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Parental social experience modulates offspring personality in the predatory mite *Phytoseiulus macropilis*

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Stephanie Rasch BA BEd

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Abstract

Despite growing research interest in animal personality and transgenerational plasticity, the impact of parental social experience on shaping offspring personality remains largely unexplored. This thesis examines whether parental social experience modulates daughters' mean and repeatable behaviour in the plant-inhabiting, group-living predatory mite *Phytoseiulus macropilis* in four personality traits: activity, aggressiveness, exploration, and sociability. The parental generation was reared in socially isolated or grouped conditions and subsequently mated to create four treatment groups of different parental social experiences. The results indicate that parental social experience modulates offspring personality, *aka* behavioural repeatability, in sociability, and to a lesser extent, in activity. Notably, repeatability was higher in offspring of parents with different social experiences, and the highest in offspring from grouped mothers and isolated fathers, and lower in those of shared social experience. Also mean offspring behaviour in activity, aggressiveness, exploration, and sociability was affected by biparental or maternal social experiences in some treatment groups. No behavioural correlations were observed between personality types in activity and the other personality types. Paternal social experience, but not maternal or biparental experience, affected the number of eggs produced by daughters. Significant correlations between personality types and oviposition were found in sociability and activity in some parental treatment groups. Sociability exhibited opposing correlations with egg production in different parental contexts, and activity was consistently negatively correlated. Overall, the findings of my thesis provide novel insights into how parental social environments influence personality expression of offspring and underscore the importance of considering parental social context in the study of animal personality.

Zusammenfassung

Trotz zunehmendem Forschungsinteresse an tierischer Persönlichkeit und transgenerationaler Plastizität ist der Einfluss elterlicher Sozialerfahrung auf die Persönlichkeitsbildung der Nachkommen weitgehend unerforscht. Diese Arbeit untersucht, ob die elterliche soziale Erfahrung das Verhalten der weiblichen Nachkommen der pflanzenbewohnenden, gruppenlebenden Raubmilbe *Phytoseiulus macropilis* in Bezug auf vier Persönlichkeitsmerkmale beeinflusst: Aktivität, Aggressivität, Exploration und Soziabilität. Die Elterngeneration wurde unter sozial isolierten oder gruppierten Bedingungen aufgezogen und anschließend gepaart, um vier Gruppen von Nachkommen mit unterschiedlichen elterlichen Sozialerfahrungen zu bilden. Die Ergebnisse zeigen, dass die elterlichen Sozialerfahrungen die Persönlichkeit, i.e. die Wiederholbarkeit des Verhaltens, in Soziabilität und in geringerem Maße auch in Aktivität moduliert. Erwähnenswert ist, dass die Wiederholbarkeit bei Nachkommen von Eltern mit unterschiedlicher Sozialerfahrung höher (am höchsten bei den Nachkommen von gruppierten Müttern und isolierten Vätern) und bei solchen mit gleicher Sozialerfahrung niedriger war. Auch das durchschnittliche Verhalten der Nachkommen wurde in einigen Gruppen durch biparentale oder mütterliche soziale Erfahrungen in Aktivität, Aggressivität, Exploration und Soziabilität beeinflusst. Es zeigten sich keine Korrelationen zwischen den Persönlichkeitstypen in Aktivität und den anderen Verhaltenskategorien. Die väterliche Sozialerfahrung, nicht aber die mütterliche oder biparentale Erfahrung, beeinflusste die Anzahl der von den Töchtern produzierten Eier. Signifikante Korrelationen zwischen den Persönlichkeitstypen und der Eiablage wurden in Bezug auf Soziabilität und Aktivität bei den Nachkommen mancher elterlicher Behandlungsgruppen festgestellt. Die Soziabilität wies in unterschiedlichen elterlichen Kontexten gegensätzliche Korrelationen mit der Eiproduktion auf, während Eiproduktion und Aktivität durchwegs in einem negativen Zusammenhang standen. Diese Ergebnisse meiner Arbeit geben neue Einblicke in den Einfluss des sozialen Umfelds der Eltern auf die Ausprägung der Persönlichkeit der Nachkommen und unterstreichen die Bedeutung der Berücksichtigung des sozialen Umfelds der Eltern bei der Untersuchung der Persönlichkeit von Tieren.

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1. Introduction

1.1. Rationale

In recent years, the concept of personality has expanded from a predominantly human characteristic to one that encompasses animals as well (Gosling, 2001). Animal personality typically manifests in behavioural repeatability and is characterised by consistent within-individual behaviours linked to consistent behavioural differences among individuals within a group (Biro & Stamps, 2008). These individual differences can affect fitness and thus contribute to evolutionary dynamics (Gosling, 2001; Réale et al., 2007). Consequently, applying the concept of personality to animals carries the potential to help better understand the mechanisms underlying animal behaviour and its ecological and evolutionary implications. Similarly, the study of parental effects, which are defined as non-genetic environmental influences in the parental generation passed on to offspring, causing phenotypic but not genotypic changes (e.g., Bonduriansky & Day, 2009), provides valuable insights into evolutionary and ecological pathways mediating phenotypic plasticity and adaptations to changing environments. Moreover, the interplay of these two phenomena, especially how parental effects contribute to animal personality formation and expression, is gaining increasing attention. Pertinent studies promise novel insights into the complex matter of individual behavioural variation and its ecological and evolutionary origins and effects (Reddon, 2012).

Research on animal personality and parental effects is spread across a multitude of taxa, including plant-inhabiting predatory mites of the family Phytoseiidae. These mites have been shown to display complex behaviours influenced by parental effects (Schausberger et al., 2017; Seiter & Schausberger, 2015). However, so far, stringent experimental studies on the effects of parental experiences on offspring personality are scarce across animals (Reddon, 2012). Regarding mites, the effect of parental social condition on offspring personality has not yet been covered and is thus unknown. Accordingly, the aim of this thesis is to address this gap in animal personality research and address the following question: Does parental social experience modulate offspring personality in activity, aggressiveness, exploration and sociability of the plant-inhabiting, group-living predatory mite *Phytoseiulus macropilis*? To answer this question, behavioural assays of these personality traits were carried out. The

analysis of the test scores entailed the calculation of repeatability, behavioural correlations and personality types. The thesis is organised into four sections. Section 1 introduces the terminology and central concepts of animal personality research, followed by an overview of parental effects and their potential impact on animal personality. Section 2 details the methodology, followed by a presentation of the results, structured by personality traits, in Section 3. A discussion of the results is found in Section 4. The thesis concludes with Section 5, summarising the key findings of the thesis.

1.2. Animal personality

1.2.1. Terminology

The term personality stands for various concepts depending on the organisms in question and the context. Moreover, several different terms have been used in place of, and in association with, personality. Consequently, it is necessary to disambiguate the terms and to clarify the concept of personality as referred to in this thesis. This section aims to provide an overview of the core terminology and concepts essential to the study of animal personality. Initially, the concept of personality had been mainly associated with the field of human psychology before it was extended to non-human animals around the turn of the millennium. While the central notion of personality is the same for humans and non-human animals, it encompasses a different range of phenomena. For instance, animal personality research, in contrast to human personality research, does not involve phenomena such as personal projects, identity, attitudes, and life stories. It instead focuses on behavioural traits and abilities in broader dimensions, which must be rigorously testable and quantifiable by pertinent natural science methodologies. With the emergence of research interest in animal personality, the need for a common framework arose (Gosling, 2001).

Currently, the generally agreed-upon definition, and the one used in this thesis, is that animal personality describes the "behavioural differences between individuals that are consistent over time and across situations" (Réale et al., 2010). Based on this definition, Kaiser and Müller (2021) have formulated three criteria for animal personality: individual differences, temporal stability, and contextual consistency. In contrast, animal personality has also been defined more broadly as "individual behavioural differences that are consistent over time and/or across situations" (Réale et al., 2007). The key distinction here is consistency throughout time and contexts, compared in the former concept to just either one of them or both in the latter broader

definition. Apart from slight conceptual differences in personality, several different terms have been used to describe it; yet, animal personality has established itself as the most commonly used one. One of these terms used in place of personality is temperament. Gosling (2001) suggests that some prefer the use of temperament over personality because it carries a smaller risk of anthropomorphism. Conceptually, though, temperament is roughly synonymous with personality.

Behavioural syndrome is another term sometimes used in place of personality; however, the concept is not entirely synonymous with animal personality. It has been defined as "a suite of correlated behaviours across multiple (two or more) observations - most interestingly, if it involves multiple contexts or situations" (Sih et al., 2004). Another understanding of behavioural syndromes defines them as "suites of correlated behavioural traits" and provides the example of a correlation between the canonical behavioural traits aggressiveness and boldness (Wolf & Weissing, 2010). The latter definition differs from animal personality, as it describes correlations between different behavioural traits and not between aspects within the same behavioural trait. Behavioural syndromes, according to Réale et al. (2010), describe the correlations "between the same behavioural trait in two different environmental contexts or between two distinct behavioural traits," which is close to a "broad-sense definition of personality." As such, behavioural syndromes describe the same phenomenon as animal personality, if it is understood as the first part of this definition. However, if it is understood as the second part, it does not match the definition of animal personality. In this thesis, behavioural syndromes are considered distinct from animal personality and understood as the correlation between distinct behavioural traits.

In their seminal review, Réale et al. (2007) proposed a framework for animal personality within evolutionary ecology and outlined, as well as operationalised, five canonical personality traits or dimensions: (1) boldness, (2) exploration, (3) activity, (4) aggressiveness, and (5) sociability. (1) Boldness describes the behaviour an individual shows when faced with a risky situation, for instance, when confronted with a predator. (2) The response to novel situations is termed exploration. New situations include novel objects or environments. Typical procedures for evaluating exploration are named novel-object and open-field test, respectively. In these tests, the distance as well as the latency to approach or explore a novel object can be measured. (3) Activity is understood as the "general level of activity" (Réale et al., 2007) and should ideally be tested in familiar and safe environments. Typical measures of activity levels are

observations of whether an individual is moving or stationary, and observations of the distance covered over a set time. (4) Aggressiveness refers to hostile behaviour towards conspecifics. It can be tested by quantifying competitive social interactions, such as physical displacement or the occurrence of fights, or measuring the latency of attack. (5) Lastly, sociability describes friendly interactions with conspecifics, such as joining behaviour, frequency and duration of social interactions, or inter-individual distances. A widely used sociability test is the so-called separation test, in which individuals are separated from conspecifics and observations on their behaviour after separation or the latency to rejoin the group are made. Each of these personality traits is a continuum with two extremes on each end, such as extremely shy and extremely bold. The term personality type is used to describe where an individual consistently scores on this continuum of a single personality trait (Kaiser & Müller, 2021; Schausberger et al., 2024). To sum up, animal personality describes the consistent inter-individual differences in behaviour within a particular group of conspecific individuals. Behaviours are commonly categorised into five personality traits: boldness, exploration, activity, aggressiveness, and sociability. Correlations between two different personality traits are called behavioural syndromes.

1.2.2. Evolutionary and ecological aspects

Animal personality is a form of phenotypic variance and, as such, it is typically determined by an interplay of genetic and non-genetic environmental factors like personal experiences and/or experiences made in ancestral generations, such as parental effects (Réale et al., 2007). In light of this, evolutionary as well as ecological approaches to the study of animal personality promise valuable insights into how this behavioural variance arises and how it is maintained. Animal personality thus adds a crucial third dimension to intraspecific variation (Wolf & Weissing, 2012). This section aims to give a broader insight into the main models and mechanisms trying to explain the phenomenon of animal personality and its ecological and evolutionary implications.

Classic evolutionary explanations appear to be insufficient to explain animal personality fully, as they do not explain the consistency aspect of inter-individual behavioural differences. Consequently, additional explanations are needed (Réale et al., 2010). In their review, Dingemanse and Wolf (2010) distinguish between three types of models explaining adaptive personality differences: models based on differences in state, models investigating the feedback between state and behaviour, and models that are not based on state differences. State-

dependent personality models are centred around the notion of underlying states of behaviour. In the context of state-dependent personality models, state refers to "any features that affect the cost and benefits of its behavioural actions" (Sih et al., 2015). Examples are morphology, age, size, physical and physiological condition, and experiences of the ecological, including the social environment. These features may influence behaviour by preventing or reducing its quality. States can be either inherently stable or labile. Stable states refer to features that are extremely costly or even impossible to change, such as sex. Labile states, in contrast, are changed very easily and quickly, such as blood pressure or energy reserves. Stable states can explain the consistency of behaviour, since the state on which the behaviour depends remains stable. Consequently, variation in stable states between individuals can result in consistent variation of behaviour among individuals (Dingemanse & Wolf, 2010; Sih et al., 2015). A clear strength of state-dependent personality models is that they can explain suites of correlated behaviours, because one state can affect more than one behaviour. However, they do not explain the initial cause for variation and the maintenance of state differences over time (Dingemanse & Wolf, 2010; Wolf & Weissing, 2010).

Labile states can explain variation in state-dependent behaviour as the behaviour changes with the state. However, consistency of behaviour depending on labile states is harder to explain, as it would require labile states to become more stable. One possible explanation is found in positive feedback-mechanisms between state and behaviour. There are two main ways in which feedback loops can stabilise behaviour dependent on labile states. Initially, a difference in state may arise and affect the dependent behaviour, which in turn affects the state in a stabilising manner. Alternatively, a difference in behaviour may result in a difference in state, which in turn stabilises the behaviour. As a result, originally minor differences in state may diverge and become more pronounced via positive feedback-loops (Wolf & Weissing, 2010). Examples of such feedback mechanisms are, for instance, the feedback between energy levels and foraging under the risk of predation, the feedback between behavioural performance and experience, and the feedback between the residual reproductive value and risk-taking behaviour (Dingemanse & Wolf, 2010). More broadly, feedback mechanisms can involve risk-reward and life history trade-offs, as well as the skill set or experience of an individual. The strength of these feedback mechanisms often depends on the environment (Sih et al., 2015). For example, a general trade-off principle concerning aggressiveness and boldness seems to be that an individual should be less willing to take risks the more it stands to lose (Wolf et al., 2007).

Regarding life-history trade-offs, Biro and Stamps (2008) compiled empirical studies on the link between life-history trade-offs and personality traits. They found that boldness, activity, and/or aggressiveness are often positively linked to life-history traits such as food intake rates and reproductive productivity. To sum up, state-dependent personality models try to explain animal personality as "an adaptive outcome of among-individual differences in state" (Sih et al., 2015).

Models not based on state instead focus on frequency-dependent selection, on responsive strategies in social contexts based on individual variation within the population, and on the co-evolution of signal emission and interpretation (Dingemanse & Wolf, 2010). Frequency-dependent selection describes the case where the outcome of selection is the equal fitness of behavioural types within a population. This occurs when the fitness of a behavioural type depends on the frequency of that type in the population, relative to alternative types. A typical scenario is a foraging situation with scroungers and producers, in which it becomes less beneficial to be a scrounger as the frequency of scroungers in the population increases. This is an example of negative frequency-dependent selection. Further examples of such mechanisms are competition avoidance, enemy avoidance, and complementation (Wolf & Weissing, 2010). Another explanation for the coexistence of behavioural types focuses on spatio-temporal variation in the environment, which results in a spatio-temporal variation of selection pressures. Under the right conditions, this can explain the coexistence of behavioural types. For instance, spatial variation can maintain variation in behavioural types if individuals cannot just freely adapt to the environment. Lastly, non-equilibrium dynamics, which occur when there is a lack of steady states, may also give rise to the coexistence of behavioural types (Wolf & Weissing, 2010).

While the above-mentioned models and mechanisms try to explain the occurrence of animal personalities, it is also worth examining the consequences of animal personalities on ecology and evolution. Wolf and Weissing (2012) formulated twelve ecological and evolutionary implications. For instance, the aspect of evolvability is an important implication. As there are many correlations between personality traits, they may optimise adaptive evolution in situations where populations experience a rapid change in conditions, because traits do not have to evolve independently. Similarly, the speed of speciation may increase. Various consequences are related to movement in space, leading to non-random distribution and

interaction. For example, the variation in personality types could lead to a higher carrying capacity if these differences reduce competition for resources. Furthermore, personality variation can lead to differences in a number of aspects. Personality variation affecting spatial distribution and social networks can lead to differences in the spread of information and diseases. Furthermore, variation in personality types can improve a population's resilience to environmental change, as well as its speed of evolution and adaptive potential. Ultimately, variation in personality can be regarded as an essential dimension of biodiversity and living together (Wolf & Weissing, 2012).

1.2.3. Research on animal personality

Research on animal personality has been conducted throughout the animal kingdom, from sea anemones to insects, spiders, mites to birds, fish and mammals. Personality in insects was examined in relation to metamorphosis. For example, Amat et al. (2018) suggest that differences in state variables such as metabolic rate, growth rate and energetic reserves in early developmental stages of holometabolous and heterometabolous insects may be too small to account for personality differences, indicating that more likely genetic or parental effects are at work. A connection between personality and tool use was examined in the ant *Aphaenogaster senilis* (Maák et al., 2020). These authors found out that personality traits could explain division of labour within a colony; ant personality predicted the use of tools, and more explorative ants took over the role of tool users after previously present tool users were removed. In arachnids, for example, the personality of spiders has been examined with regard to behavioural, physiological and environmental factors (Hernández Duran et al., 2021). For instance, the bridge spider *Larinoides sclopetarius*, which is abundant in urban areas, showed high between-individual variability in many behavioural traits such as aggressiveness and boldness. Moreover, spiders with higher levels of aggressiveness suffered from higher mortality and males were much more aggressive than females (Kralj-Fišer & Schneider, 2012).

In vertebrates, juvenile lemon sharks, *Negaprion brevirostris,* were found to display consistent individual differences in sociability (Finger et al., 2017). Moreover, it was shown that the environmental factors can generate behavioural syndromes; in particular, exposure to predation risk induced a correlation between boldness and aggressiveness in sticklebacks *Gasterosteus aculeatus* (Bell & Sih, 2007). The effect of another environmental factor, namely the degree of human disturbance, was studied in little penguins *Eudyptula minor* (Colombelli-Négrel &

Katsis, 2021). Four colonies of little penguins were studied, which had different levels of human disturbance, ranging from low to high and even unregulated disturbance by unauthorised vehicles or people walking on top of nests. It was found that penguins from colonies with a high degree of unregulated nest disturbance by humans displayed a higher degree of nest defence behaviour than penguins in less disturbed environments (Colombelli-Négrel & Katsis, 2021). The nest defence behaviour observed in the little penguin study was used to infer aggressiveness; however, in the framework by Réale et al. (2007), the personality trait aggressiveness is more narrowly defined as aggressive behaviour only towards conspecifics. According to this framework, the tests carried out in the little penguin study are more indicative of boldness, as the experiment involved a researcher with a tennis-ball contraption approaching the nest. Portugal et al. (2017) examined the link between dominance hierarchies and exploration in homing pigeons, *Columba livia*, revealing no connection between exploration and dominance rank. Another study on birds, black-capped chickadees, *Poecile atricapillus,* examined the connection between exploratory behaviour and urbanisation (Thompson et al., 2018). The authors found that urban birds were more exploratory than non-urban birds and that among-individual variation was greater in urban environments than in non-urban environments.

Smith and Blumstein (2008) performed a meta-analysis on the consequences that personality traits can have on fitness. They surmised that boldness and aggression increased reproductive success, and that boldness reduced survival while exploration increased survival. In contrast, another meta-analysis by Moiron et. al (2020) concluded that bolder behavioural types did not suffer from higher mortality. To sum up, animal personality has been studied across multiple taxa. Evolutionary stable variation in personality types can be explained via various models and mechanisms that can be grouped into models depending on the difference in states and models based on other factors than state, such as frequency-dependent selection. Moreover, according to Wolf and Weissing (2012) personality traits have adaptive value as they can influence evolutionary outcomes and should be regarded as a third dimension of intraspecific biodiversity, next to commonly studied variation due to life history and morphological and physiological differences.

1.3. Parental effects

1.3.1. Overview

Parental effects are one cause of variation in offspring and are mostly described for mothers, i.e. maternal effects. Commonly, parental effects are defined as the non-genetic influence of the parental phenotype or environmental conditions experienced by the parents on the offspring phenotype (Mousseau & Dingle, 1991; Mousseau & Fox, 1998; Wolf et al., 2007). However, different fields of study have different perspectives on specifics, such as which phenomena should be regarded as parental effects (Badyaev, 2009). According to Wolf and Wade (2009), an important distinction should be made between the broader phenomenon of parental inheritance and parental effects. Their definition of parental effects explicitly excludes phenomena such as maternal cytoplasmic inheritance and genomic imprinting, which should rather be understood as parental inheritance in a broader sense. A phenomenon embracing, or closely related to, parental effects is non-genetic inheritance. It is described as "any effect on offspring phenotype brought about by the transmission of factors other than DNA sequences from parents or remote ancestors" and used in place of parental effects to avoid ambiguity (Bonduriansky & Day, 2009). The term transgenerational effect encompasses not only parental effects, but also grandparental effects (Schausberger & Rendon, 2022), as it is used to describe the influence of an ancestral generation's environment or behaviour on subsequent generations (Yin et al., 2019). The specific case of parental effects, occurring when the environment a parent experienced has an effect on their offspring phenotype but not genotype, is also one type of transgenerational plasticity. Transgenerational plasticity may span across multiple generations (Bell & Hellmann, 2019). The interest of this thesis lies in parental effects, specifically how the social conditions experienced by parents affect offspring personality.

Parental effects can be categorised according to outcomes into three types: developmentally entrenched, context-specific parental effects, and passive parental effects (Badyaev & Uller, 2009). Developmentally entrenched parental effects are essential to an individual's proper development and are not dependent on environmental conditions. They enable context-specific parental effects to occur. These effects vary depending on the environmental conditions and can have diversifying or directional effects on offspring phenotypes. Passive parental effects occur under stressful conditions that cause the expression of developmental variation that was hitherto unexpressed (Badyaev & Uller, 2009). The mechanisms by which parental effects can

mediate offspring phenotypes are manifold, as are the offspring' traits that are affected. Parental effects may modulate offspring phenotypes via pre-zygotic mechanisms in the form of messenger RNAs, or post-zygotic mechanisms in the form of nutritional provisioning and choice of nest sites, among others. Though most studies on parental effects focus on, and presume, maternal effects (Wolf & Wade, 2009), parental effects can be mediated by the mother (maternal), the father (paternal) or both. Paternal effects are likely more widespread than anticipated, but much more difficult to pinpoint than maternal effects (Crean & Bonduriansky, 2014).

Regarding insect life histories, maternal effects can influence the intensity and incidence of diapause, the production of sexual forms, wing polyphenism, dispersal behaviour, developmental time, growth rate, resistance to chemicals or microbial infection, and survival and reproduction (Mousseau & Dingle, 1991). In particular, maternal oviposition behaviour can influence offspring growth and survival by choosing the oviposition site, manipulating offspring sex ratio, and clutch size, all of which can affect the level of resource competition among the offspring (Mousseau & Fox, 1998). In general, parental effects may affect offspring in all developmental stages and can also last for life (Wolf & Wade, 2009).

Another perspective on how to regard the mechanism of parental effects is to view it as a multistep communication process. In this process, a parent initially experiences an environmental cue, processes this information, and uses it to modify the environmental conditions experienced by their offspring or to send different signals or cues to their offspring, which must be detected by the offspring to have an effect. Additionally, the offspring further process this information and combine it with other non-parental cues, which implies that offspring are not necessarily only passive receivers. On the contrary, mechanisms to manage possibly deceptive parental cues can occur (Bell & Hellmann, 2019).

Parental effects represent an essential aspect of evolution, specifically by overcoming some limitations of genetic inheritance, such as the transmission of acquired traits, and by increasing the speed of adaptation to environmental changes compared to genetic adaptation (Bonduriansky & Day, 2009). A more comprehensive understanding of how parental effects may affect evolutionary and ecological phenomena is due to the fact that parental effects integrate developmental variation, natural selection, and inheritance. This integration results in various patterns of parental effects in evolution and ecology to emerge. Overall, parental effects

constitute a generator of evolutionary innovation and diversification (Badyaev & Uller, 2009). Adaptive innovations can arise and be maintained via parental effects. They might also simultaneously cause coordinated changes in several offspring phenotypes. As a result, parental effects may facilitate the swift evolution of ontogenies across generations, or they may accomplish the opposite by restricting diversification and adaptability when parental and offspring environments do not match. They may enhance heredity by facilitating the non-genetic transmission of adaptive modifications or by maximising the similarity between parents and offspring.

Parental effects may also reduce hereditability if they have a diversifying effect, thus decreasing similarity between parents and offspring. Additionally, parental effects can be short-term or long-term, where short-term parental effects can either become long-term or weaken and vanish over time (Badyaev & Uller, 2009). Lastly, a meta-analysis concludes that parental effects can improve offspring performance across different environments and not only in those matching the parental environments (Yin et al., 2019).

To understand how parental effects may arise and be maintained, conditions under which parental effects are selected for have been examined. Uller et al. (2008) formulated three conditions under which parental effects are favoured by evolution, based on models that predict within-generation developmental plasticity. Parental effects are a type of parentally induced developmental plasticity, differing from general developmental plasticity by occurring between and not within generations (and are then accordingly called a type of transgenerational plasticity; Bell & Hellmann, 2019). First, the environment must be heterogeneous across generations. Second, the parental environment or other parental traits can be predictive of the offspring environment (Uller, 2008). A similar condition is also proposed in relation to maternal effects in plants (Galloway, 2005). Third, gathering and appropriately reacting to information must not incur costs that are too high. Also, there should be no parent-offspring conflict, which represents divergent evolutionary interests of parents and offspring (Uller, 2008). Parent-offspring conflict potentially limits the evolution of parental effects by creating conditions in which it is not ideal for the offspring to trust potentially misleading parental signals. However, empirical evidence is too sparse to clearly state how parent-offspring conflict impacts the evolution of parental effects (Bell & Hellmann, 2019). All in all, parental effects play a significant role in shaping the phenotypes of the next generation, bringing together evolution, ecology, and development (Uller, 2008).

1.3.2. Parental effects on animal personality

The study of parental effects on animal personality combines two major areas of research (Reddon, 2012). As previously mentioned, parental effects can influence animal personality. Behaviour in general is not only one of the many aspects influenced by parental effects, but can also act as the cause for parental effects. Within context-dependent parental effects, anticipatory or diversifying effects may occur, based on the predictability of the offspring environment. Unpredictable environments or insufficient information about the offspring' environment usually lead to diversifying parental effects, resulting in greater variation of behavioural or personality types within a population. This is beneficial, under the assumption that a greater variety of behavioural or personality types within a population increases the chance that at least some individuals are a good fit, in comparison to a more homogeneous composition. This strategy is also known as bet-hedging (Reddon, 2012). Anticipatory parental effects may explain populations with slight behavioural or personality variation, while diversifying parental effects may explain greater variation in behavioural or personality types (Reddon, 2012). Moreover, the adaptive value of behavioural traits can be modulated by parental effects in three main ways. First, parental effects may affect the fitness cost/benefit trade-offs associated with the behavioural trait. Second, they may influence the fitness implications of social interactions. Third, they may alter behavioural traits that are themselves also parental effects (Kilner et al., 2015).

1.3.3. Research on parental effects and animal personality

Several studies have examined the parental effects on mean behavioural traits and/or personality (behavioural repeatability). For example, the experience of mild stress (husbandry procedures) by the mothers of the viviparous guppy *Poecilia reticulata* led to more aggressive offspring and higher inter-individual variation, thus showing diversifying parental effects (Eaton et al., 2015). In contrast, Cortez et al. (2016) examined the effect of maternal stress (caused by handling or cortisol treatment) on learning and boldness in brook trout *Salvelinus fontinalis* and found no effect on boldness. However, in this study, boldness was tested only once, not repeatedly, which does not conform to the definition of personality as behavioural repeatability by Réale et al. (2007). A study on the freshwater snail *Physa acuta* examined the effect of parental experience with predator cues on personality diversity and escaping behaviour (Tariel et al., 2020). These authors found no effect of parental environment on the

level of personality diversity within the group, but snails with parents that experienced predator cues took longer to escape. Thus, parental effects modulated mean behaviour. While they did not lead to greater diversity in personality, personal experience of predator cues by developing snails did have an effect (Tariel et al., 2020). The native Australian rodent *Melomys cervinipes* was tested in a study on maternally mediated genetic and non-genetic effects on offspring exploration and anxiety-like behaviours (Rowell & Rymer, 2024). While evidence for genetic effects was found in open-field tests for exploration, maternal care did not affect offspring personality in exploration. Interestingly, anxiety and exploration assayed via novel-object tests displayed more variable results, possibly indicating that developmental factors more strongly influence the observed behaviours than genetic or non-genetic maternal effects (Rowell & Rymer, 2024). To sum up, parental effects have high potential to contribute to the occurrence of personality, the degree of variation in personality and the diversity of personality types.

1.4. Aims of the thesis

The previous sub-sections have provided an overview of research on parental effects and animal personality in predatory mites and other animals. Most studies on behaviour have focused either on parental effects of environmental cues other than social ones (e.g., Eaton et al., 2015; Nguyen & Schausberger, 2025b; Schausberger & Rendon, 2022; Seiter & Schausberger, 2015) or the effect of social experiences within the same generation (e.g., Groneberg et al., 2020; Jäger, 2019; Schausberger et al., 2017; Schausberger & Nguyen, 2025), except for a study on the effects of paternal social isolation on offspring activity in zebrafish (Hellmann & Rogers, 2024). However, no study has explicitly focused on the parental effects of social isolation on offspring personality in any animal. My thesis' aim was to determine whether the social conditions of the parental generation modulate offspring personality in the predatory mite *Phytoseiulus macropilis*. Specifically, four of the five personality traits defined by Réale et al (2007) were selected: activity, aggressiveness, exploration and sociability. Accordingly, the overarching research question was: Does parental social experience modulate offspring personality in activity, aggressiveness, exploration and sociability of the plant-inhabiting, group-living predatory mite *Phytoseiulus macropilis*?

Six specific research questions were formulated. (1) Does parental social experience (grouped or isolated) affect offspring behaviour (mean and personality) in activity, aggressiveness, exploration and sociability? (2) Is there significant repeatability (i.e. inter-individual behavioural consistency) across treatment groups? The purpose of this question is to establish whether parental social experience could increase or decrease repeatability. (3) Which parent (mother, father or both) causes behavioural variation in offspring? (4) Are activity types correlated with aggressiveness types, exploration types or sociability types? This question tries to address whether any behavioural syndromes may be present. Because I also observed oviposition during and between the repeated assays, two fitness-related questions were raised. (5) Does parental social experience affect the number of eggs produced? (6) Are personality types correlated with the number of eggs produced?

2. Materials & Methods

2.1. Study organism *Phytoseiulus macropilis*

Phytoseiulus macropilis is a plant-inhabiting predatory mite belonging to the family Phytoseiidae, among species like *Phytoseiulus persimilis*, *Neoseiulus californicus, Neioseiulus cucumeris, Amblyseius swirskii*, which have been predominantly studied and used as biological control agents against phytophagous spider mites, also known as *Tetranychidae* (Helle & Sabelis, 1985; McMurtry & Croft, 1997). Some phytoseiid mites are generalist predators, feeding on pollen, fungal spores, spider mites, and thrips, while others are specialised predators of spider mites (Fathipour & Maleknia, 2016). *P. macropilis* is such a specialised predator that mainly feeds on spider mites of the genus *Tetranychus* spp. (Ali, 1998). While *P. macropilis* is also able to feed on other tetranychid mite species, a preference for two-spotted spider mites, *Tetranychus urticae,* has been observed (Majolo & Ferla, 2014). *P. macropilis* feeds on all stages of *T. urticae*, but predates the eggs more than subsequent mobile stages (Blackwood et al., 2001; Oliveira et al., 2007). During the larval stage, *P. macropilis* do not consume any food (Ali, 1998; Schausberger & Croft, 1999).

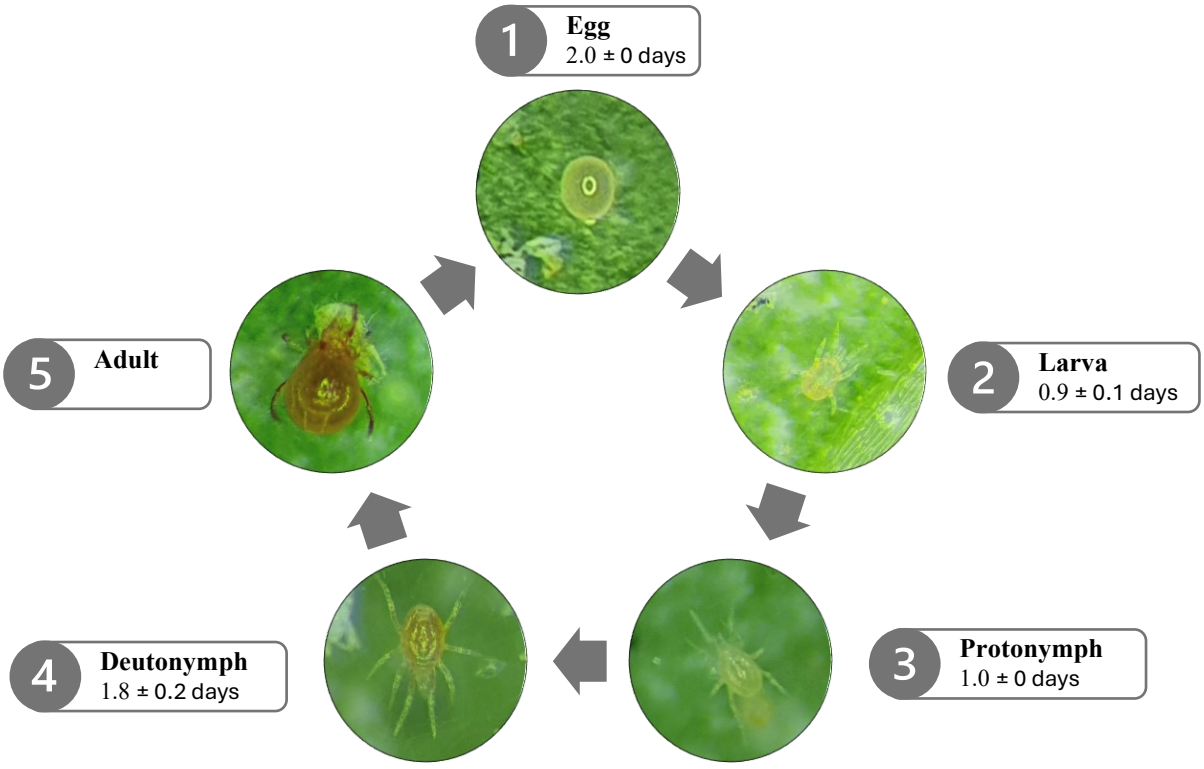

Figure 1**. Life cycle of** *Phytoseiulus macropilis.* Duration of life stages are mean durations of females as observed by Ali (1998) at 25°C when fed on *T. urticae* eggs (photos © Stephanie Rasch).

The predatory mite *P. macropilis* goes through five life stages (Figure 1). As poikilothermous organisms, their rate of development, oviposition rate and longevity depend on temperature. Research on the influence of temperature shows that from 20 to 30 °C the development from egg to adult was faster the higher the temperature, but slowed down again at 32 °C (78 ± 2% RH, 16h light 8h dark photoperiod). Males have shorter developmental times than females (Ali, 1998). Overall, development from egg to adult takes approximately 6 days at 25 °C and 7 days at 20 °C, and from egg to egg 7 days (25 °C) and 11 days (20 °C) (Ali, 1998). Souza-Pimentel et al. (2017) observed shorter mean developmental phases than Ali (1998) for both males and females at 25 ± 2 °C (70 ± 10% RH, 14h light 10h dark photoperiod), which they suggest may be due to differences in the supplied prey stages of *T. urticae*, among other factors. Males display shorter developmental duration, but also experience a shorter lifespan than females. Female longevity spans approximately 43 days at 25 °C and 57 days at 20 °C, whereas males live 38 and 48 days, respectively, at the aforementioned conditions (Ali, 1998).

Although previous research on *P. macropilis* has mainly focused on their use as biological control agents, there are many studies on the behaviour and ecology of *P. macropilis* and closely related phytoseiid mite species such as *Phytoseiulus persimilis*. Due to their global occurrence, ease of rearing in the laboratory and accessibility for experimental manipulation, phytoseiid mites, as well as their prey, spider mites, are widely used model animals in scientific fields such as genetics, ecology, evolution and behaviour (Schausberger, 2022). For instance, cannibalism, aggressiveness and prey preferences among phytoseiid mites have been examined, as well as the impact of intraguild predation risk experienced by phytoseiid mothers on the behaviour and learning of their offspring (Seiter & Schausberger, 2015), and phenomena such as kin-recognition (Schausberger, 2007). Another example is how *P. persimilis* was shown to be more aggressive when reared in isolation compared to grouped rearing conditions, indicating their suitability as a model species in behavioural ecology (Schausberger et al., 2017). It is likely that the closely related species *P. macropilis* is similarly suited to the study of animal behaviour, even though it has not received as much attention. Specifically, no study has yet explored the effect of parental social conditions on personality in *P. macropilis,* nor any other animal species.

2.2. Rearing and pre-experimental treatments

The predatory mites used in this thesis were taken from a laboratory population that had been founded by specimens collected in the wild in the state of São Paulo, Brazil. They were kept in two separate rearing arenas in an air-conditioned room at 23 ± 1 °C, 50 to 60% RH and 16:8 h L:D photoperiod. Leaves of common bean (*Phaseolus vulgaris*) infested with two-spotted spider mites, *T. urticae,* were piled up in the rearing arenas to feed the predatory mites. The spider mites used for feeding were reared under the same environmental conditions on whole common bean plants. To generate mites for the experiments, predatory mites were taken from the rearing units, and the steps listed in Table 1 were followed.

Table 1. Procedure for generating mites used in experiments (light grey - parental generation F0, darker grey - generation of the experimental mites F1)

Day	Procedure
0	Transfer of *Phytoseiulus macropilis* females from the rearing units
	Preparation of small (for isolated) and large (for grouped) leaf discs
1-2	Egg collection Transfer of eggs onto leaf discs to generate isolated and grouped mites
6 (7)	Isolation of deutonymphs in acrylic cages
8 (9)	Pairing of adult female and male mite (four treatments; Figure 2)
	Preparation of small leaf arenas
9 (10)	Transfer of isolated females back onto their leaf discs Transfer of grouped females onto new small leaf arenas.
10 (11)	Removal of eggs after 24 h
(11-13) (12-14)	Daily collection of eggs. Transfer of eggs to small leaf arenas on the last day.
	Preparation of 8 small leaf arenas one day before the last day of egg collection
~20	Checking if there are enough male *Phytoseiulus macropilis* present on each arena to ensure fertilisation of females. If necessary: transfer of male predatory mites from the rearing room.
~ 21	Predatory mites of the four treatments are ready for experiments

First, around 30 *P. macropilis* females were removed from the rearing units and evenly distributed onto two large spider mite-infested leaf arenas (described below) using a fine paint brush. These arenas were stored in a climate chamber at 23 ± 1°C, a relative humidity of 60 ± 5%, and 16h light 8h dark. Over two days, eggs were collected daily from these leaf arenas. To ensure that the eggs developed concurrently, the eggs collected on the first day were

refrigerated at 8 °C to temporarily halt their development. Once at least 80 eggs were collected, they were assigned to two treatments: one half of the eggs were placed in isolation on small leaf discs (Ø 1.1 cm; one egg per disc), and the other half was placed in groups of six to eight eggs on large leaf discs (Ø 2.2 cm). All discs harboured surplus spider mites serving as prey for the predators during development. For each leaf disc (Figure 3b), a solidified agar cylinder (isolated: Ø 1.1 cm, grouped: Ø 2.2 cm), prepared from a 1.5 g agar/100 ml water solution, was placed in the middle of a round insect breeding dish (Ø 5 cm, h = 1.5 cm), closable by a lid containing a mesh-covered (mesh size 0.05 mm) opening (1.3 cm Ø) for ventilation (SPL Life Sciences Co. Ltd., S-Korea). The dish was half-filled with tap water, and a filter paper disc was placed on top. Lastly, a leaf disc was punched out from a trifoliate bean leaf using a cork borer and put on top of the filter paper, abaxial side down. Before adding the predators, one *T. urticae* female was placed on each small leaf disc to generate isolated predatory mites, and three *T. urticae* females were placed on each larger leaf disc to generate grouped mites.

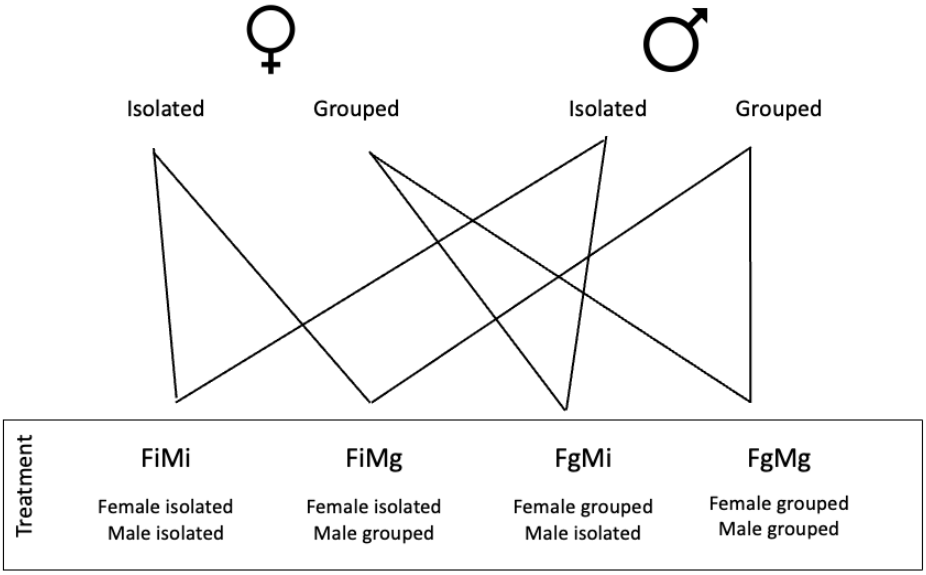

Figure 2. Pairing of the parental generation to produce four parental social treatments

As soon as the predatory mites reached the deutonymphal stage, they were isolated in acrylic cages to prevent random mating. After another two days, the predatory mites had reached adulthood and were paired to create four parental treatments (Figure 2). Pairs were left in their acrylic cages for around 24 h, after which the females were placed back onto the leaf discs in isolation or in groups, according to their early-life experience. The isolated females were placed back onto their leaf discs, and the previously grouped females were placed in groups on new small leaf arenas. To account for a possibly disruptive effect of the transfer and to allow for

(re-) familiarisation with their environment, all eggs laid in the first 24 h were discarded. Over the following four days, eggs were collected daily and intermittently refrigerated at 8 °C until around 20 eggs for each of the four treatments had been collected. These eggs were then distributed onto small spider mite-infested leaf arenas in groups of 10 and allowed to develop to adult and mate in the arenas. Spider mites were replenished as needed. One day before the first experiment, the number of males in each arena was checked to ensure that all females were fertilised, as only gravid females were used. If necessary, the arenas were supplemented with males from the general rearing units.

The large and small leaf arenas used for rearing the predatory mites consisted of common bean leaves singly placed on top of a water-saturated foam block set inside a plastic box (large: 20 × 20 × 6 cm; small: 10 × 10 × 6 cm), half-filled with tap water (Figure 3a). The foam block was covered with moist filter paper and a whole primary (for large arenas), or trifoliate (for small arenas) leaf of common bean was placed on top, abaxial side up. The leaf edges were covered with moist tissue paper, reaching down into the surrounding water to maintain leaf turgidity and to deter the mites from leaving the leaf arena. The leaf arenas harboured mixed life stages of *T. urticae*, which were replenished as needed by brushing spider mites from infested leaves in the arena. To avoid any cross-contamination among treatments, the plastic boxes with the leaf arenas were stored on trays with a layer of soapy water.

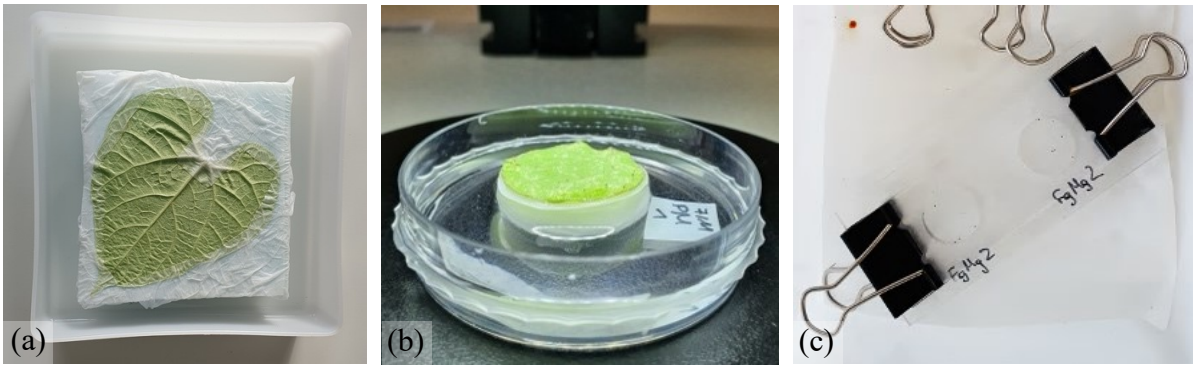

Figure 3. Construction of leaf arena (a), leaf disc (b) and acrylic cage (c).
(© Stephanie Rasch)

The acrylic cages used for isolating the mites in their deutonymphal stage and pairing of female and male mites consisted of a large cavity (Ø 1.5 cm) drilled into an acrylic plate (80 x 35 x 3 mm). Each cavity had a mesh on the bottom and was closed with a microscope slide on top, fastened with foldback clips (Schausberger, 1997). The acrylic cages were stored in a plastic

container with soaked water beads (polyacrylamide) to provide sufficient humidity inside the cages. Two *T. urticae* females were placed in each cavity during moulting of the deutonymphs, and four *T. urticae* were provided during pairing.

2.3. Behavioural Assays

To avoid any inadvertent influence among behavioural assays, different sets of experimental mites were used for the assays on aggressiveness, exploration and sociability.

2.3.1. Aggressiveness

To assess aggressiveness, the females' propensity to cannibalism was examined. More precisely, the occurrence of cannibalism and the latency of attack were used as indicators of aggressiveness. To this end, experimental females were singly placed into an acrylic cage with an unrelated, unfamiliar conspecific larva. The aggressiveness assay was repeated three times with varying contexts and one day break between assays. The contexts differed in the experimental predatory mite females' nutritional state and the presence or absence of spider mite cues inside the cage. In the first assay, the predatory mite females were well-fed before testing and no additional cues were present. In the second assay, spider mite cues were present inside the cage. This was achieved by placing spider mites in the cage one day before the test and removing them immediately before testing. In the third assay, the predatory mite females had been starved for 12 h before testing. Each assay was started by adding the larva to the cage. In between assays, the predatory mite females were placed individually on small leaf discs and stored inside the climate chamber.

In each of the three assays, the predatory mite females were observed every 30 min over 5 h and once more after 24 h to check if the larva had been attacked overnight. A successful attack on the larva was defined as the larva being killed by the experimental predatory mite female. In all three assays, the acrylic cages harbouring the predatory mite females were stored in a plastic container on top of saturated water beads. The construction of the acrylic cages was the same as those described in section 2.2. After the initial 5 h observation period, the cages were transferred to the climate chamber overnight.

If the predatory mite female did not attack the larva within the 5 h window, but within the 24 h, the latency of attack was estimated as 720 min in the analysis. If the female did not attack

the larva within 24 h, a ceiling time of 1440 min was used in analysis. To evaluate the composition of personality types within each treatment, the personality types in aggressiveness were categorised from 0 to 5, based on the degree and consistency of aggressiveness, with 0 being consistently non-aggressive and 5 being consistently highly aggressive (Table 2).

Table 2. Personality type categorisation in aggressiveness.

Aggressiveness	attack (yes/no)	attack latency(min)
0	0	no attack
1	1	=720
2	1	≤300
3	2	≥300, ≥300 or ≤300
4	2	≤300, ≤300
5	3	attack in each assay

2.3.2. Exploration

To examine the exploration propensity of the predatory mite females, three assays were conducted, i.e., an open-field test and two novel object tests (Figure 4). The parameters used to quantify exploration were latency to leave a shelter or release site, latency to arrive at a novel object and, in case of the open-field test, latency to have visited all quadratic sections of the open-field arena at least once. The three assays represented varying contexts and were conducted over the span of five days with one day break in between assays. After each assay, the mites were placed individually on small leaf discs and stored inside the climate chamber.

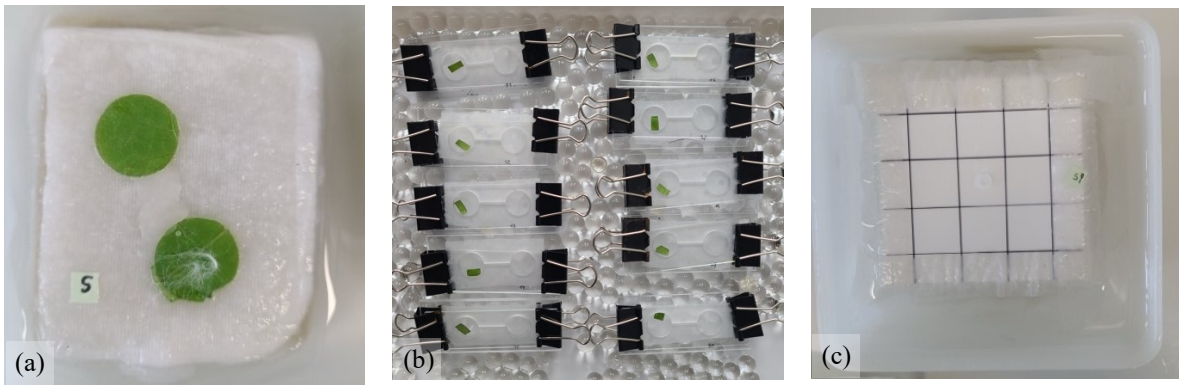

Figure 4. Exploration test arenas
(a) novel object test 1 (b) novel object test 2 (c) open-field test (© Stephanie Rasch)

As shown in Figure 4a, the set-up of the arena for the first test consisted of two leaf discs on top of a water-saturated foam block placed in a plastic box half-filled with water (10 x 10 x 6 cm). The foam block was covered with a cotton pad. The two leaf discs (Ø 1.8cm) were connected by a wax bridge, which was blocked with wet tissue paper until releasing the

experimental animal.One spider mite female was placed on each disc one day before the assay to lay eggs; the spider mite female was removed before releasing the experimental predatory mites. A cotton wool tuft was placed on one leaf disc to serve as a novel object. The experimental predatory mite was placed on the leaf disc without cotton wool and left to acclimatise for 15 min. The experiment was started by removing the wet tissue barrier from the wax bridge. Latency to leave was defined as the time until the predatory mite moved onto the wax bridge with all eight legs. Latency to arrive was defined as the time the predatory mite took to reach the other leaf disc and touch the novel object (cotton wool tuft). The experiment lasted until the predatory mite had arrived at the cotton wool or until the maximum observation period of 20 min was reached, in which case the maximum latency score of 20 min was given. Latency times were measured using a stopwatch app.

In the second assay, acrylic cages with two connected cells were used (Figure 4b). Access to the corridor connecting to the cells was blocked, using a small piece of a silicon tube, until release of the experimental animal. A freshly cut rectangular leaf fragment (8 x 2 mm) of an untreated and clean pepper plant (*Capsicum annuum)* was placed on one side to serve as the novel object. Two adult spider mites were placed on the other side. Each acrylic cage was covered with a microscope slide fastened with foldback clips (Figure 4b). The experimental predatory mite was placed in the cell with the spider mites and left to familiarise for 15 min. The experiment started by removing the silicon piece blocking the corridor to the novel object. Latency to leave was defined as the time until the predatory mite had entered the corridor with all eight legs. Latency to arrive was defined as the time until the predatory mite had reached the other cell containing the leaf fragment with all eight legs. The maximum observation time was the same as in the first assay, i.e. 20 min.

The third assay was an open-field test (Figure 4c). To construct an open field, a 6 x 6 cm acrylic tile platform was sectioned into nine quadrats (each 1.6 x 1.6 cm), leaving a border, made from moist tissue paper, of 0.6 cm on each side. The acrylic tile was put on top of a sponge within a water-filled plastic container (10 x 10 x 6 cm). A small plastic washer (Ø 5 mm outside, 3 mm inside) was placed in the centre of the tile and loaded with 4 spider mite eggs. The predatory mite was placed inside the washer, and the washer was closed with a cover slip to allow the predatory mite to acclimatise for 10 min. The experiment was started by removing the cover slip and videotaping the setup for 5 min. From the videos, the following measures were extracted: the latency to leave was defined as the time until the predatory mite had completely

(with all four leg pairs) left the inside area of the washer. Latency to visit all quadrats was defined as the time elapsed until the predatory mite had visited all quadrats with all eight legs.

To evaluate the composition of personality types within each treatment, the personality types in exploration were categorised from 0 to 5 for latency to leave (A) and latency to arrive (B) based on the degree and consistency of exploration, with 0 being consistently little explorative and 5 being consistently highly explorative (Table 3). For type 0, mites either never (A) left or (B) arrived, or they (A) left or (B) arrived only once throughout all three trials. Types 1 to 3 all (A) left or (B) arrived twice, and types 4 and 5 always (A) left or (B) arrived.

Table 3. Exploration type categorisation

Exploration	A/B	A	B
	leaving/arriving (yes/no)	latency to leave (min) (Trial 1&2/Trial 3)	latency to arrive (min) (Trial 1&2/Trial 3)
0	0-1		
1	2	>10/2.5, <20/5	>10/2.5, >10/2.5
2	2	<10/2.5, <10/2.5	<10/2.5, >10/2.5
3	2	<5/1, <5/1	< 5/1, <10/2.5
4	3	>1/0.01, 1>0.01, 1>0.01 or >1/0.01, 1>0.01. >10/2.5	5/1>x<20/5, 5/1>x<20/5, 5/1>x<20/5
5	3	<1/≤0.01, <10/2.5, <10/2.5	<5/1, <20/5, <20/5

2.3.3. Sociability

To examine sociability, separation tests were conducted. The test parameter was latency to re-join a group of conspecific mites after separation. Three assays were conducted, each with a different context, over five days with one-day breaks between assays. The contexts differed by group size and familiarity of the mites. In the first and second assays, the group size was three adult predatory mites, including the target individual. However, in the first assay, the predatory mites were familiar, whereas unfamiliar mites were used in the second assay. The group of the third assay consisted of five unfamiliar mites, including the target mite. The four non-target unfamiliar mites were taken from the rearing units, whereas the familiar mites were taken from the same rearing arena as the mite being tested. Before and in between the assays, the predatory mites were placed individually on small leaf discs stored in the climate chamber.

The standard procedure for all assays was to mark the target animals with a tiny dot of watercolour (Jolly, Supertabs) on their dorsal shields before testing. The set-up of the experimental arrangement used in all three sociability tests was basically the same as the one described for the first exploration assay (see Figure 4a), apart from using three leaf discs, a larger one (Ø 2.2 cm) and two smaller ones (Ø 1.8 cm), instead of two. Two wax bridges connected each of the two smaller leaf discs with the larger leaf disc. Five spider mite females were placed on the large leaf disc and ten spider mite eggs on each of the small leaf discs. The wax bridges were blocked with wet tissue paper. This set-up allowed for one disc arrangement to be used to test two mites, released for re-joining on different small leaf discs

In all three assays, at the beginning, the target predatory mites were placed within a group of conspecifics on the large leaf disc and left to acclimatise for 10 min. After acclimatisation, the target predatory mite was removed from the group and placed on one of the smaller leaf discs. The assay started by removing the moist tissue barrier from the wax bridge. The assay lasted until the target predatory mite had re-joined the group or the maximum observation time of 30 min was reached. Latency to re-join the group was defined as the time until the target predatory mite had reached the larger leaf disc with all eight legs. Latency times were measured using a stopwatch app. If the predatory mite did not re-join the group, the maximum latency score of 30 min was assigned.

To evaluate the composition of personality types within each treatment, personality types in sociability were categorised from 0 to 4, based on the degree and consistency of sociability, with 0 being consistently non-sociable and 4 being consistently highly sociable (Table 4).

Table 4. Sociability type categorisation

Sociability	Re-joined (yes/no)	latency (min)
0	2 or 3	>1, >1, >1
1	3	>1, >1, <1
2	3	>1, <1, <1
3	3	>1, <1, <0.2
4	3	<1, <1, <1

2.3.4. Activity and Oviposition

The activity of the predatory mites was observed on top of each of the previous personality assays. Activity was quantified on the off days between and after the other personality assays (Table 5). On each observation day, the mites were checked on their familiar leaf discs in 30 min intervals over 2 hours, whether they were stationary or moving. To evaluate the composition of personality types within each treatment, the personality types in activity were categorised from 0 to 4, based on the degree and consistency of activity, with 0 being consistently little active and 4 being consistently highly active (Table 6). Oviposition by the predatory mite females was measured by counting and removing the eggs daily from their leaf discs. In case of the aggressiveness tests, eggs were also counted after the 24 h period in the test cages.

Table 5. Experimental schedule

	Day 1	**Day 2**	**Day 3**	**Day 4**	**Day 5**	**Day 6**
Tests	Test 1	Activity 1	Test 2	Activity 2	Test 3	Activity 3
Eggs	/	1st count	2^{nd} count	3^{rd} count	4^{th} count	5^{th} count

Table 6. Activity type categorisation

Activity	**activity (moving out of 5 observations per day)**
0	0, 0, 0
1	0, 0, 1
2	0, ≤2, ≤2
3	0, ≤2, >2
4	>0, >0, >0

2.4. Statistical analyses

Statistical analyses were conducted using IBM SPSS Statistics for macOS ver. 29.0.2.0 (IBM Corp., Armonk, NY, USA). Time-dependent data in aggressiveness, exploration and sociability were log-transformed before analyses. Generalised estimating equations (GEEs; normal distribution, identity link) were used to analyse the effect of maternal and paternal treatment on mean aggressiveness, exploration and sociability across the repeated assays. Generalised linear models (GLM) were used to analyse the effects of maternal and paternal treatment on mean oviposition and activity (for both: Poisson, log link). To assess repeatability, the

Intraclass Correlation Coefficients (ICC; two-way random, consistency) were calculated for each trait pooled across treatments and for each treatment and maternal/paternal treatment separately. Correlations between personality types and the total number of eggs were calculated using Spearman's rank correlation coefficient. The correlation graphs were made in IBM SPSS Statistics for macOS ver. 29.0.2.0 (IBM Corp., Armonk, NY, USA) and edited in Microsoft Word (Microsoft Corporation, 2024). The graphs of the population means, forest plots and personality type distributions were created using JMP® Version *18* (SAS Institute Inc., Cary, NC, 1989–2023).

3. Results

3.1. Aggressiveness

3.1.1. Population means

Aggressiveness scores across the three assays were collected for a total of 116 mites, with oviposition data available for all of them, while activity was quantified in 84 mites. The sample size per treatment was similar across treatments for both aggressiveness (FgMg 28, FgMi 30, FiMg 28, FiMi 30) and activity (FgMg 19, FgMi 24, FiMg 23, FiMi 20).

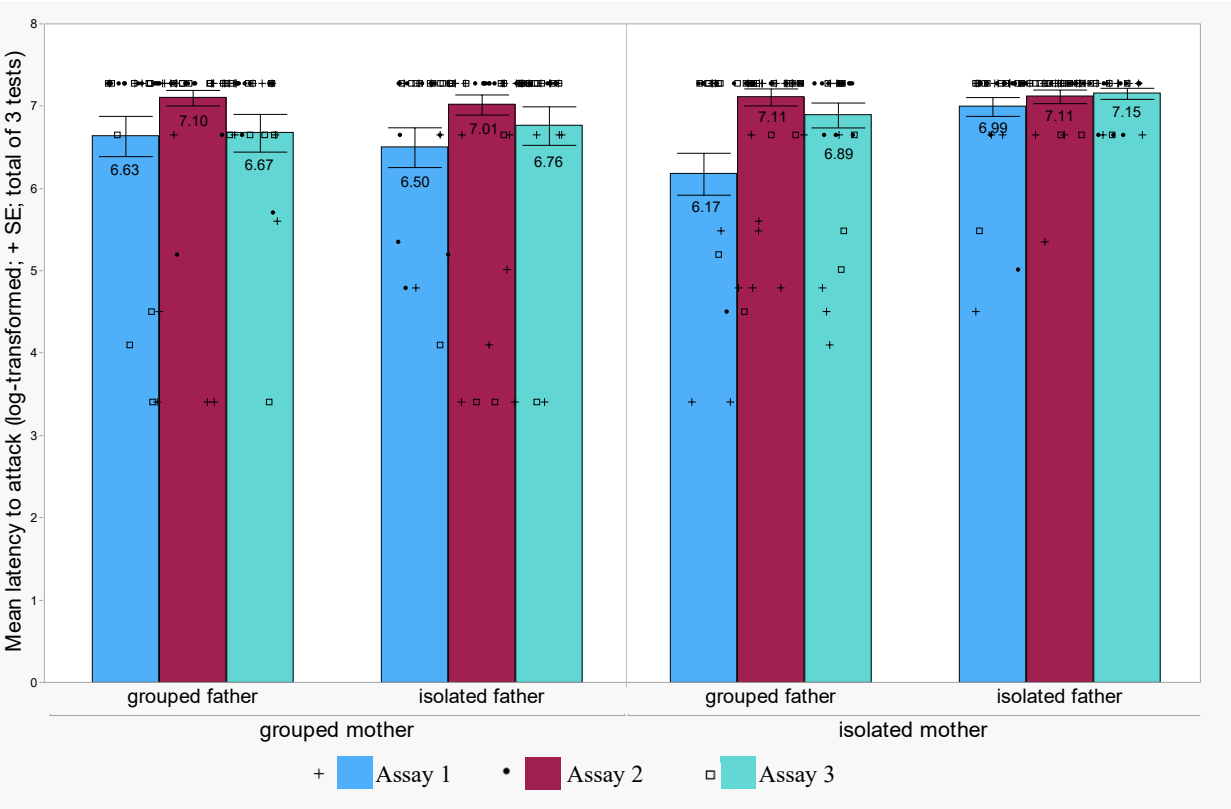

Figure 5. Log-transformed mean (± SE) latency of predatory mite females to attack a conspecific larva across three assays and treatments

In the aggressiveness experiment, the 116 mites were tested over three assays, resulting in 373 observations on attack latency, out of which 288 mites did not attack the larva during the observation period. Among the 85 mites that did attack, slightly more than half (44) did so within the first five hours. Among assays, the most attacks occurred during the first assay (42), accounting for almost half of the attacks overall. In the remaining two assays, 18 attacks were counted during the second and 25 attacks during the third assay.

Figure 5 shows the log-transformed mean scores of the latency to attack across treatments and assays. Averaging the log-transformed mean scores of all three assays, the treatment group FiMi scored the least aggressive ($\bar{x}$ = 7.00), FiMg the most ($\bar{x}$ = 6.71). FgMg ($\bar{x}$ = 6.82) and FgMi ($\bar{x}$ = 6.84) scored in-between and very similarly. When dividing the parental treatments into maternal (Fg, Fi) and paternal (Mg, Mi) treatments, the log-transformed mean aggressiveness scores suggest that offspring of females mated to grouped males ($\bar{x}$ = 6.76) were slightly more aggressive than those mated to isolated males ($\bar{x}$ = 6.92) and offspring of grouped mothers ($\bar{x}$ = 6.78) were slightly more aggressive than those of isolated mothers ($\bar{x}$ = 6.91).

Table 7. Results of GEEs and GLMs for the effects of maternal and paternal state (isolated or grouped) on the mean number of eggs, activity, and aggressiveness in all individuals and in only attacking individuals.

Dependent variable	Independent variables	Wald Chi-Square	df	Sig.
Aggressiveness all individuals	**Fem_state**	1.458	1	0.227
	M_state	2.376	1	0.123
	Fem_x_M_state	3.829	1	0.05
Aggressiveness only attacking	**Fem_state**	4.99	1	0.025
	M_state	1.418	1	0.234
	Fem_x_M_state	4.181	1	0.041
Eggs	**Fem_state**	1.384	1	0.239
	M_state	4.873	1	0.027
	Fem_x_M_state	0.006	1	0.939
Activity	**Fem_state**	0.142	1	0.706
	M_state	0.604	1	0.437
	Fem_x_M_state	1.102	1	0.294

The GEEs (Table 7) revealed a significant effect of maternal treatment on aggressiveness in only attacking individuals and a significant effect of the interaction of maternal and paternal treatment on aggressiveness in all and only attacking individuals. Offspring of parents that had both been socially isolated in early life were the least aggressive across treatments (Figure 5). Paternal treatment had a significant effect on the mean number of eggs oviposited, with grouped fathers as mates allowing females to produce more eggs (Figure 6). No significant effect of parental treatment on activity was found.

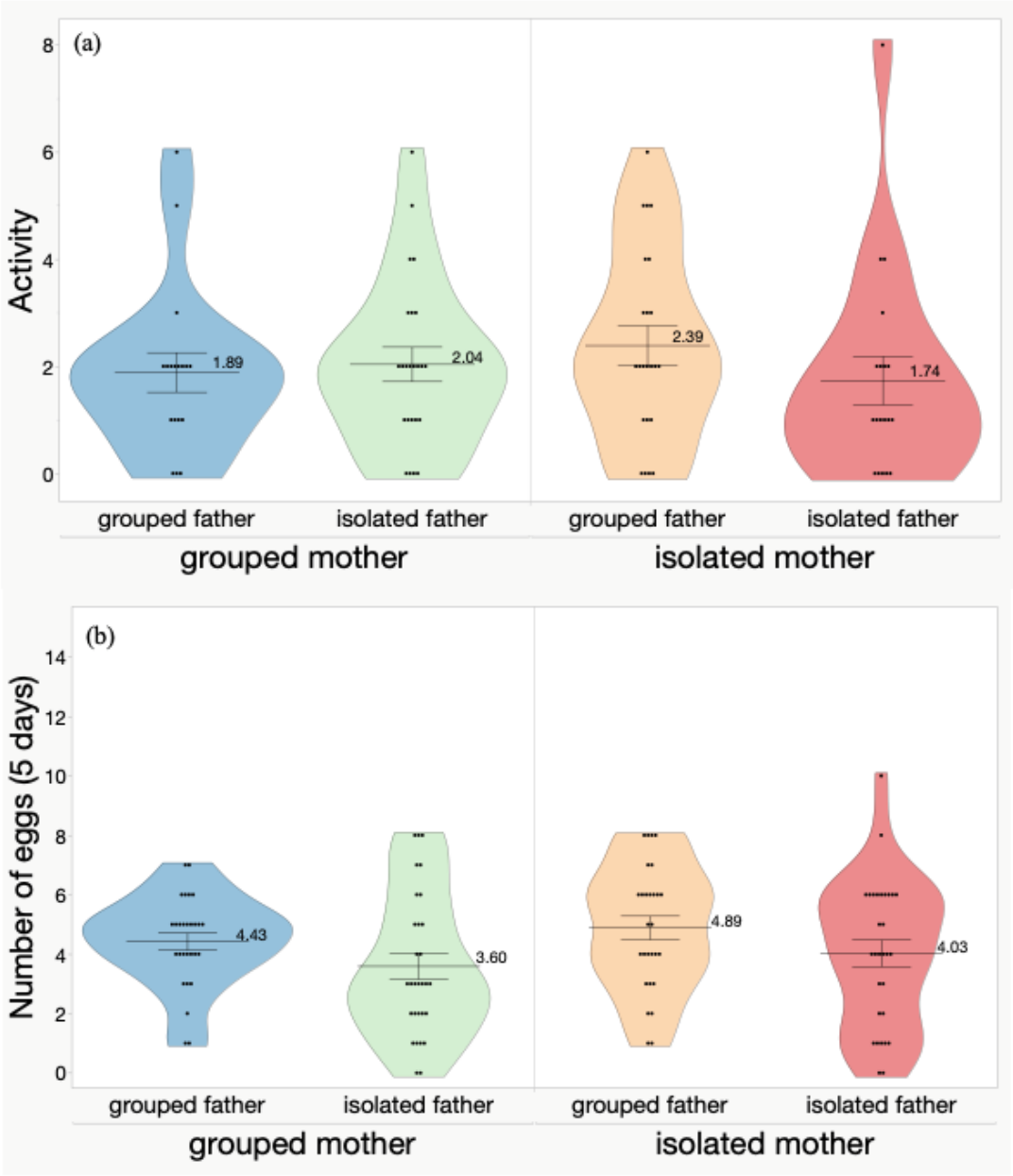

Figure 6. Mean (± SE) activity (a) and oviposition (b) across treatments during the aggressiveness experiment. Dots are the individual data.

3.1.2. ICC aggressiveness and activity

All ICC scores for aggressiveness were non-significant, with p-values well above 0.05 (Figure 7a), suggesting no consistency in aggressiveness. In contrast, activity was repeatable when all treatments were combined (p=0.042), and in treatments that included isolated parents such as FiMi (p=0.019), Fi (p=0.017), and Mi (p=0.031). Socially isolated parents produced daughters that were repeatable in activity during the aggressiveness tests (Figure 7b).

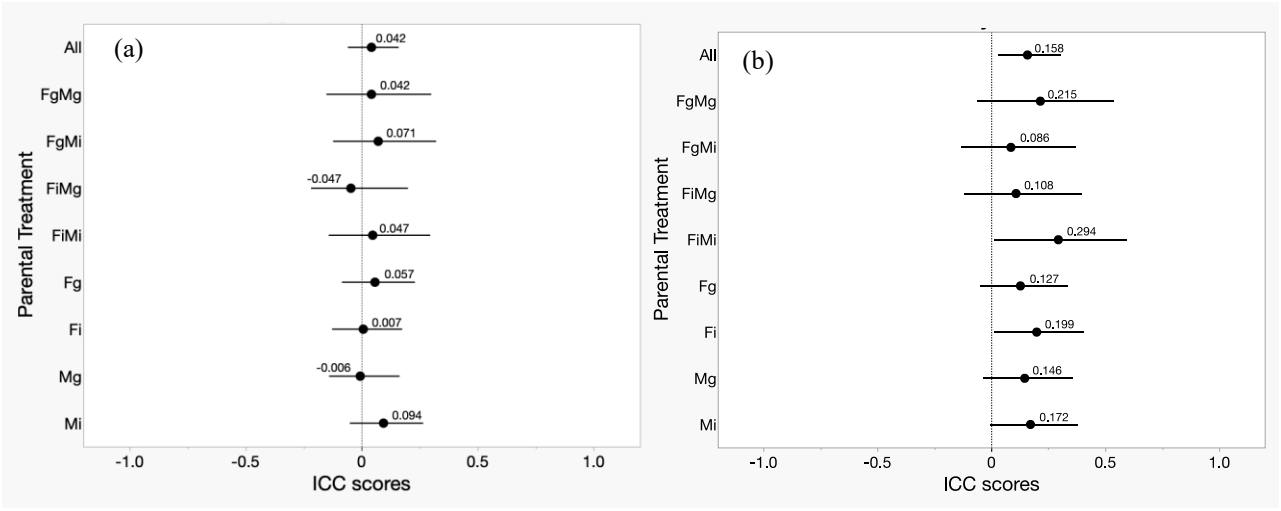

Figure 7. ICC scores (± 95% CI) for aggressiveness (a) and activity (b) across parental treatments. Parental treatments: female grouped (Fg), female isolated (Fi), male grouped (Mg), male isolated (Mi).

3.1.3. Aggressiveness and activity types

Figure 8 shows the distribution of the personality types in aggressiveness and activity within treatments. For aggressiveness, most types fall on the less aggressive side of the scale, the least aggressive type 0 being the most frequent, with 53 out of 116 individuals (61%). This type is also the most frequent among almost all treatment groups, making up around half of all types (FgMg=50%, FgMi= 40%, FiMi= 60%). Only in FiMg, type 0 is the second-most frequent, surpassed by type 2 as the most frequent, with more than a third (36%). Combined, the little aggressive types 0 and 1 account for the majority of types, except for FiMg, in which the combined medium aggressive types 2 and 3 are as frequent (46%). The two highly aggressive types 4 and 5 are the least frequent, making up only around 3% each. Regarding activity, types are more evenly distributed among the group. The most frequent type is type 1, with 31 out of 84 cases, more than a third (37%). This holds true for all treatments, except for FgMi, which has an equal amount of type 2 and type 3 (33%). Highly active types 3 and 4 are overall the least frequent, at only a tenth each. In group FiMg, however, type 3 (13%) and type 4 (17%) make up roughly as much as the less active types, except for type 1. To sum up, aggressiveness and activity types are skewed towards little aggressive and little active types overall, although distribution varies among treatments. Multinomial GLM results of parental treatment on within-group aggressiveness type composition show no significance of maternal (p= 0.814), paternal (p=0.158) treatment, nor their interaction (p=0.098). Similarly, none of the GLM results were significant for the activity type composition in the aggressiveness assay.

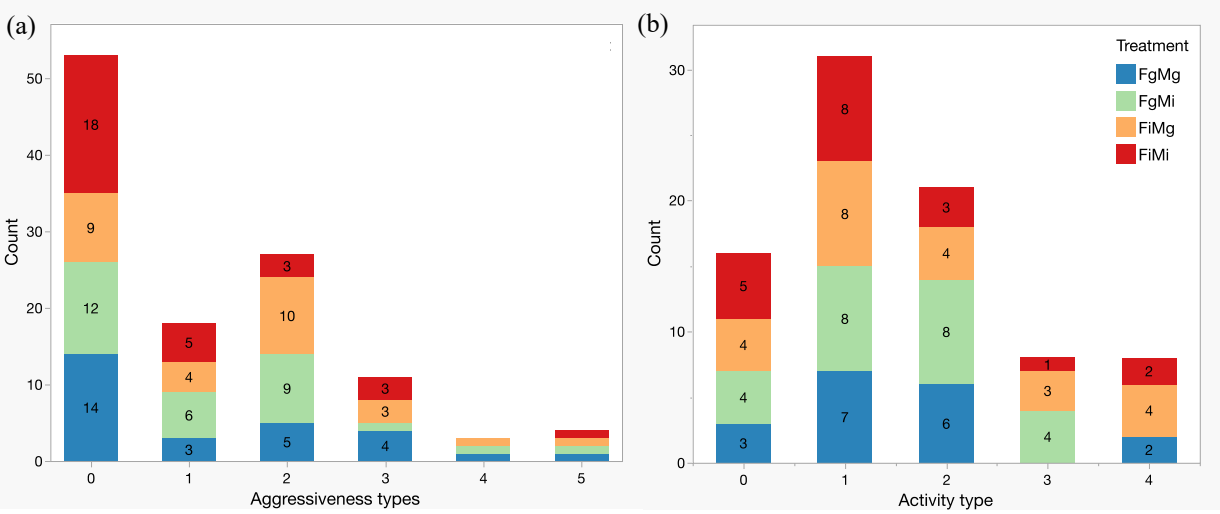

Figure 8. Within-group personality composition of (a) aggressiveness and (b) activity types across treatment groups. Aggressiveness types from 0 (not aggressive) to 5 (extremely aggressive), activity types from inactive (0) to highly active (4).

3.1.4. Correlations

No statistically significant correlations were found between aggressiveness types and activity types, nor between aggressiveness types and mean oviposition. A marginally significant negative correlation was found between activity types and mean oviposition in offspring of isolated females mated to isolated males (r_s=-0.724; p=0.066). A significant negative correlation was found between activity type and oviposition in offspring of isolated females (r_s=-0.563; p=0.019).

3.2. Exploration

3.2.1. Population means

A total of 87 predatory mite females were tested across the three assays on exploration, activity and oviposition. The sample sizes of the four treatments were distributed relatively evenly among treatments (FgMg 24, FgMi 18, FiMg 24, FiMi 21). The distribution of mean latency to leave and to arrive across the four treatments and three assays is presented in Figure 9. The minimum latency score for leaving was 0.02 min in the novel object tests and 0.001 min in the open-field test, which represents experimental mites that began immediately to explore the surroundings after release. In contrast, in each of the three assays there were some individuals that did not move out of the shelter or leave the release site during the experiment.

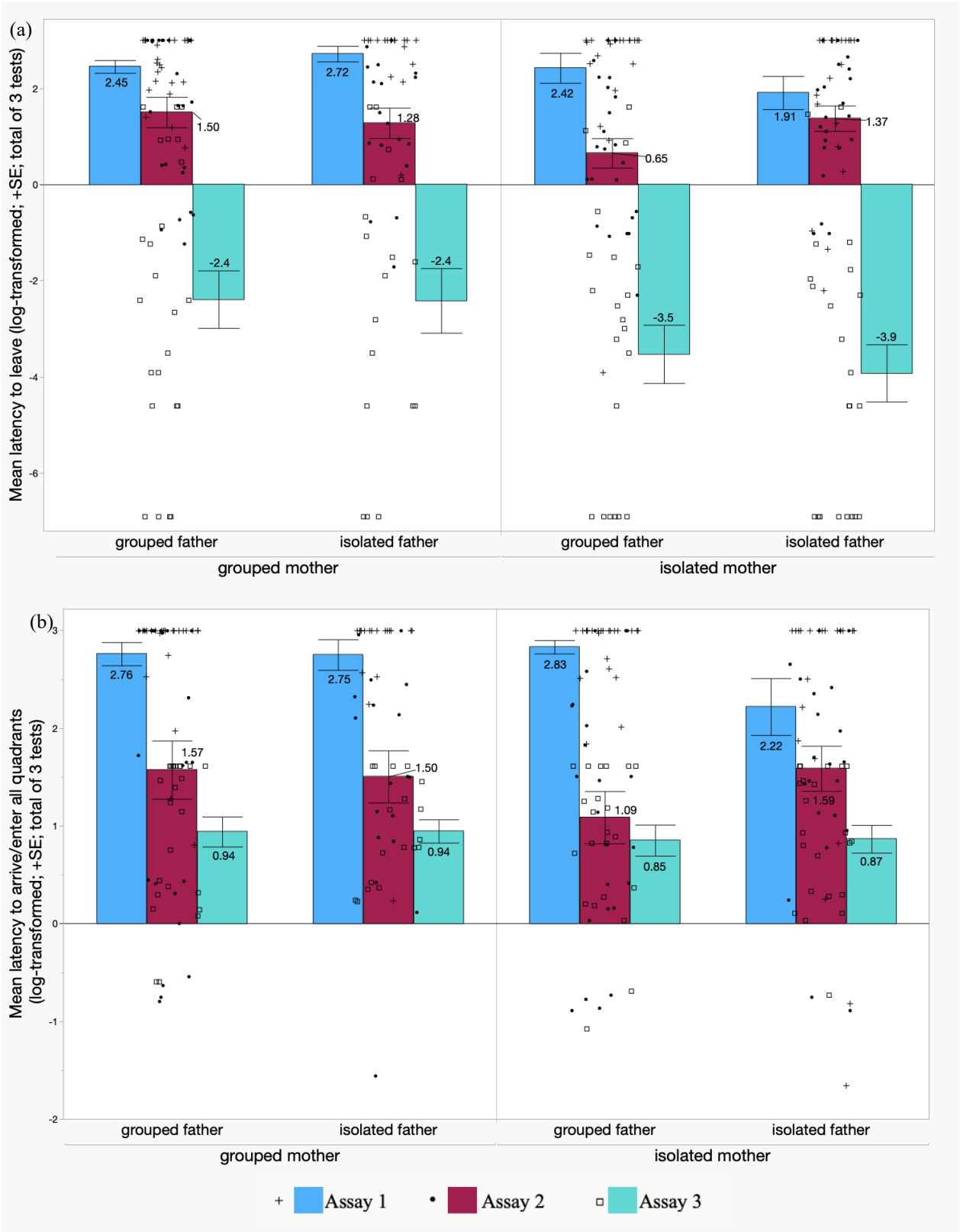

Figure 9. Log-transformed mean latency (±SE) to leave (a) and arrive (b) according to treatment and exploration assay. Dots are the individual data points. Contexts: 1) novel-object: cotton wool, arena: leaf discs with wax bridge 2) novel-object: unfamiliar leaf fragment, arena: acrylic cage with connecting corridor 3) open-field test. Observation period: 30min in the first two trials, and 5min in the third trial. If the mite did not leave/arrive within the observation period, the respective maximum score of 30min/5min was recorded.

Looking at the average of the log-transformed mean latency scores across all three assays, FiMi were the fastest in leaving ($\bar{x}$ = 0.56) and in arriving ($\bar{x}$ = 1.77), followed by FiMg and then by FgMi and FgMg coming last (Figure 9). Moreover, this pattern was also true for each parameter (Figure 9). When dividing the parental treatments into maternal (Fg, Fi) and paternal (Mg, Mi) treatments, the mean exploration scores suggest that in latency to leave, the offspring of females mated to grouped males were faster than offspring of isolated males. However, in latency to arrive, offspring of isolated males were on average faster than those of grouped males. Offspring of isolated females were on average faster in leaving and in arriving than grouped females (Figure 9).

Maternal treatment had a highly significant effect on latency to leave, but not on latency to arrive (Figure 9; Table 8). Daughters from isolated mothers were the fastest explorers (Figure 9). There was no influence of paternal treatment on exploration.

Table 8. Results of GEEs and GLMs for the effects of maternal and paternal state (isolated or grouped) on the mean number of eggs, activity and the exploration parameters, latency to leave and to arrive.

Dependent variable	Independent variables	Wald Chi-Square	df	Sig.
Exploration latency to leave	**Fem_state**	9.017	1	0.003
	M_state	0.089	1	0.766
	Fem_x_M_state	0.101	1	0.751
Exploration latency to arrive	**Fem_state**	2.133	1	0.144
	M_state	<0.001	1	0.988
	Fem_x_M_state	0.036	1	0.849
Eggs	**Fem_state**	0.252	1	0.615
	M_state	0.067	1	0.795
	Fem_x_M_state	0.024	1	0.878
Activity	**Fem_state**	0.875	1	0.35
	M_state	3.587	1	0.058
	Fem_x_M_state	0.39	1	0.532

Paternal treatment influenced daughter activity marginally significantly, with daughters from isolated fathers being more active (Figure 10; Table 8). Egg production did not differ among treatments (Figure 11; Table 8).

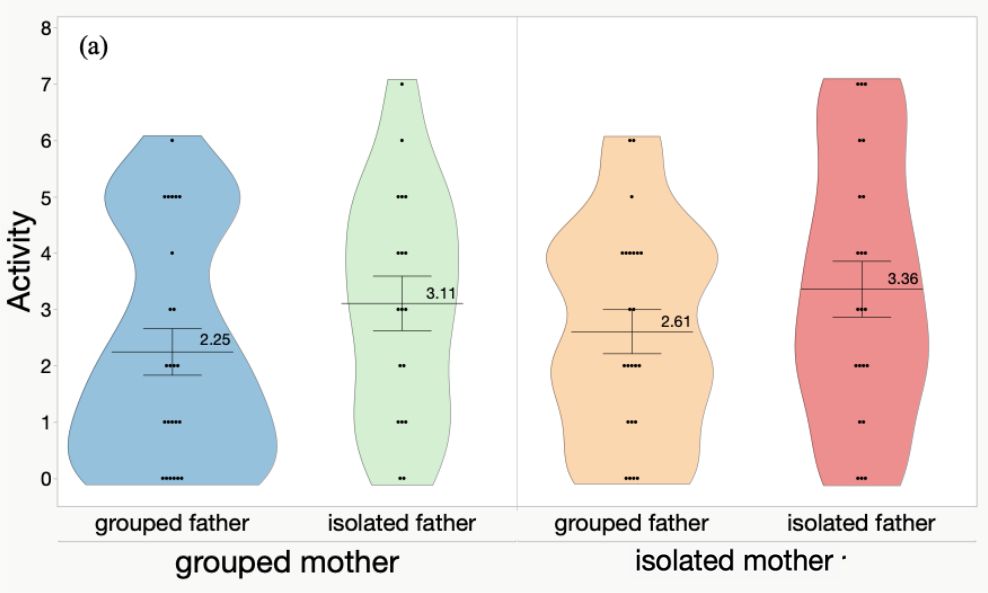

Figure 10. Mean (±SE) activity across treatments during the exploration experiment.

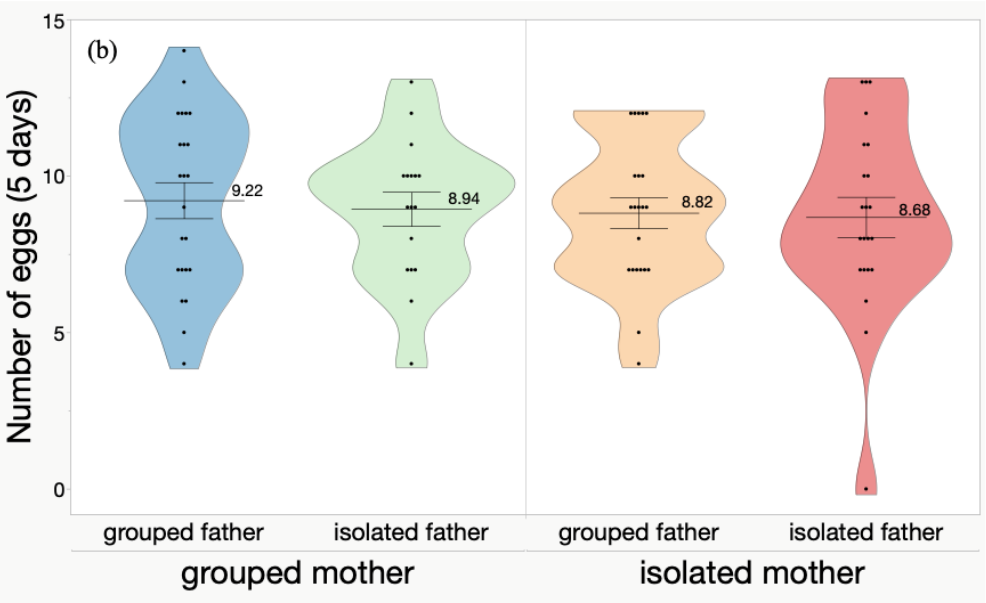

Figure 11. Mean (± SE) oviposition across treatments during the exploration experiment. Dots represent individual data.

3.2.2. ICC exploration and activity

None of the ICC scores for exploration and for activity during the exploration experiment were significant (Figures 12, 13).

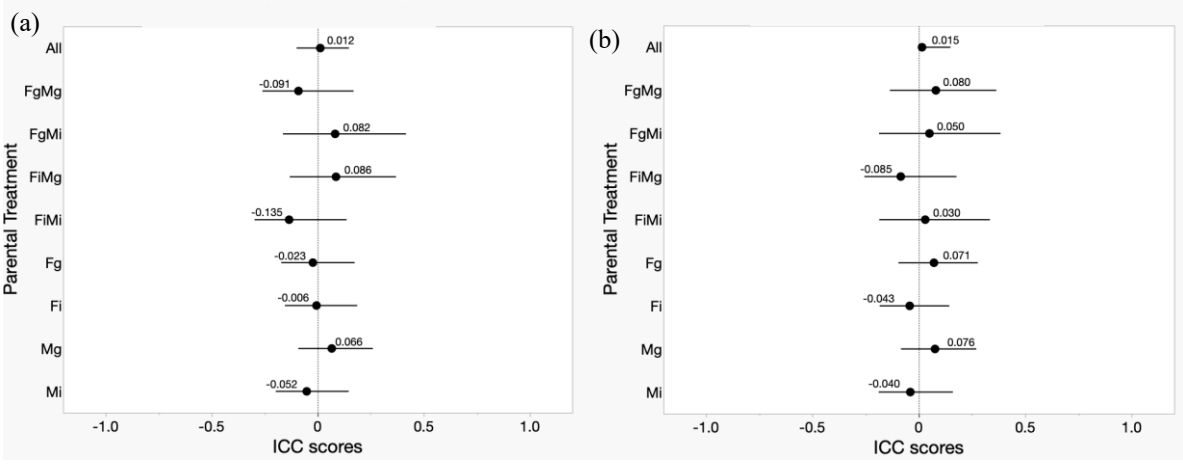

Figure 12. ICC scores (±95 % CI) in exploration (a) latency to leave, (b) latency to arrive according to parental treatment (F and M for females and males; i and g for isolated and grouped).

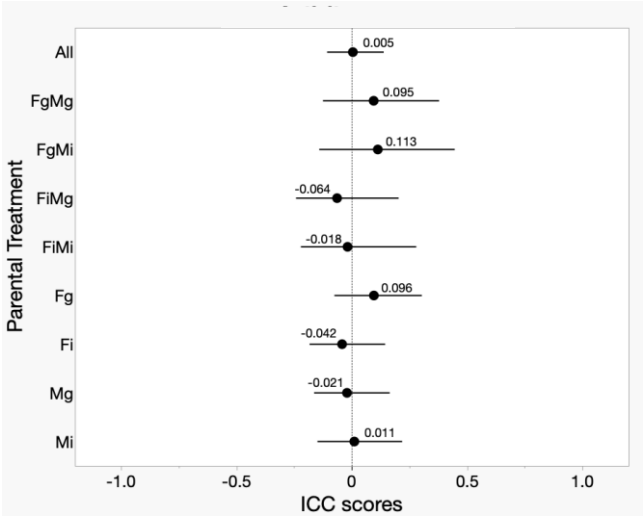

Figure 13. ICC scores (± 95% CI) for activity during the exploration assays according to parental treatments (F and M for females and males; i and g for isolated and grouped).

3.2.3. Exploration and activity types

The distribution of exploration types within treatments in latency to leave (Figure 14a) and latency to arrive (Figure 14b) differed between the two exploration parameters. While in latency to arrive, the most frequent type was type 0, with 29 cases out of 87 (33%); it was type 3 with 24 cases in latency to leave (28%). Moreover, the least frequent type in latency to leave was type 2 with 8 cases (9%) and type 1 in latency to arrive with 4 cases (5%), followed closely by type 4 with 5 cases (6%). Overall, the distribution of personality types in latency to leave seems to be more equal than that in latency to arrive (Figure 14a,b). Multinomial GLM results of parental treatment on within-group exploration type A composition show that only the

maternal treatment had a marginally significant effect (p=0.065), while paternal treatment (p=0.493) and their interaction (p= 0.876) were not significant. For exploration type B, paternal treatment (p=0.063) was marginally significant, while maternal treatment (p=0.383) and the interaction of maternal and paternal treatment (p= 0.382) were not significant.

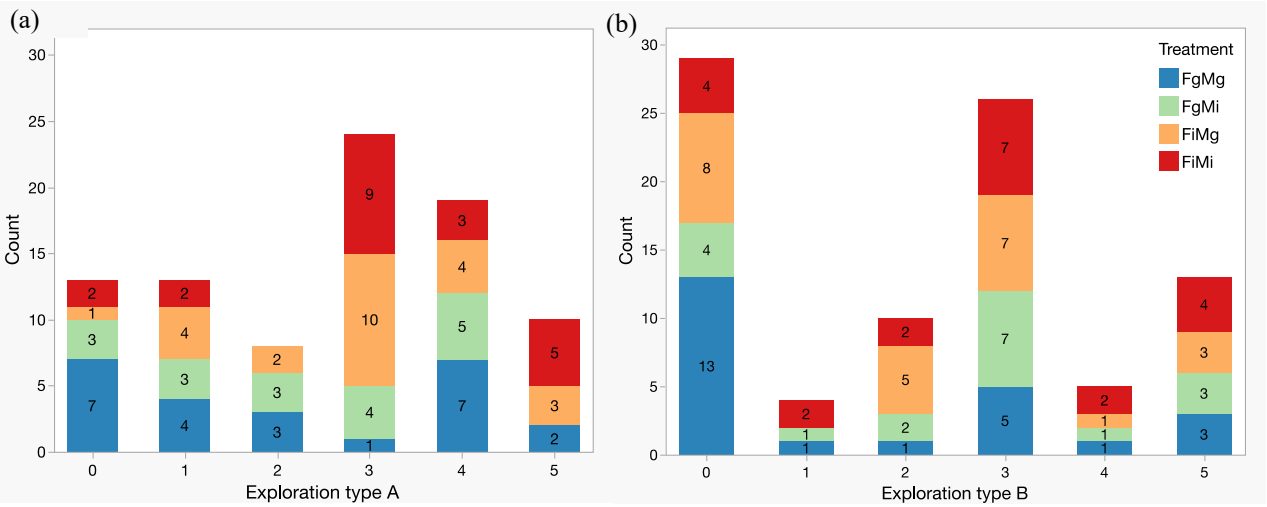

Figure 14. Within-treatment composition of personality types in exploration, (latency to leave (a) and arrive (b).

The distribution of activity types during the exploration assays shows a clear dominance of type 1 with 32 out of 87 cases (37%, Figure 15). However, this was not the case in all treatments. Whereas FgMg and FiMg had the highest frequency of type 1(FgMg=42%; FiMg=46%), the other two treatments had more homogeneous distributions of personality types (Figure 15). Multinomial GLM results show that paternal treatment had a marginally significant effect (p=0.070 on activity type composition, while maternal (p=0.565) and the interaction of maternal and paternal treatment (p=0.116) were not significant.

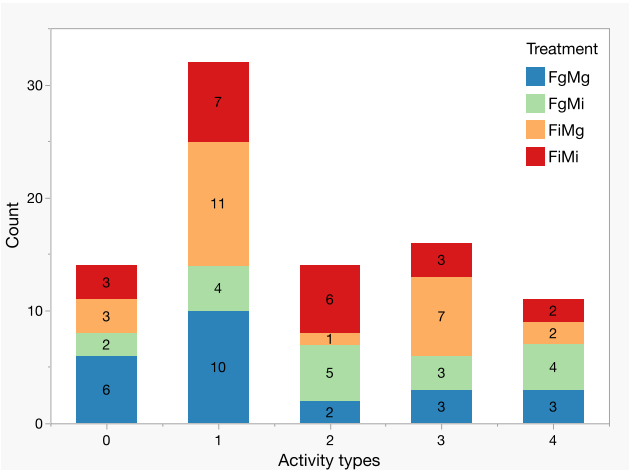

Figure 15. Within-treatment composition of personality types in activity during the exploration assays.

3.2.4. Correlations

No statistically significant correlations were found between exploration and activity types and between exploration types and mean oviposition. A significant negative correlation was found between activity types and oviposition in offspring of grouped mothers and isolated fathers (r_s=-0.491; p=0.045) as well as grouped mothers (r_s= -0.321; p=0.044).

3.3. Sociability

3.3.1. Population means

A total of 79 experimental mite females were tested in three assays for sociability and 78 for activity and oviposition. The sample sizes were similar across the four treatments (FgMg 17, FgMi 21, FiMg 18, FiMi 23). In the sociability experiment, the 79 mites were tested over three assays, totalling 237 observations on latency to re-join the group, out of which only 6 experimental mites did not re-join the group within the observation period. Among the mites that did re-join the group, the fastest re-joined the group immediately after release (Figure 16).

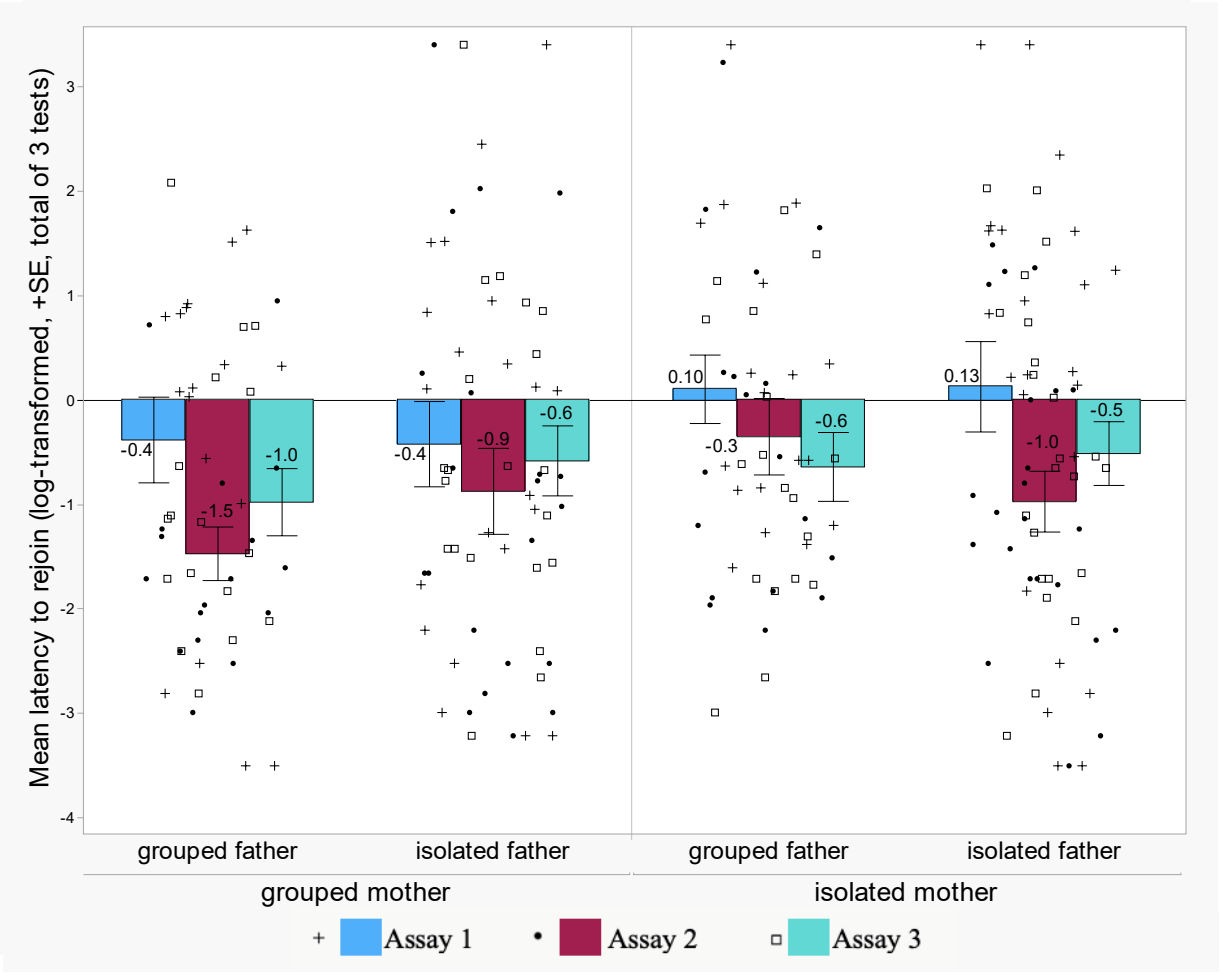

Figure 16. Log-transformed mean (± SE) latency to re-join the group according to treatment in the sociability experiment.

Looking at the average of the log-transformed mean scores across all three assays, offspring of treatment FgMg ($\bar{x}$ =-0.68) were the fastest, followed by FgMi, then by FiMi and lastly FiMg (Figure 16). When dividing the parental treatments into maternal (Fg, Fi) and paternal (Mg, Mi) treatments, the mean sociability scores suggest that offspring of grouped mothers were faster re-joiners than those of isolated mothers. In contrast, offspring of isolated fathers were on average faster re-joiners than those of grouped fathers.

GEEs and GLMs revealed that maternal treatment had a significant effect on sociability. Daughters from grouped mothers were more sociable than those from isolated mothers; daughters in the FgMg treatment were the most sociable (Table 9;Figure 16). Parental treatment did not affect activity and oviposition in the sociability experiment (Table 9; Figure 17).

Table 9. Results of GEEs and GLMs for the effects of maternal and paternal state (isolated or grouped) on the mean number of eggs, activity and sociability.

Dependent variable	Independent variables	Wald Chi-Square	df	Sig.
Sociability	**Fem_state**	3.806	1	0.050
	M_state	0.147	1	0.702
	Fem_x_M_state	1.269	1	0.260
Eggs	**Fem_state**	1.639	1	0.201
	M_state	0.474	1	0.491
	Fem_x_M_state	0.817	1	0.366
Activity	**Fem_state**	2.051	1	0.152
	M_state	0.562	1	0.453
	Fem_x_M_state	2.143	1	0.143

Parental treatment did not have any effect on activity and oviposition during the sociability experiment. The experimental mites were relatively inactive, with no mite moving more than 5 times out of 15 observations, and many being consistently inactive. Regarding oviposition, the highest score was 15 eggs in total over 5 days, while the lowest was 3.

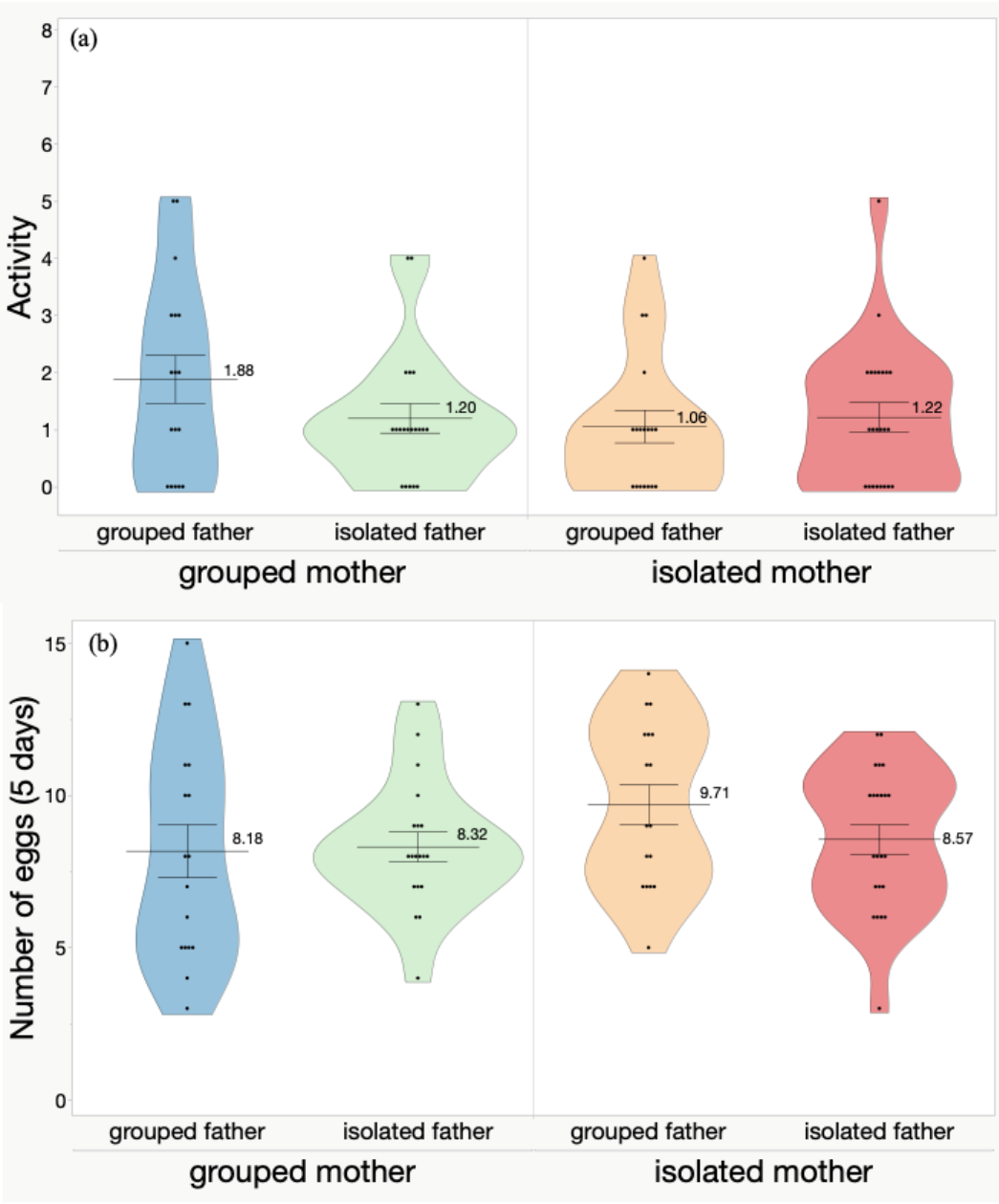

Figure 17. Mean (±SE) activity and oviposition across treatments during the sociability experiment. Dots are the individual data.

3.3.2. ICC sociability and activity

All ICC scores for sociability were clearly significant ($p<0.05$), except for the treatment FiMi, which was only marginally significant ($p=0.063$) (Figure 18a). In contrast, activity during the sociability experiment was not repeatable, as indicated by $p>0.05$ of all ICC scores (Figure 18b). The sociability ICC scores ranged from 0.193 to 0.578, indicating moderate to high repeatability in sociability (Figure 18a). Daughters from grouped mothers mated to isolated fathers were the most repeatable (ICC=0.578), whereas daughters from both isolated parents were the least repeatable (ICC=0.198) (Figure 18a).

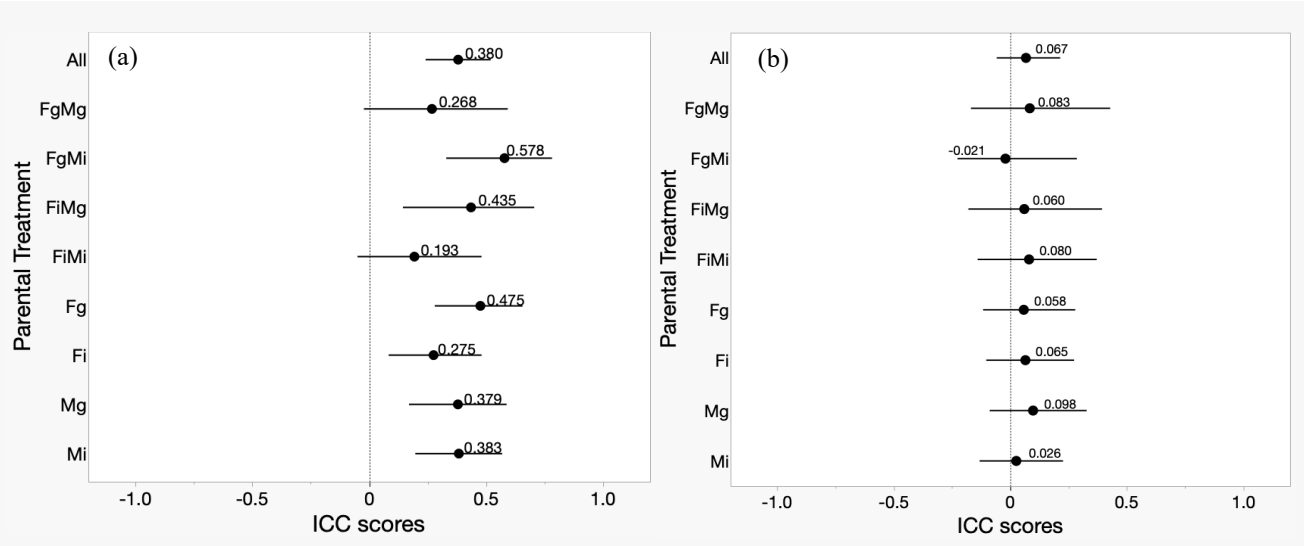

Figure 18. ICC scores (± 95% CI) for sociability (a) and activity (b) across parental treatments (F and M for female and male parents; i and g for isolated and grouped)

3.3.3. Sociability and activity types

Scrutiny of the distribution of sociability types shows that type 3 was the most frequent, with 27 cases out of 79 (34%), and type 2 was the least frequent, with 9 cases (11%). As such, the distribution was skewed towards more sociable types. The distribution of activity types during the sociability experiment was biased towards consistently little active types, with almost three-quarters of all cases being type 0 or 1 (58 out of 78 cases; 74%; Figure 19).

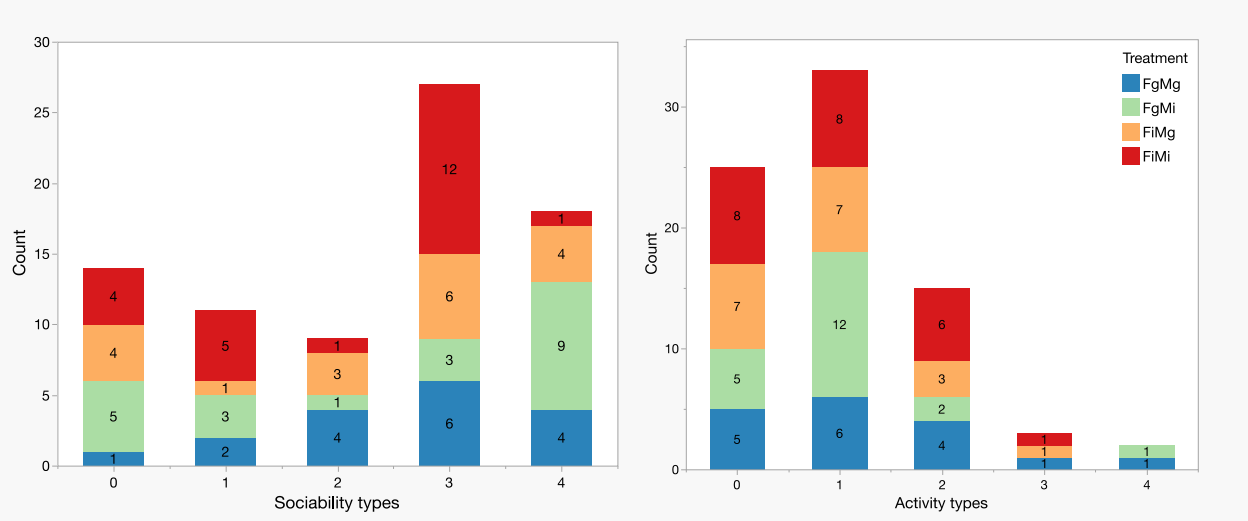

Figure 19. Within-treatment composition of personality types in sociability (a) and activity in the sociability experiment (b).

The results of multinomial GLM of parental treatment on sociability type composition and activity type composition show no significant effects ($p>0.05$).

3.3.4. Correlations

A statistically significant and strong positive correlation was found between the sociability types and mean oviposition in the FgMg treatment ($r_s= 0.809$; $p=0.009$; Figure 20). A significant moderate negative correlation was found between sociability types and oviposition in mites with isolated fathers ($r_s= -0.341$; $p= 0.027$; Figure 20).

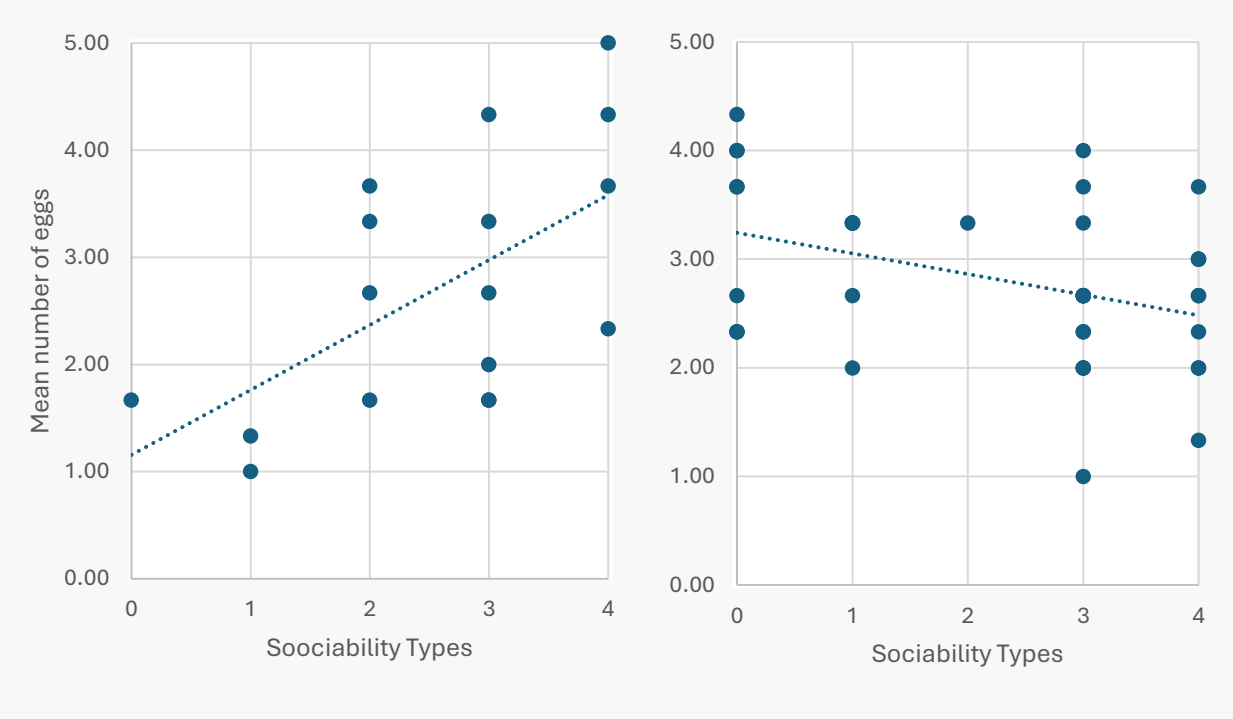

Figure 20. Relationship (linear regression) between mean number of eggs and sociability types in mites of (a) grouped females and grouped males (b) isolated males. Sociability types from least (0) to most (4) sociable.

No statistically significant correlations were found between sociability and activity types. Activity types and oviposition were not correlated overall nor across treatment groups except for a moderate negative correlation in offspring of isolated females mated to isolated males ($r_s= -0.501$; $p= 0.013$).

4. Discussion

My experiments revealed that parental social experience has pronounced effects on mean aggressiveness, exploration and sociability of offspring. Across behavioural traits and analyses, offspring sociability was the strongest affected by parental social experience. Regarding personality expression, sociability and activity, but not aggressiveness and exploration, were repeatable, depending on parental social experience. Both mean trait expressions and personalities varied with the mother's and father's social experience and the combination thereof. Daughters from grouped females and isolated males were the most repeatable in sociability. Oviposition by daughters from grouped parents correlated positively with the personality types in sociability.

4.1. Parental effects on mean behavioural trait expression

On average, daughters of isolated females mated to isolated males behaved the least aggressively, the most exploratory and second to last sociable compared to the other treatments. In comparison, a study on within-generational social isolation observed that isolated *P. persimilis* were, on average, less active and less sociable than grouped mites during the protonymphal stage (Schausberger et al., 2017). Offspring of grouped females mated to grouped males were, on average, the least exploratory, the most sociable and the second most aggressive. Daughters of one isolated and one grouped parent ranked between the offspring of parents with the same social experience in aggressiveness and exploration, but not in sociability, where offspring of isolated females mated to grouped males behaved the least sociable on average. Comparing the mean behaviour between offspring of isolated females with grouped females, offspring of isolated females behaved, on average, less aggressively, more exploratory and less sociable than offspring of grouped mothers. Offspring of isolated males behaved on average less aggressively, less exploratory in leaving, more exploratory in arriving and more sociable than offspring of grouped males.

Significant parental effects of social experience on the offspring' behavioural traits were only found in some groups and for some traits, as shown in Table 10. In aggressiveness, the interaction of paternal and maternal social experience had an effect overall. Maternal experience also had an effect when exclusively considering attacking individuals. Thus,

paternal effects did not account for the difference in mean aggressiveness between offspring of isolated and grouped males.

Table 10. Comparison of parental effects of social experience on offspring' aggressiveness, exploration and sociability. Offspring behaviour of isolated females was compared to that of grouped females. Offspring behaviour of isolated males was compared to that of grouped males. Arrows indicate whether offspring behaviour was more (↑) or less (↓) aggressive, exploratory or sociable. The significance of parental effects on offspring' behavioural traits are given (see Table 7, Table 8 and 11).

Offspring mean behaviour	**Offspring of isolated parents compared to those of grouped parents.**		**Ranking of treatment groups from most (1) to least (4)**
	♀ isolated	♂ isolated	
Aggressiveness	↓ sig. (only attacking)	↓ not sig.	1. FiMg 2. FgMg 3. FgMi 4. FiMi (sig.)
Exploration (latency to leave)	↑ sig.	↓ not sig.	1. FiMi 2. FiMg 3. FgMi 4. FgMg (not sig.)
(latency to arrive)	↑ not sig.	↑ not sig.	
Sociability	↓ sig.	↑ not sig.	1. FgMg 2. FgMi 3. FiMi 4. FiMg (not sig.)

The exploratory behaviour, measured in latency to leave, was only affected by maternal social experience, while no parental effect on exploration was found, when measured as latency to arrive. Maternal social experience of conspecifics also enhanced daughters' sociability. However, neither paternal nor the interaction of maternal and paternal social experience affected daughters' sociability and exploration. To sum up, these findings indicate that the interaction of maternal and paternal effects modulates aggressiveness, but not exploration or sociability. Maternal social experience affected aggressiveness (only in attacking individuals), exploration (latency to leave) and sociability, while paternal social experience did not have a main effect on these traits. However, main paternal influences were detected in the number of eggs produced by daughters during the aggressiveness assays and in activity during the exploration assays.

Only few studies examined the effects of parental social conditions, though not social isolation, on similar behavioural traits as in my study. For example, the paternal effect of social isolation has been shown to affect offspring' anxiety-like behaviour in sticklebacks, in that predator-exposed fathers produced less anxious offspring (Hellmann & Rogers, 2024). He et al. (2016) have shown that prolonged stress by restraining mice for 60 days reduced anxiety-like behaviour in offspring. Effects of other forms of social stress in the parental generation have been observed, such as the paternal effect of unpredictable maternal separation on offspring in mice (Gapp, 2014) and the effect of paternal social status on offspring activity in zebrafish (Zajitschek et al., 2017). Social instability affected offspring behaviour in mice (Kong et al., 2021; Saavedra-Rodríguez & Feig, 2013). A significant effect of maternal stress on aggressiveness has been observed in guppies, where mild stress from husbandry procedures for pet fish tanks affected offspring, by increasing aggressiveness towards their mirror image (Eaton et al., 2015). In comparison, in mites, offspring of socially isolated mothers behaved on average less aggressively than those of mothers that had not been isolated (Figure 5). Overall, these studies clearly demonstrate that social conditions can have important transgenerational effects on offspring mean behaviour. However, to the best of my knowledge, information on the maternal and paternal contribution of parental social isolation effects on offspring' aggressiveness, exploration and sociability was not available before my thesis. Other contexts of parental effects, such as diet experience, largely did not affect mean activity and exploration in offspring of *P. persimilis* and *P. macropilis*, while it influenced offspring' repeatability in activity and exploration (Nguyen & Schausberger, 2025a).

The more pronounced effects of mothers on mean aggressiveness, sociability and exploration could be explained in various ways. Nonetheless, the extent of offspring provisioning is the most notable. In many animals, mothers invest more resources by producing and nourishing the growing eggs inside their body while fathers only contribute the tiny sperm, though these may contribute important non-genetic information. Generally, Bell & Hellmann (2019) summarised that, in some instances, maternal effects may be stronger than paternal effects as observed in paternal post-traumatic stress disorder (PTSD) in humans (Yehuda et al., 2008). In other cases, paternal effects may be stronger than maternal ones. This has been found in trans-generational immune priming in pipefish (Beemelmanns & Roth, 2016) and in paternal prenatal alcohol exposure on head circumference in humans (Zuccolo et al., 2016). It is, thus, possible that maternal effects of social isolation are generally stronger than paternal effects. Alternatively, parental effects can have sex-based differences in which trait they affect, as well

as what effect they have (Crean & Bonduriansky, 2014). In my study, fathers but not mothers had an effect on other offspring traits such as egg production during the aggressiveness assays and activity during the exploration assays. It is also important to note that only daughters were tested. This is relevant because parental effects can have different impacts on sons and daughters (Bell & Hellmann, 2019). Since there are no data on sons in this thesis, potential paternal effects on sons can neither be confirmed nor disproved. All in all, the results of the experiments demonstrate that social conditions can impact offspring' mean behavioural trait expression and thus should be considered in future research.

Activity was also observed between the repeated assays on aggressiveness, exploration and sociability. The levels of mean activity varied among experiments, which was likely due to using different setups in the assays between the activity measures. Overall, the highest activity was observed in the exploration experiment and the lowest in the sociability experiment. While daughters of isolated females mated to isolated males were the least active in the aggressiveness assay, compared to the other treatment groups, they were the most active in the exploration assay. Daughters of grouped females mated to grouped males were the most active in the sociability experiment, but the least active in the exploration experiment. In contrast to inter-experimental differences in activity levels, within experiments, activity varied little with parental experiences. Nonetheless, paternal social experience had a significant effect on activity in the exploration experiment. Daughters of females mated to isolated males were more active than those of females mated to grouped males. No such paternal effects on activity were observed in the aggressiveness and sociability experiments. While no study has yet inspected the effect of paternal social isolation on offspring' activity, other social conditions, such as paternal social status, have been shown to affect offspring activity in zebrafish (*Danio rerio*) (Zajitschek et al., 2017).

4.2. Personality expression

My experiments demonstrate that female predatory mites *P. macropilis* are repeatable, i.e. have personality, in sociability and partly in activity. Aggressiveness and exploration were not repeatable. In the predatory mites *P. persimilis* and *A. swirskii*, personality has been reported for aggressiveness, boldness (Schausberger et al., 2024), activity, exploration (Nguyen & Schausberger, 2025b) and sociability (Schausberger & Nguyen, 2025). In crickets, within-generational social experiences have been shown to modulate the repeatability of

aggressiveness (Jäger, 2019). No study has yet examined the effect of parental social isolation on offspring personality expression and changes in within-offspring personality composition. My thesis provides evidence for repeatability in sociability and partly in activity across treatment groups. Within-group personality composition was analysed via categorisation and count of personality types. Statistical analyses of parental treatment on within-group personality type composition revealed only marginally significant effects in some traits.

Sociability was repeatable across treatments as well as within treatments, except for daughters of isolated females mated to isolated males, which was only marginally significantly repeatable. Scrutiny of within-treatment personality composition for sociability revealed a skew towards highly sociable types across and within treatments (Figure 19). Daughters of grouped females mated to isolated males were the most repeatable, followed by daughters from isolated females mated to grouped males. Thus, daughters from parents with different social experiences were more repeatable than daughters from parents with the same social experience. Moreover, isolated females produced less repeatable offspring than grouped females, whereas grouped and isolated males produced offspring that were similarly repeatable. Personality in sociability has been shown to be modulated by within-generational social isolation in predatory mites; isolated gravid female *P. persimilis* were only repeatable in the number of immediate neighbours compared to grouped mites, which were highly repeatable in several sociability measures (Schausberger & Nguyen, 2025). Regarding parental effects, information is scarce. Mild maternal stress increased inter-individual variation in the behaviour of guppies (Eaton et al., 2015). There is no information available on the transgenerational effects of social isolation on offspring' repeatability in sociability for any animal.

Activity was only repeatable in the aggressiveness assays in daughters of one or both parents that had experienced isolation (FiMg, FgMi, FiMi), but not in offspring of grouped females mated to grouped males. During the other behavioural assays, activity was not repeatable. Within-group personality composition revealed that during the aggressiveness assays, most individuals belonged to consistently little active personality type, and only some ranked as consistently highly active types. There was a slight variation in within-group personality composition among treatments. On the inactive to highly active scale, however, most treatments were similarly composed except for offspring of isolated females mated to grouped males, which had a disproportionate number of highly active types. Since activity was only consistent in one of the three behavioural assays, these results deserve further research.

Whether social isolation could specifically increase or decrease offspring consistency in activity has not been tested before this thesis. Schausberger & Nguyen (2025) found that activity in the presence of conspecifics was not repeatable in predatory mites reared in isolation compared to grouped mites. However, when no conspecifics were present, isolated mites remained consistent in activity while grouped mites did not. Thus, within-generational social isolation has been shown to influence repeatability in activity. Whether parental social isolation has a similar effect on activity, as observed in the aggressiveness assay, will need to be examined further.

4.3. Behavioural Syndromes

There were no significant correlations between activity and the other personality traits aggressiveness, exploration and sociability. Lacking correlation between activity and exploration indicates that the associated experimental procedures tapped into separate behavioural dimensions (Reale et al, 2007). Assaying different individuals for aggressiveness, exploration and sociability did not allow to check for behavioural syndromes among these traits.

4.4. Egg production

Biparental and maternal social experience did not affect oviposition in any of the behavioural assays. However, paternal social experience modulated the number of eggs produced by the daughters in the aggressiveness experiment. Considering that parental effects can be context-specific and passive, occurring only under stressful conditions (Badyaev & Uller, 2009), the more stressful conditions during the aggressiveness experiment, compared to the exploration and sociability experiments, might explain the evidence of significant paternal effects. Parental effects on offspring' fecundity have been observed in zebra finches, where maternal perception of mate attractiveness influenced the offspring' number of eggs via maternal investment (Gilbert et al., 2012); and maternal nutritional state prior to laying influenced the offspring's fecundity measured by clutch size and survival over two years in zebra finches (*Taeniopygia guttata)* (Gorman & Nager, 2004).

Regarding the relationship between personality types and oviposition, personality types were not correlated with egg production pooled across treatments, but within some treatments in sociability and activity; in previous experiments with the predatory mite *P. persimilis*, egg production was correlated with personality scores in both boldness and aggressiveness (Schausberger et al., 2024). In male red flour beetles, their personality traits in activity and boldness affected mating behaviour and the number of eggs produced by their female mates, yet body size had the strongest effect (Li et al., 2025). According to Biro and Stamps (2008), the correlation of personality traits such as activity, aggressiveness and boldness with fecundity as life-history trait has been documented across various animal taxa.

In my experiment, the personality types in sociability were strongly correlated with oviposition in daughters of grouped females mated to grouped males and in daughters of isolated males. Interestingly, in the former treatment more sociable daughters produced more eggs, whereas in the latter treatment, more sociable daughters produced fewer eggs. These results indicate that parental social experience may modulate the occurrence and direction of the relationship between the personality types in sociability and egg production, thus indirectly affecting reproductive success.

Activity types were not correlated with oviposition across treatments, but were negatively correlated in some treatments and experiments. Daughters of isolated females mated to isolated males showed a marginally significant negative correlation in the aggressiveness experiment, and a significant negative correlation in the sociability experiment. In the exploration experiment, the activity types of daughters of grouped females mated to isolated males were negatively correlated with oviposition. Despite the differences in treatments and strength of correlation, the direction of the relationship, if present, was the same: consistently more active personality types produced fewer eggs.

Biro and Stamps (2008) proposed that consistent individual differences in life-history traits can explain behavioural consistency and personality expression, as long as there is a correlation between them. They further stressed that personality traits cannot only be positively, but also negatively correlated with reproduction, as it depends on the function of the personality trait in the respective species (Biro & Stamps, 2008). Another important aspect to consider is that parental effects may modulate offspring personality to improve offspring survival and reproduction (Reddon, 2012), possibly by affecting fitness costs or influencing the fitness of

social interactions (Kilner et al., 2015). Schausberger et al. (2024) observed that the positive correlation between aggressiveness and egg production was only present in individuals that had experienced stress through the presence of intraguild predators compared to individuals who had not, suggesting an adaptive benefit of modifying personality traits in response to early-life experiences. It might prove insightful to further explore the role of stress-inducing situations, such as social isolation in the parental generation on offspring personality and fecundity, as well as their relationship.

4.5. Limitations

Firstly, only four of the five canonical personality traits could be addressed due to the scale of my thesis. Secondly, only gravid females were tested. Due to the ratio of female to male eggs, the inclusion of male mites would have gone beyond the scope of this thesis to reach a large enough male sample size. Thirdly, *Phytoseiulus macropilis* revealed the ability to swim across the water surrounding the small leaf discs in the insect breeding dish. As a result, some mites were able to leave their leaf discs and reach the lids of their insect breeding dish. This meant that some eggs were deposited on the lids, which were then harder to find. Additionally, some mites escaped when opening the lid, reducing the number of mites that underwent all three trials. Luckily, their ability to swim did not affect the other arenas, as cross-contamination of the leaf arenas was successfully avoided by surrounding the plastic containers with soapy water.

5. Conclusion

The overarching aim of my thesis was to find out whether parental social experience modulates offspring personality in activity, aggressiveness, exploration and sociability of the plant-inhabiting, group-living predatory mite *Phytoseiulus macropilis*. My study addresses a notable gap in the behavioural ecology literature, considering that such effects have not yet been looked at before in any animal. By creating four parental treatments differing in social experience (isolated or grouped) during rearing and after mating, data on mean and repeatable behavioural trait expressions, as well as egg production, were collected using different behavioural assays modelled after five canonical personality traits (Réale et al., 2007) and previous behavioural research on predatory mites.

The most important finding of this thesis is that parental social experience modulates offspring personality in sociability, and to a lesser extent, in activity. Additionally, the detailed research questions reveal further insights. (1) Significant parental effects were found in some treatments on offspring' mean activity, aggressiveness, exploration and sociability. Offspring of isolated females behaved on average less aggressively, more exploratory and less sociable. Paternal social experience did not have an effect on these traits, revealing sex-specific differences in the parental generation. (2) Personality, defined as consistent inter-individual variation, was only observable in sociability and, within some treatments, in activity. Parents with the same social experience produced less repeatable offspring than parents with differing social experience in sociability, suggesting that shared parental social experiences may constrain, while mixed experiences may enhance repeatability of sociability. Activity was only repeatable in offspring when one or both parents had experienced isolation. Within-group personality composition revealed a tendency towards more sociable and less active types. (3) Personality types in activity were not correlated with the personality types in aggressiveness, exploration, and sociability. (4) Paternal social experience, but not maternal or biparental experience, affected the number of eggs produced by offspring. (5) Relationships between personality types and oviposition were found in sociability types and activity types in some parental treatments. The offspring in some treatments that were more active produced fewer eggs. While sociability was positively correlated in offspring of grouped females mated to grouped males, it was negatively correlated in offspring of isolated females mated to grouped males, suggesting that parental

social experience modulates not only the occurrence, but also the direction of the relationship between personality and egg production.

The findings of my thesis present unique first insights into the potential effects of social conditions on the next generation's personalities, particularly in sociability. They add to the existing knowledge on transgenerational behavioural plasticity, suggesting that the social environment of parents can serve as indicators for environmental conditions, which may optimise the behaviour of their offspring and subsequently increase offspring fitness. These insights widen the knowledge base for future studies on animal personality expression, and its potential link to reproductive success, highlighting the importance of considering the parental social conditions in studies on animal personality.

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