



The indirect influence of potential mates on survival and reproduction of *Tyrophagus curvipenis* (Acari: Acaridae)

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Research Paper

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Abstract

The social-sexual environment is well known for its influence on the survival of organisms by modulating their reproductive output. However, whether it affects survival indirectly through a variety of cues without physical contact and its influence relative to direct interaction remain largely unknown. In this study, we investigated both the indirect and direct influences of the social-sexual environment on the survival and reproduction of the mite *Tyrophagus curvipenis* (Acari: Acaridae). The results demonstrated no apparent influence of conspecific cues on the survival of mites, but the survival and reproduction of mated female mites significantly changed, with the females mated with males having a significantly shortened lifespan and increased lifetime fecundity. For males, no significant difference was observed across treatments in their survival and lifespan. These findings indicate that direct interaction with the opposite sex has a much more profound influence on mites than indirect interaction and highlight the urgent need to expand research on how conspecific cues modulate the performance of organisms with more species to clarify their impacts across taxa.

Introduction

Animals exhibit phenotypic plasticity in diverse social environments, especially ones involving their conspecifics. In response to the social context, they often demonstrate behavioural changes, which modify their survival and reproduction (Morgan *et al.*, 2022). These changes can be adaptive or maladaptive, ultimately influencing the ecological success of individuals and populations (Forsman, 2015). For example, animals may adjust their aggression levels or mating strategies based on the presence or absence of competitors or potential mates. These adaptations can enhance an individual's chances of survival and reproduction (Cremer *et al.*, 2011; Tolvanen *et al.*, 2020).

Extensive studies have shown that the social environment changes the behaviour, alters the physiology and shifts the life-history strategy of organisms across a wide range of taxa (Carvalho *et al.*, 2006; Rush *et al.*, 2007; Travers *et al.*, 2015; Liu and Hao, 2019; Garratt *et al.*, 2020; Kohlmeier *et al.*, 2021) through intra- and inter-sexual interactions. For example, a recent study reported that the male fruit fly, *Drosophila melanogaster*, shifted reproductive behaviour according to the intensity of competition. When housed with other competitors, they prolonged their mating duration and transferred much larger ejaculates than males housed alone (Filice *et al.*, 2020). Furthermore, females mated with males housed with rivals laid more eggs in their early life but few eggs in later life, and showed reduced lifespan (Filice *et al.*, 2020). The social environment has also been well documented to reduce immune function and alter digestive processes through mating, which is the most common process being social interaction (McKean and Nunney, 2001; Rolff and Siva-Jothy, 2002; White *et al.*, 2021). Social interaction, one of the most important biotic factors, is now well known for its tremendous influence on many aspects of animals' fitness (Boulay *et al.*, 1999; Koto *et al.*, 2015).

Over the past few years, we have gained much knowledge about how social context influences the fitness of organisms through direct physical interaction. However, relatively few research projects have been devoted to the consequences of perceiving cues from conspecifics without any direct contact. Recently, there has been emerging evidence that many organisms can detect various types of stimulation from conspecifics, including visual, auditory, olfactory and chemical cues (Mokany and Shine, 2003; Mcleman *et al.*, 2005; Poschadel *et al.*, 2006; Wijenberg *et al.*, 2008; Lecchini *et al.*, 2014). These perceived cues can trigger behavioural and physiological changes, ultimately determining the organism's short-term or long-term fitness. In model organism rats, males fed *ad libitum* reduced anxiolytic-like behaviour when exposed to olfactory cues from male mice under 25% calorie restriction (Abbott *et al.*,

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2009). More interestingly, the perception of conspecific cues even regulated the long-term fitness traits of fruit flies and mice. Fruit flies avoided the side of the T-maze containing a group of flies infected with the lethal pathogen *Pseudomonas aeruginosa* 24–48 h earlier. Moreover, when the fruit flies were chronically exposed to dead conspecifics, their lifespan decreased significantly, a finding that was robust for all experimental strains (Chakraborty *et al.*, 2019). In mice, compared with females exposed to water, female mice exposed to odours from adult females from the 3rd day to the 60th day old had a longer lifespan (Garratt *et al.*, 2022).

Although there is evidence that cues from the social environment can be successfully perceived and profoundly influence animals, how the cues of conspecifics shape the long-term fitness of animals is still little known. A few previous studies only addressed mating and reproductive success in response to sexual perception, one of the major fitness traits of adults, but neglected survival and lifespan (Corbel *et al.*, 2022a, 2022b), both of which are also of critical importance. Furthermore, lifespan and reproduction were reported to be associated with each other, and sometimes trade off under energy limitations in much life-history research. Therefore, measuring both of these traits is of particular interest and may enhance our understanding of the fitness consequences of social interaction. Also, up till now, research in this field has focused on model organisms, including nematodes, fruit flies and mice. No comparative studies have been conducted on non-model organisms, to the best of our knowledge. Thus, whether this profound influence is common for animals is largely unknown.

In this study, we aim to investigate how interaction with the opposite sex affects long-term fitness traits in a non-model species, *Tyrophagus curvipenis*, through direct and indirect interaction via sensory perception. Previous studies on immature life-history traits showed that this species has three developmental stages, including larval, protonymphal and tritonymphal, but without the deutonymphal stage, ranging from 10 to 25 days depending on the food source (Ye and Zhang, 2014). To clarify the effect of direct interaction with the opposite sex on the fitness of mites, we exposed adult females to males of the same age to allow for insemination. The influence of cues from the opposite sex without physical contact was explored by isolating the mites from the opposite sex with a fine mesh so that they could perceive cues by olfaction, while the mites in the control group were kept individually. If the opposite sex has any influence, both directly and through indirect cues, it was predicted that, compared with the control, the mites will have different lifespans and reproduction in response to socio-sexual cues.

Materials and methods

Mite rearing

The mite species used was first collected from capsicum leaves in the greenhouse of Manaaki Whenua – Landcare Research, Auckland, New Zealand. It was identified by Professor Qing-Hai Fan from the Ministry for Primary Industries as *T. curvipenis*. The population has been established in our laboratory since 2012 (Ye and Zhang, 2014) and is sustained with dry yeast (*Saccharomyces cerevisiae*, produced by Goodman Fielder Limited, New Zealand), a common product used in bakery. The mites and yeast were placed on a black plastic sheet (about 12 cm in diameter) over a wet sponge inside a Petri dish (15 cm in diameter), which is put into a box

with sponge. The box was filled with water regularly to keep the sponge wet and prevent mites from escaping. This rearing container was kept at $25 \pm 1^\circ\text{C}$, with a relative humidity of 65–75% and a photoperiod of 16L:8D.

Experimental cells

The experimental cell is a cylinder hole with its top 6 mm in diameter and bottom 3 mm in diameter in plexiglass slides (38 mm in length, 25 mm in width and 3 mm in thickness). The cell was covered on each side with a transparent plastic sheet to facilitate observation, and fixed with two metal clips. The experimental cell was modified from Ye and Zhang (2014).

Preparations for experiment

To obtain mites of the same age, females from the laboratory population were collected, fed with yeast and allowed to lay eggs. Twenty-four hours later, the females were removed and these newly produced eggs were allowed to develop. They were kept one mite per cell during development. On the 10th day, their sex was determined and they were randomly assigned to different treatments. The sex of the mites was determined by checking the ventral and genital shields under a dissecting microscope.

Experimental procedures

Four treatments were set up to determine the influence of mating and the possible fitness consequence of sexual perception (fig. 1). In the first treatment, the males and females were kept virgin and one mite per cell throughout their lives (single). In the second treatment, the virgin females and virgin males were kept in different cells side-by-side with a fine mesh isolating them, so that they could perceive the presence of the opposite sex via visual or olfactory cues but did not have any physical or sexual interactions (isolated). In the third treatment, the virgin male and virgin female were paired and kept together until dead, so they were allowed to mate frequently (mated together). In the last treatment, the male and female were kept together and allowed to mate for 24 h, after which they were separated into different cells and received the same treatment as that in treatment 1 until death (mated for 1 day). The survival of each individual and the number of eggs produced by females were checked every day until all the mites were dead. If one mite in a pair (focal mite) was lost or dead accidentally, a mite from the lab population of the opposite sex was introduced to ensure the focal mite were still under the treatment as before. However, the newly introduced mites were not included in the data collected. This replicated experiment had a sample size that ranged from 44 to 21 for each treatment and sex, respectively.

Data analysis

The survival data were fitted in the Cox proportional hazard model to see how multiple variates and covariates modulate this parameter. In this model, we evaluated the influence of two main factors, mating regimes and sex, with block as a covariate. The covariate did not significantly influence survival, indicating no real difference between these three blocks, so it was removed from the following analysis. The Kaplan–Meier survival analysis was performed to further explore the effects of each factor, including treatment and sex. The survival analyses were conducted with R packages ‘survival’ and ‘survminer’. The lifespan of mites in

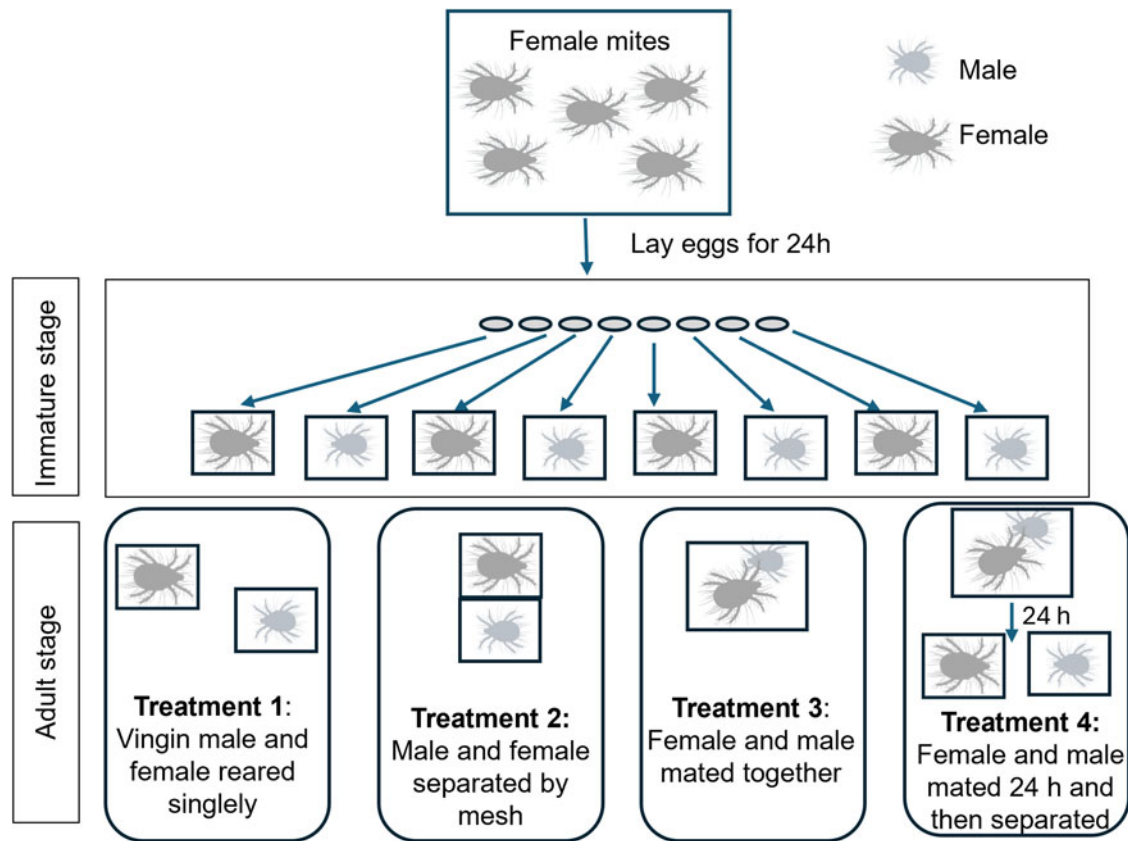


Figure 1. Schematic diagram of the experimental procedures.

each social environment was analysed with two-way ANOVA, with treatment and sex as the main factors. The differences in lifespan among the four treatments were compared with TukeyHSD, and the sex-specific difference in each treatment was compared using *t*-test.

In our experiment, only females in two treatments produced eggs: those kept with males throughout life and those kept with males for 24 h and then separated. Lifetime reproduction (all the eggs produced by each female) was first checked for normality by Shapiro–Wilk’s method with R function `shapiro.test`, since it meets the assumption of normality. An unpaired two-sample *t*-test was conducted to compare the difference between these two groups with R function `t.test`. The relationship between reproduction and adult lifespan was first explored for all females in this study with linear regression, and was then analysed for the females mated with males for their lifetime and females mated for 1 day, respectively. The difference in slope between these two treatments was compared with a *t*-test with R package ‘`lsmeans`’ (Lenth *et al.*, 2015). Data analyses were carried out and visualised using R version 4.0.0 (R Core Team, 2020).

Results

No significant effect of blocks on the survival rates ($Z = -0.961$, $P = 0.337$) was observed, so the data in each block were pooled. The survival of females and males differed significantly, with males living longer than females ($Z = 2.274$, $P = 0.023$; *fig. 2A*). The mated females kept together with a male for their whole life showed dramatically lower survival rates than the females

kept singly, isolated and mated for 1 day ($\chi^2 = 25.6$, $P < 0.001$), but females in the later three treatments did not show any differences from each other (all $P > 0.05$). The social context did not have a significant effect on the survival of males across treatments ($\chi^2 = 6$, $P = 0.1$; *fig. 2B*).

Since no block effects on lifespan were detected ($F_{2,215} = 0.935$, $P = 0.394$), data from three blocks were pooled. Significant effects of treatment ($F_{3,210} = 8.099$, $P < 0.001$) and sex ($F_{1,210} = 7.485$, $P = 0.007$) on lifespan were demonstrated, without interactions between them ($F_{3,210} = 0.896$, $P = 0.444$; *fig. 3*). By comparing the mean lifespan of mites across four treatments, it was found that mites mated together for their whole life showed an obviously shorter average adult lifespan than mites in the other treatments. The female mites that were single and isolated did not differ in adult lifespan from the males in the same treatments ($t_{1,64} = -1.3044$, $P = 0.1968$; $t_{1,51} = -0.15557$, $P = 0.877$; *fig. 3*), while females mated for 1 day showed a marginal difference from males, and females mated together for their whole life showed a profound difference from males ($t_{1,45} = -1.8133$, $P = 0.076$; $t_{1,50} = -2.1466$, $P = 0.037$; *fig. 3*).

The females allowed to mate with males for their whole life laid 61% more eggs than those that mated for only 1 day, and this difference was significant ($t = 3.670$, $P < 0.001$; *fig. 4*). For the former, the females with a longer life span produced more eggs, indicating a significant positive relationship ($F_{1,18} = 11.4$, $P = 0.003$; *fig. 5*). For the latter, no apparent linear relationship between adult lifespan and lifetime fecundity was found ($F_{1,21} = 0.207$, $P = 0.653$; *fig. 5*). Moreover, the difference between these two treatments was significant ($t_{1,39} = 3.051$, $P = 0.004$; *fig. 5*).

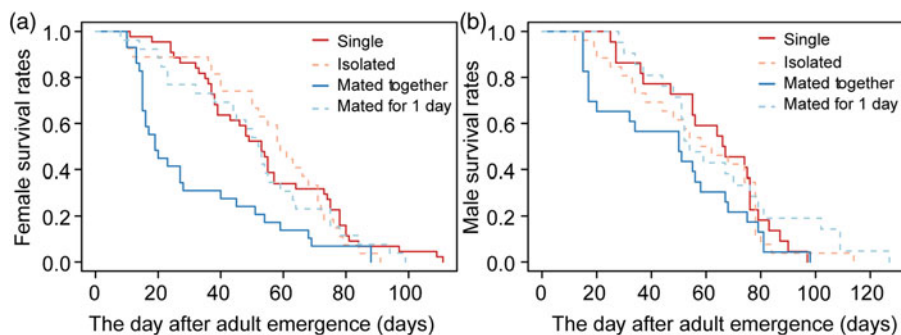


Figure 2. Survival plots of female (A) and male (B) mites *Tyrophagus curvipenis* in four different social contexts: single, isolated, mated together, mated for 1 day.

Discussion

This study investigated the indirect and direct influences of social-sexual environment on the long-term fitness of the mite *T. curvipenis*. The results showed there was no significant difference in survival rate and lifespan between mites kept singly and those kept isolated but exposed to cues of the opposite sex, indicating that cues of the opposite sex did not shift the life-history strategy of adults. We also showed that direct sexual interaction – mating and housed together with males – shortened the lifespan but increased the lifetime fecundity of female mites. In contrast, the adult lifespan of males was not influenced when they mated with females.

Indirect influences of social-sexual environment

Organisms can employ a wide range of cues to perceive the environment they are exposed to and adjust their behaviour and physiology to adapt. In Acari, many species have been reported to be capable of receiving biotic cues from their prey, predators, competitors and conspecifics and show responses to these cues (Azandémè-Hounmalon *et al.*, 2016; Schausberger *et al.*, 2017; Li and Zhang, 2019a; Gu *et al.*, 2022a, 2022b; Wei *et al.*, 2023). It is generally accepted that the species in this class evolved to identify vibratory and olfactory cues despite their limited visual perception. This study found that the adult mite *T. curvipenis* exposed to cues of the opposite sex did not show a significant difference in survival and lifespan compared with their counterparts kept single, indicating that neither females nor males were affected by the cues of the opposite sex. This was partially in line with a study on the Mediterranean flour moth (*Ephestia kuehniella*, Esfandi *et al.*, 2015), in that the survival of males was not affected by stimuli of additional females. However, it conflicts with results from the model species fruit fly

(*D. melanogaster*): Gendron *et al.* (2014) reported that male flies exposed to female donor pheromones exhibit a shorter life-span than flies exposed to male donor pheromones. This study proposed that the perception of sexual characteristics may modulate the health and lifespan of conspecifics by affecting a set of molecular processes.

The divergence among these studies might have resulted from differences in the experimental set-up. In the non-model species (mites and moths), the cues of conspecifics were generated by exposing the focal ones to cues without any physical contact by separating them with a mesh. However, the focal flies were housed with pheromone-donor flies in the same cage, which allowed homosexual interactions among flies. Previously, it was documented that male fruit flies displayed homosexual courtship and aggressive behaviours, with frequency, intensity and directionality varying according to their experience (Svetic and Ferveur, 2005). These behaviours were already proven to influence the survival of males in many insects and mites (Maklakov and Bonduriansky, 2009; Stojković *et al.*, 2010; Benelli *et al.*, 2013; Li and Zhang, 2021b).

Although both this study and the previous study with moths (Esfandi *et al.*, 2015) provide evidence that males do not have a survival cost when exposed to cues of the opposite sex, behavioural changes and reproductive success were significantly affected by cues from females. Specifically, Mediterranean flour moth (*E. kuehniella*) males that perceived auditory stimuli from females exhibited intense sexual flirtation behaviour and shortened mating duration (Esfandi *et al.*, 2015). Their lifetime fecundity was decreased as a result of reduced lifetime copulation frequency. Nevertheless, it was found that perception of female cues increased mating duration but did not affect the other behavioural traits of male flies, including mating latency, which determines the short-term fitness of males (Corbel *et al.*, 2022b). Furthermore, it was reported that short-term exposure to female

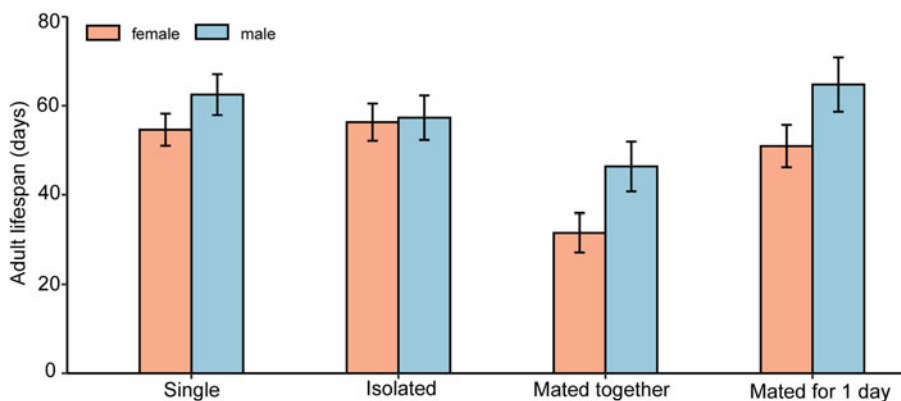


Figure 3. The adult lifespan of female and male *Tyrophagus curvipenis* in four different social contexts: single, isolated, mated together, mated for 1 day. Data are shown as mean ± SE in days.

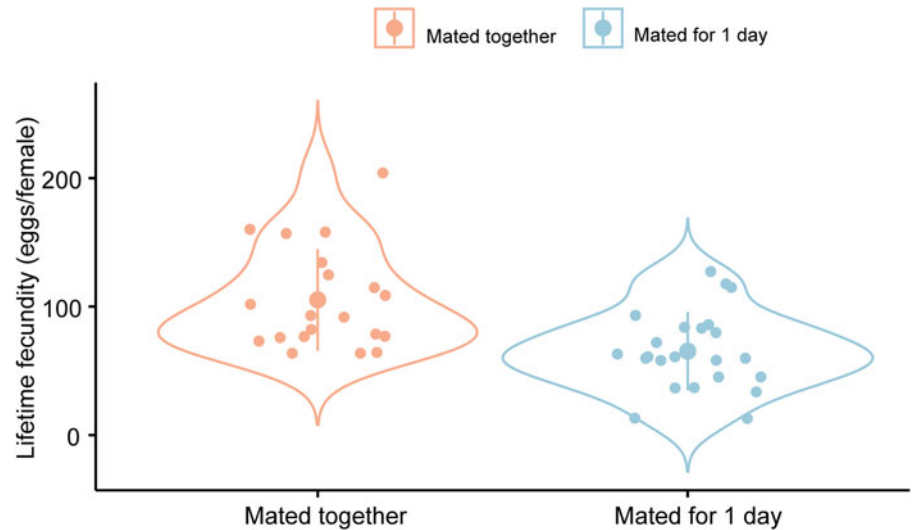


Figure 4. Violin plot of lifetime fecundity for female mites *Tyrophagus curvipenis* mated with males together throughout life and females mated with males for only 1 day.

cues increased male relative lifetime reproductive success in a competitive environment. In contrast, extended exposure to female cues decreased it (Corbel *et al.*, 2022a).

This research with different species differed in behavioural response to female cues, but it was in line with the finding that lifetime reproductive success is negatively influenced when males are exposed to female cues for a long period. This reproductive cost can be attributed to their great devotion to pre-copulatory behaviour. The flour moth has wing-fanning behaviour, which is energy intensive and considered costly for males. Also, there is evidence that the wing-fanning duration of males exposed to cues from five additional females was 5–8 times longer than that exposed to cues from five additional males and none (Esfandi *et al.*, 2015). Higher activity was also elicited as a response to female cues in fruit flies (Gendron *et al.*, 2014).

Direct influences of social-sexual environment

When females were allowed to have direct contact with males, they initiated reproduction after mating, suggesting that fertilisation is necessary for reproduction for this species, and it reproduces sexually. Moreover, compared with females that mated for 1 day, the females mated all their life produced many more eggs, proving that sperm acquired in one day is not enough to inseminate all eggs throughout the life of a female, and re-mating is necessary to obtain more sperm for insemination in later life. Also, the females mated with males showed a much shorter

lifespan than males, indicating that the socio-sexual environment significantly modified sex difference in lifespan. This finding was consistent with the notion that mating is costly for females (Fowler and Partridge, 1989; Ueyama and Fuyama, 2003; Rodrigues *et al.*, 2020; Li and Zhang, 2021a, 2021b). The decreased lifespan of females mated with males can result from their higher investment in egg production (Harshman and Zera, 2007) given that they produce significantly more eggs than their counterparts that were not mated or only mated for 1 day. However, we cannot exclude the possibility that the reduction in lifespan is due to seminal factors because there is evidence that sterile females of *D. melanogaster* showed decreased lifespan after mating (Ueyama and Fuyama, 2003).

The two crucial life-history traits – lifespan and reproduction of females mated – showed a significant positive relationship: with the increase of adult lifespan their lifetime fecundity showed an increasing trend, similar to another species of spider mite, *Tetranychus urticae* (Li and Zhang, 2019b). However, no apparent association was found for mites mated for 1 day. This is in line with a study on a closely related species *Tyrophagus putrescentiae* (Wei *et al.*, 2023). These studies contribute to the accumulating evidence that the life-history trade-off between adult lifespan and reproduction is not universal (Jasienska, 2009).

In conclusion, this study demonstrated that the social-sexual environment profoundly influences the life-history traits of female mites through direct interaction – mating. In contrast, indirect interaction and perceived cues of conspecifics have no

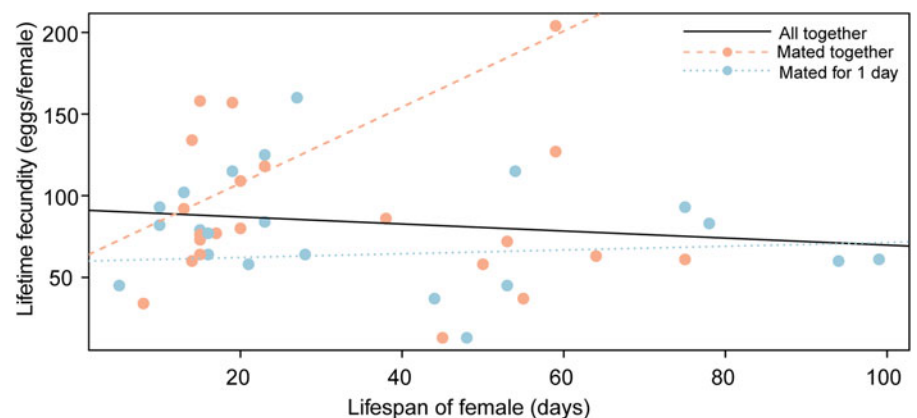


Figure 5. Correlations between adult lifespan and lifetime fecundity of female mites *Tyrophagus curvipenis* mated with males throughout life and females mated with males for only 1 day.

influence on mite survival and reproduction. It seems that some insects and mites show different responses to conspecific cues. It is possible that the divergent responses of the animals across taxa may result from differences in their degree of sociality. Given that work on this topic has focused on model species up to now, further research on animals across taxa, including both solitary and social insects, would be of great importance to generalise the potential influence of socio-sexual environment, and expand our understanding of how indirect social interactions, such as phenotypic plasticity in response to conspecific cues, modulate the fitness of different organisms.

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Author contributions. Z.-Q. Z. conceived the idea and designed the experiment. W. L. and G.-Y. L. carried out experiments and collected data. G.-Y. L. conducted statistical analysis and drafted the manuscript. All authors discussed the analyses and results, contributed to the writing and approved the final manuscript.

Competing interests. None.

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