploration propensity. By contrast, at the individual level, the offspring of IGP-experienced mothers were significantly repeatable in exploration. This is different from the study on zebrafish, where there was a paternal influence on the exploration behaviour of offspring. The offspring were moderately repeatable in exploration when both parents were IGP-experienced or the mates of the IGP-experienced females were IGP-naive. This maternal influence could represent a potentially adaptive, long-lasting response to the predation risk to increase the survival success of the offspring. However, this potential explanation needs additional experimentation and further scrutiny. As mentioned before, as a consequence of changed exploration personality, *P. persimilis* females could change their oviposition behaviours, by postponing oviposition or reducing the number of produced eggs, as a defence mechanism (Walzer and Schausberger, 2011), which would be considered a behavioural syndrome. In any case, to the best of my knowledge, the potential effects of parental IGP risk on the repeatability in exploration of offspring were hitherto untested and unknown for any animal.

4.3 Parental Effects on Offspring' Sociability

Sociability refers to an individual's tendency to engage in friendly social interactions and maintain proximity to conspecifics (Réale et al., 2007). This behavioural trait is crucial in shaping group dynamics and cohesion, cooperation, and survival strategies in many animal taxa. Group living can provide benefits such as enhanced foraging

efficiency, predator avoidance through group vigilance, and increased mating opportunities (Rubenstein, 1978). However, it can also come with costs, such as stronger resource competition, enhanced disease transmission and increased exposure to predators (Rubenstein, 1978).

In arthropods, sociability, sociality and group-living vary widely across species. While some exhibit strong and highly sophisticated group-living tendencies, such as eusocial insects like ants, termites or bees (Gordon, 1996) and colonial spiders (Whitehouse and Lubin, 2005), others, like many predatory arachnids, are more solitary (Whitehouse and Lubin, 2005). In mites, except for eusociality, many other forms of social organization can be found, from solitary to predominantly living together in groups. For instance, the two-spotted spider mite *Tetranychus urticae* and another spider mite, *T. kanzawai*, cooperate by joint web construction and web sharing, joint dispersal and getting closer to each other when they are exposed to predators (Yano, 2012; Schausberger et al., 2021). Some spider mites, such as species living on bamboo and other grasses, have cooperative parental care and nest defence. Males of bamboo spider mites can even kill the immature stages of phytoseiid predators that try to intrude the nests (Saito, 1986). Also, some predatory mite species such as *Phytoseiulus* spp. are predominantly living in groups and evolved sophisticated group-living behaviours. For example, gravid *P. persimilis* females preferentially join familiar groups and deposit their eggs in prey patches occupied by familiar females during group joining assays (Muleta and Schausberger, 2013). When *P. persimilis* individuals are socially isolated in early life, they change in mean behavioural traits such as mate choice and group cohesion (Schausberger et al., 2017), as compared to those growing up in groups. Strikingly, social isolation in early life also disrupts adult personality expression in the group-living *P. persimilis* (Schausberger and Nguyen 2025).

In my study, sociability was quantified based on the propensity to re-join a group after separation. The results revealed a significant maternal effect at the population level, suggesting that mothers' early-life experiences of IGP risk influence their offspring's sociable tendencies. Offspring of IGP-experienced females had stronger propensities to re-join the familiar group, which behaviour could likely be favourable in anti-predator contexts. However, sociability was not repeatable, indicating that despite maternal influences on mean behavioural traits, sociability within individuals may remain highly plastic in response to changes of the immediate

socioenvironmental conditions. Subjecting the experimental animals to several other tests on exploration and boldness before testing them for sociability may have interfered with personality expression. In the study by Schausberger and Nguyen (2025), group-reared *P. persimilis* were highly repeatable in sociability such as in inter-individual distances and the propensity to be in close proximity to conspecifics. The experimental conditions before the sociability assays could have also blurred inherited repeatability in sociability, as similarly observed in *Polistes fuscatus* wasps, where laboratory-rearing conditions disrupted social traits shown under natural conditions (Jandt et al., 2015). Another potential explanation is that group-living predatory mites could exhibit context-dependent sociability, where the benefits of social interactions fluctuate based on environmental factors such as resource availability and experiences of predation risk.

Overall, the findings on sociability suggest that parental IGP experiences can influence offspring' sociability in *Phytoseiulus persimilis*, mainly through maternal effects. Future studies could explore the underlying mechanisms driving these maternal effects, such as hormonal, nutritional or epigenetic changes passed on to offspring, and investigate whether similar patterns also occur in other predatory mite species.

4.4 Parental Effects on Offspring' Egg Production

The number of eggs produced is a highly critical component of reproductive success and typically strongly affected by the environmental conditions. Accordingly, many animals adjust egg production such as egg number, composition, sex, size, laying time etc. to previously prevailing or immediate environmental conditions. For instance, *P. persimilis* females reduce the size of eggs and increase the number when food is abundant but do the opposite under food stress (Walzer and Schausberger, 2015). Grasshoppers *Ageneotettix deorum* decrease egg production when they are exposed to predation risk by lycosid wolf spiders (Danner and Joern, 2004). Similarly, egg production by *P. persimilis* is influenced by the presence of heterospecific predators, by postponing oviposition and changing oviposition site choice as defence mechanisms (Walzer and Schausberger, 2011). Another study with *P. persimilis* showed that maternal IGP risk exposure changes offspring'

response to predator cues (Seiter and Schausberger, 2015). Together, these studies suggest that parental exposure to stress factors such as IGP can induce physiological changes that affect egg production rates and/or individual egg quality, potentially optimising offspring survival in risky environments. In the present study, parental early-life IGP experience significantly influenced fecundity in *P. persimilis*, with the highest number of eggs produced when both parents were IGP-experienced, which suggests a potentially synergistic effect of maternal and paternal experience on reproductive output. In contrast, IGP-experienced females mated to IGP-naïve males produced the fewest eggs. These results indicate that both maternal and paternal experiences contribute to reproductive strategies of offspring.

4.5 Conclusion

My study demonstrates that parental early-life IGP experience can influence offspring personality traits and reproduction in the plant-inhabiting predatory mite *Phytoseiulus persimilis*. The observed parental effects were either mediated by the mother, the father or both. While mean boldness was mainly influenced by paternal experience, mean sociability and mean exploration were affected by maternal experience. Activity and egg production were infuenced by both parents' experiences. Offspring personality was mainly evident in boldness and activity during the boldness assays, with the level of repeatability depending on the parental treatments. The findings of my study highlight the complexity of transgenerational effects, with both maternal and paternal influences contributing to offspring behaviour in different ways. Understanding these dynamics provides valuable insights into the mechanisms of non-genetic behavioural inheritance and the potential for adaptive responses across generations.

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ABSTRACT

Animal personality, i.e. behavioural repeatability, refers to consistent within-individual behaviours that vary among individuals across time and contexts. Animal personalities can either be a response to environmental factors and/or be genetically determined. Major environmental contexts shaping an individual's personality are the social conditions, diet availability, and predation risk. Environmental factors can influence animal personality at any life stage and phase, but the most pronounced and lasting effects are often caused by early-life experiences. While many studies focused on how early-life experiences affect animal personality later in life, the transgenerational effects of early-life experiences remain poorly understood. This study investigated sex-specific parental effects on offspring' repeatability in boldness, exploration, and sociability in the group-living predatory mite *Phytoseiulus persimilis*. To this end, I exposed the parents in early life to intraguild predation (IGP) risk or not, as IGP has been shown to influence the personality of *P. persimilis*, particularly in terms of boldness (risk-taking) and activity. The experimental animals emerged from four parental treatments, defined by IGP experience (+ yes, - no) of the mother (F, female) and father (M, male): F+M+, F+M-, F-M+, and F-M-. This design allowed examining the sex-specific parental influence of IGP on mean behavioural trait expression of offspring as well as their personality. At the population level, paternal early-life IGP experience significantly influenced offspring boldness, while maternal IGP experience influenced activity, sociability, and egg production. Offspring mean exploration was not influenced by parental IGP experience. Intraclass Correlation Coefficients (ICCs) revealed that offspring' personality in boldness and exploration were influenced by parental IGP experiences. Pooled across parental treatments, offspring were repeatable in boldness but less so when both parents had IGP risk experience (F+M+). Repeatability in exploration was primarily mediated by maternal IGP experience. Mean sociability was significantly influenced by maternal IGP experience, but neither parental treatment resulted in significant offspring' repeatability in sociability. Egg production was significantly influenced by maternal IGP experience, and marginally significantly by paternal experiences with the lowest reproductive output observed when mothers but not their mates had been exposed to IGP risk. Overall, the results of this thesis suggest that parental early-life IGP experience can have parental sex-specific impacts on

offspring mean behavioural traits as well as their personality. The findings highlight the complexity of transgenerational effects, with either maternal or paternal or both influences contributing differently to trait expression. Understanding how parental experiences can shape offspring personality is important for unravelling the pathways mediating animal behaviour and how personality traits develop across generations. This research provides insights into the complexities of how environmental stressors and parental experiences can shape the behaviour of future generations, contributing to further our understanding of animal personality occurrence and evolution.

ZUSAMMENFASSUNG

Tieren wird Persönlichkeit zugeschrieben, wenn sie wiederholbar in ihren Verhaltensweisen sind (*repeatability*). Das Phänomen tierischer Persönlichkeiten (*animal personality*) beschreibt konsistente Verhaltensweisen innerhalb eines Individuums, die zwischen den Individuen einer Gruppe über Zeit und Kontext hinweg variieren. Tierische Persönlichkeiten können entweder eine Reaktion auf Umweltfaktoren sein und/oder genetisch bedingt sein. Die wichtigsten Umweltfaktoren, die die Persönlichkeit eines Individuums beeinflussen, sind die sozialen Bedingungen, die Verfügbarkeit von Nahrung und das Prädationsrisiko. Umweltfaktoren können die Persönlichkeit von Tieren in jedem Lebensstadium und in jeder Lebensphase beeinflussen, aber die ausgeprägtesten und nachhaltigsten Auswirkungen werden häufig durch Erfahrungen in der frühen Lebensphase verursacht. Während sich viele Studien damit befassten, wie sich Erfahrungen in der frühen Lebensphase auf die Persönlichkeit von Tieren im späteren Leben auswirken, sind die transgenerationalen Auswirkungen von Erfahrungen in der frühen Lebensphase noch wenig erforscht. Diese Masterarbeit untersuchte die geschlechtsspezifischen elterlichen Auswirkungen auf die Wiederholbarkeit von Risikobereitschaft, Explorationsverhalten und Geselligkeit (Soziabilität) der Nachkommen in der gruppenlebenden Raubmilbe *Phytoseiulus persimilis*. Zu diesem Zweck wurden die Elterntiere in ihrer frühen Lebensphase dem Risiko von Intragilden Prädation (IGP; *intraguild predation*) ausgesetzt oder nicht. IGP kann nachweislich die Persönlichkeit von *P. persimilis* beeinfluss en, insbesondere in Bezug auf Risikobereitschaft und Aktivität. Die Versuchstiere waren die Nachkommen von vier Elternpaartypen (*parental treatments*), die jeweils durch die IGP-Erfahrung (+ ja, - nein) der Mutter (F, *female*) und des Vaters (M, *male*) definiert wurden: F+M+, F+M-, F-M+, und F-M-. Dieses experimentelle Design ermöglichte die Untersuchung des geschlechtsspezifischen elterlichen Einflusses von IGP Erfahrung auf die mittlere Ausprägung von Verhaltensmerkmalen der Nachkommen sowie auf deren Persönlichkeit. Auf Populationsebene beeinflusste die väterliche IGP-Erfahrung in der frühen Lebensphase signifikant die Risikobereitschaft der Nachkommen, während die mütterliche IGP-Erfahrung die Aktivität, Geselligkeit und Eiproduktion beeinflusste. Die durchschnittliche Explorationsfreudigkeit der Nachkommen wurde durch die IGP-Erfahrung der Eltern nicht beeinflusst. Die

Intraklassen-Korrelationskoeffizienten (ICC; *intraclass correlation coefficient*) zeigten, dass die Persönlichkeit der Nachkommen in Bezug auf Risikobereitschaft und Explorationsverhalten von den elterlichen IGP-Erfahrungen beeinflusst wurde. Über alle Elternpaartypen (*parental treatments*) waren die Nachkommen wiederholbar in ihrer Risikobereitschaft, aber weniger, wenn beide Elternteile Erfahrung mit IGP-Risiko hatten (F+M+). Die Wiederholbarkeit im Explorationsverhalten wurde in erster Linie durch die mütterliche IGP-Erfahrung bestimmt. Die mittlere Sozialität der Nachkommen wurde durch die IGP-Erfahrung der Mutter signifikant beeinflusst, aber keine der elterlichen Erfahrungen mit IGP Risiko führte zu einer signifikanten Wiederholbarkeit der Sozialität bei den Nachkommen. Die Eiproduktion der Nachkommen wurde signifikant von der mütterlichen IGP-Erfahrung beeinflusst und geringfügig von der väterlichen IGP-Erfahrung, wobei die geringste Reproduktionsleistung beobachtet wurde, wenn die Mütter, aber nicht ihre Partner, einem IGP-Risiko ausgesetzt waren. Insgesamt deuten die Ergebnisse meiner Arbeit darauf hin, dass elterliche IGP-Erfahrungen im frühen Lebensalter geschlechtsspezifische Auswirkungen auf die mittleren Verhaltensmerkmale der Nachkommen sowie auf ihre Persönlichkeit haben können. Die Ergebnisse unterstreichen die Komplexität transgenerationaler Effekte, wobei entweder mütterliche oder väterliche oder beide Einflüsse unterschiedlich zur Merkmalsausprägung in den Nachkommen beitragen. Studien die zeigen wie die elterlichen Erfahrungen die Persönlichkeit der Nachkommen beeinflussen und formen können, sind wichtig, um die Entstehung und Ausbildung von tierischen Persönlichkeiten zu entschlüsseln.