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Article

Does size matter? Fecundity and longevity of spider mites (*Tetranychus urticae*) in relation to mating and food availability

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Abstract

Bigger animals tend to live longer than the small ones across species, but whether body size also has a robust relationship with survival within species remains to be determined. Here, the association between body size and fitness traits was examined through two food treatments (starvation and fed *ad libitum*) for both virgin and mated spider mites, *Tetranychus urticae*. The longevity of spider mites differed significantly across treatments, with feeding *ad libitum* increasing the survival of both males and females, mating decreasing male survival when starved and female survival when fed *ad libitum*. The body size of females but not of males increased with food. For each treatment, no clear correlations between body size and longevity were found. However, female fecundity was shown to have a positive relationship with body size. These results suggested that within species, for spider mites, there is no clear association between body size and longevity, but the fecundity increased with the body size, although this association is weak.

Keywords: food availability, starvation tolerance, mating status, body size, fecundity, longevity

Introduction

The body size of organisms varies greatly across taxa and considerably within species (Brown *et al.* 2004). It evolves as a consequence of opposing forces of natural selection and sexual selection acting on two main fitness components—survival and reproduction (Blanckenhorn *et al.* 2006). The direction and degree of these selection forces shape the degree of sexual size dimorphism, with female-biased dimorphism, male-biased dimorphism, and monomorphism (Andersson 1994; Dale *et al.* 2007). Body size is an important morphological trait that covaries with many physiological, behavioural, life history (Brown *et al.* 2004), ecological (Cohen *et al.* 2005), and evolutionary (Blanckenhorn 2005) organism traits.

The possible influences of body size on interrelated life history traits of animals have been extensively explored for vertebrates across a wide range of taxa, because of the great importance of body size in ecological and evolutionary studies. For example, small animals can have a relatively lower energy requirement (West *et al.* 1999; Ackerman *et al.* 2004), generally developed faster (Depczynski & Bellwood 2006), and reproduced more quickly (Munday & Jones 1998; Ménard *et al.* 2012; Nash *et al.* 2013). Larger animals, on the other hand, tend to show a great advantage over the small ones because of the dramatic decline of mortality rates with increasing body size under predation pressure (Goatley & Bellwood 2016). Additionally, larger animals live longer than small ones do, as indicated by the obvious fact that human beings live many times longer than small mice, which in turn greatly outlive insects such as fruit flies. The correlation between body size and lifespan has also been further examined within vertebrate classes such as birds and mammals,

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suggesting that body size can be a predictor of lifespan (Wilkinson & South 2002; Speakman 2005; Ricklefs 2010; Valcu *et al.* 2014; Scharf *et al.* 2015).

In empirical studies on birds and mammals males are typically bigger than females (Blanckenhorn 2005; Isaac 2005; Székely *et al.* 2007). Generally larger animals live longer than small ones for vertebrates with male-biased sexual size dimorphism. However, invertebrates differed from vertebrates with female-biased dimorphism, male-biased dimorphism, and monomorphism (Fairbairn 1997), and have received relatively little attention. Moreover, despite clear evidence of the positive relationship between body size and life expectancy in across-taxa research, increasing studies within species have resulted in controversy. In numerous studies with populations from different countries and people of different occupations, height was observed to be negatively correlated with longevity for both genders due to the increased risk of chronic diseases (Samaras 2007; Samaras 2014).

Within species level, difference in body size is also substantial. The most striking example is human beings, with the women being generally shorter in height and lower in weight than men. Some researchers have proposed that variation in body size may be attributable to the sex difference in longevity—a notion supported by evidence that men from America, Poland and Sweden who were taller than females had a shorter life expectancy (e.g. Samaras, Storms & Elrick 2002). However, the relationship between body size and lifespan between genders for small invertebrates such as arthropods is not clear, although there are extensive reports on how body size covaries with lifespan and reproductive success. Further studies on how body size is related to longevity within species and between gender are therefore important to understand the interrelationship of life history traits.

Here, we examined the potential influence of body size on the fitness of two-spotted spider mites, *Tetranychus urticae*, a species with female-biased sexual dimorphism. Males and females do not differ in size until the deutonymphal stage, with the larger female have an oval-shaped body, while small males have tapered abdomen (Delgado *et al.* 1994; see also Fig. 1). Usually, the body mass of female spider mites continues to increase during the early adult stage, by about 100% to 150% and eases at around 6-day post-adult emergence, while the male mite rarely grow after the protonymphal stage. Evidently, food availability in the adult stage can alter the body size to a large extent. Another factor that influences resource allocation of the adult is the mating status. Being mated can induce the female mites to shift energy and resources from growth and somatic maintenance to reproduction. Although spider mites may re-mate (Oku 2010, Macke *et al.* 2012), only the first mating can effectively inseminate the female, unless it is interrupted (Satoh & Takafuji 2001). The male has a shorter immature stage than the female and guards the quiescent deutonymphs after emerging to assure paternity (Satoh *et al.* 2001). To clarify to what extent body size is related to the fitness (i.e. longevity and fecundity), we scored the fitness components of spider mites in different mating status (virgin/mated) and food availability (*ad libitum* fed/starvation). In this study, we aimed to (1) determine the two main fitness traits: survival and reproduction of spider mites on starvation and feeding ad libitum; (2) explore the association between body size with longevity and female fecundity; (3) check whether mating status would be an influential factor on the fitness of spider mites and the association of body size with fitness traits.

Material and Methods

Mite species

To study the effects of mating status on starvation tolerance and longevity, we used the two-spotted spider mites of which the mating behaviour and reproductive system were well known. The spider mites used in the study were from a laboratory-reared population established on common bean

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(*Phaseolus vulgaris* L.) for nearly 3 years in a greenhouse of Manaaki Whenua – Landcare Research, Auckland.

Experiment preparation and rearing unit

At the commencement of this experiment, we randomly picked about 240 quiescent males and 240 quiescent females in their deutonymphal stages from the bean leaves using a fine brush and transferred them individually onto each leaf disc. The freshly emerged adults were used to establish the experiment. The rearing unit for spider mite fed *ad libitum* is a round leaf disc (80 mm in diameter) floating on the water filled in each well of the cell culture plate (24 well plate). The leaf disc was a little smaller than the well in size (well volume 3.4 ml, diameter 15.6 mm), so water around the leaf disc can function as a barrier that prevents mites escaping. Spider mites in starvation were raised in similar units, except that the leaf discs were replaced by a black plastic sheet so that the mites had access to water but no food.

Experiment manipulation

We fully crossed two factors, both with two levels: the mating status (mated=a male paired a female and virgin =isolated male or female without mating) with food availability (starvation and with food *ad libitum*), thus generating four treatments. Two days after the adults emerged, females and males were haphazardly assigned to each treatment. The survival of males and females was checked daily until death. The number of eggs produced by the females was also recorded daily. Mites were identified as not dead when they were active or could move when they were disturbed on their legs by a soft hairy brush. The experiment was conducted in a laboratory under the condition of 25 ± 1 °C, 12:12 light cycle, with relative humidity of 65 ± 5%.

The body width of the mites was also measured as an index of body size for each individual after death to examine whether body size was associated with the starvation tolerance and lifespan of the mites. The dead body of each mite was collected and mounted in Hoyer's medium on microslides, pressed flat, and heated in an oven at 50 °C for 2 weeks. The specimens were then measured in μm at 20-fold magnification using an optical microscope connected to a video camera with NIHimage software on a computer. The body width was measured as the distance between the bases of paired *sce* setae on the propodosoma (shown in Fig. 1), which is reliable index reflecting the body size of Tetranychidae (Sato *et al*. 1999). Initially forty eight replicates were set up for each treatment; owing to accidental death and missing, the final sample size ranged from 26 to 44.

Data analysis

The survival difference of the spider mites was analysed with Cox's proportional hazard model with mating treatment, food availability, and sex as fixed factors and the body width as a covariate. The possible three- and two-way interactions mating treatment × food availability × sex, mating treatment × food availability, mating treatment × sex, food availability × sex were also included in this model. The Kaplan-Meier survival analysis was used for comparisons of survival times across treatments, with Log Rank (Mantel-Cox) tests. The lifetime fecundity of females was analysed using the general linear models, with the mating treatment and food availability as two main factors with the interaction included. The dorsal width of spider mites was fitted in the general linear models with the mating treatment, food availability, sex, and all the possible interactions as explanatory variables. Correlations between longevity and body size were tested using the Pearson's product moment correlation.

The analyses were performed in R studio (R version 3.4.3). The Cox's proportional hazard model was performed using function "*coxph"* in R package *survival* (Therneau & Thomas, 2015),

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and general linear models were performed using the function "*aov*". Data are given as mean± SE throughout the text, unless stated otherwise.

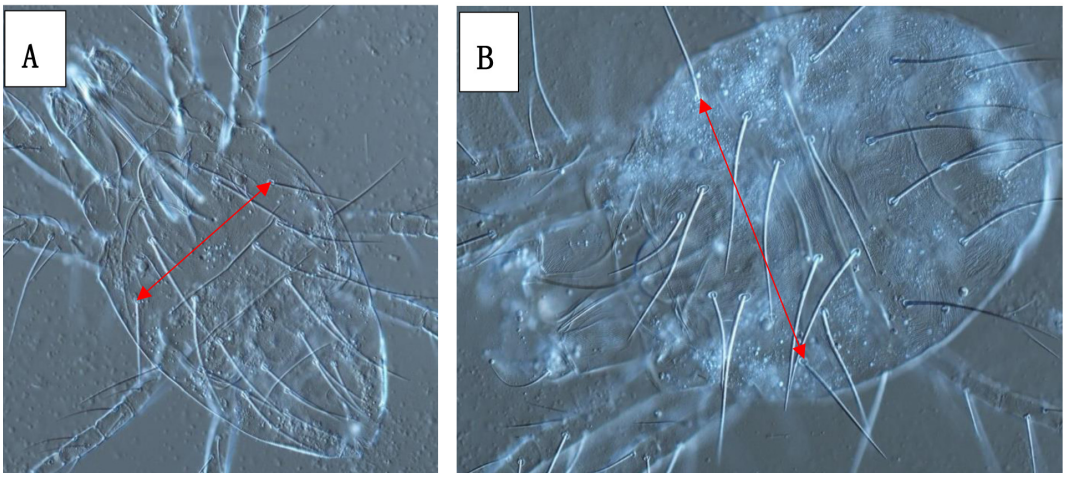


FIGURE 1. Dorsal side of *T. urticae* showing the measured distance between paired setae *sce* marked with red double-headed arrows for a male (A) and female (B). The females are much larger than the males.

Results

Effects of mating status, sex on survival time of starved mites

The longevity of mites varied significantly, with main factors including their mating status, sex, and food availability. The spider mites showed a sex difference in response to food deprivation, with the females more resilient to starvation—showing a much higher survival rate than the males during starvation (χ^2= 71.5, *df*=1, *P* <0.000, Fig. 2A) regardless of their mating status. When they were deprived of food for 2 days, the survival rates for females and males were 100% and 86.96%, respectively. The median survival time of males was 3 days on average, much shorter than females (6 days). Maximum survival time for males and females were 7 days and 11 days, respectively. There is also a significant interaction between sex and mating status on the survival of starved mites (*z* = 3.288, *P* =0.001): the female lifespan under different mating status did not differ (*P* >0.05), whereas the mated males showed a lower survival than the virgins (χ^2= 15.4, *df*=1, *P* <0.000).

Body size and its relationship with the survival time of starved mites

The female spider mites were significantly larger than males, with the female being about 480 µm and male being 325 µm in dorsal length (Fig. 3A). For both sexes, the survival time in absence of food did not demonstrate significant correlation with their body size indicated by the linear regression ($F_{1,38}$= 0.5918, *P*=0.4465 for mated female; $F_{1,44}$= 2.411, *P*=0.1276 for mated male; $F_{1,33}$=3.993, *P*= 0.05399 for virgin female; $F_{1,44}$= 0.4127, *P* = 0.524 for virgin male, Table1). This is consistent with the results of Cox proportional hazards model, which argues that body size showed no effects on the survival time of mites at food deprivation (*z* = 0.04, *P* =0.96).

Effects of mating status and mating on lifespan of mites fed ad libitum

Spider mites fed *ad libitum* lived longer than the starved ones (*z* = 13.1, *P* <0.000). When fed, the males showed a longer mean lifespan than the females (25 days for males and 12 days for females; $F_{1,145}$= 59.06, *P* <0.001). The mating status had a significant influence on the survival of

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mites fed *ad libitum*: mated females showed a significant decrease in longevity, while the male longevity was not significantly influenced (P>0.05)—consistent with the results obtained from survival analysis for mites fed *ad libitum* (Fig. 2B).

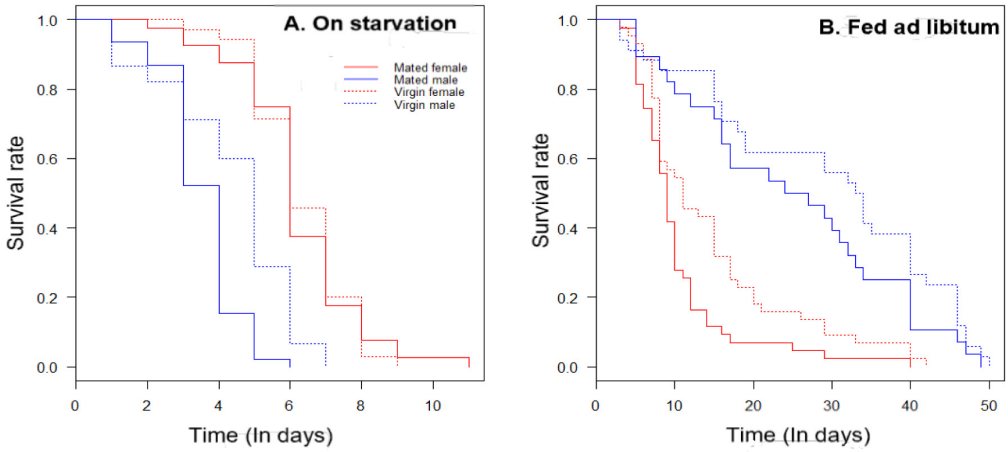


FIGURE 2. The proportion of surviving adult mites on starvation (A) and fed *ad libitum* (B), with the solid red lines for the mated females, dash red line for virgin females, the solid blue line for mated males, dash blue line for the virgin males.

Body size and its relationship with the lifespan of mites fed ad libitum

As with those mites on starvation, the females were larger than the males in dorsal width ($F_{1,158}$= 740.98, P <0.001 Fig. 3B). In comparison with starved mites, the body size of females significantly increased when they were fed at adult stage ($F_{1,158}$= 40.18, P<0.001). However, food availability did not alter male body size (P>0.05). The lifespan of mites showed no significant relationship with body size within each treatment (All P>0.05, Table1), suggesting that body size did not contribute to the longevity difference of mites. Across treatments, the influence of body size on the survival of mites was also insignificant (z = -1.258, P=0.21).

Effects of food and mating status and body size on female fecundity

The starved females mostly ceased reproduction on the second day of starvation. Thus, their lifetime fecundity averaged 1.8 eggs per female, significantly lower than that of females fed *ad libitum* (76 eggs per female for fed female; $F_{1,154}$=117.51, P<0.001, Fig. 4). While mating status also influenced female fecundity, as the mated females produced fewer eggs than virgins ($F_{1,154}$=10.33, P =0.002), its interaction with food availability is non-significant ($F_{1,154}$=2.971, P=0.086). Regression analysis showed that for mated starved females, the relationship between lifetime fecundity and body size was not significant ($F_{1,38}$=0.60, P= 0.44, Table 2). However, the body size of mated females fed *ad libitum* positively correlated with their fecundity; however, the significant level was marginal ($F_{1,41}$=3.573, P=0.067). For the virgin females, there is a significant positive relationship between these two parameters, regardless of food availability ($F_{1,33}$=10.44, P=0.003 for starved virgin females; $F_{1,42}$=4.818, P= 0.033 for fed *ad libitum* virgin females).

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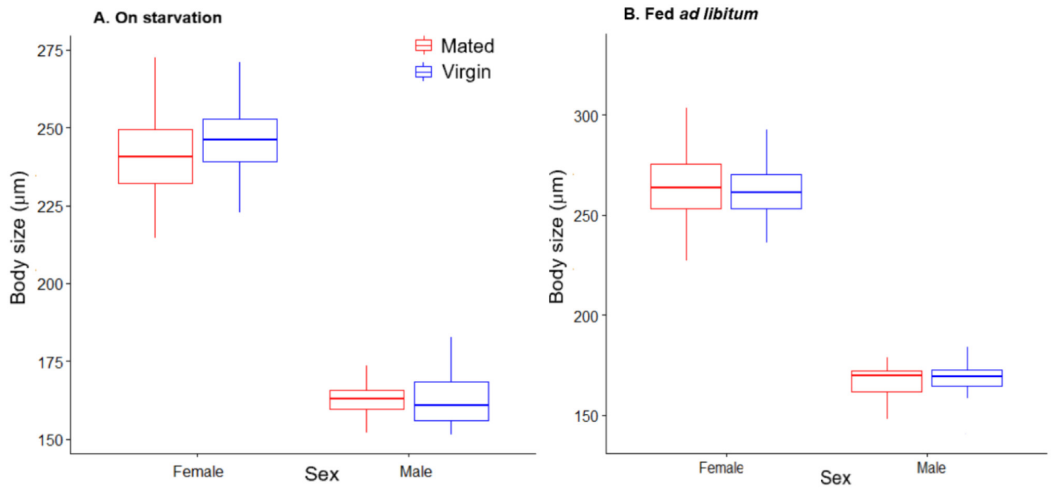


FIGURE 3. Body size (Means±95% percentile) of the mated and virgin mites under different conditions (A: on starvation; B: fed *ad libitum*). In both figures, the red boxes denote the mated mites, and the blue boxes represent the virgin mites.

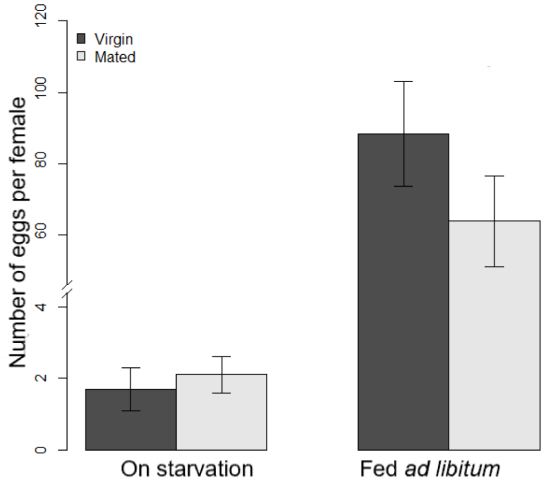


FIGURE 4. Fecundity (Mean±SE) of mated and virgin females as a function of food availability (feed *ad libitum* and starvation). Note there is a break on the y-axis, with the lower half for the fecundity of mites on starvation, and upper for the fecundity of females feed *ad libitum*.

TABLE 1. The correlation between body size and adult lifespan of mated and virgin mites with different food availability (on starvation and fed *ad libitum*).

Food availability	Sex	Mated			Virgin		
		slop	R^2	N	slop	R^2	N
On starvation	Female	-0.007	0.01	38	-0.016	0.0809	33
	Male	0.017	0.03	44	0.017	0.009	43
Fed *ad libitum*	Female	0.014	0.018	41	0.055	0.029	42
	Male	0.035	0.029	26	-0.08	0.03	32

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TABLE 2. The correlation between body size and female fecundity of mated and virgin mites with different food availability (on starvation and fed *ad libitum*).

Food availability	Mated			Virgin		
	slop	R^2	N	slop	R^2	N
On starvation	0.007	0.01	38	0.033	0.217	33
Fed *ad libitum*	0.321	0.056	41	0.379	0.081	42

Discussion

In this study, we determined the fitness traits of spider mites and their body size, as well as the possible relationship of body size with two main fitness components: survival time and lifetime fecundity. The results showed sex-specific tolerance to starvation, with large females surviving much longer than small males, regardless of their mating status. For males, the mated males that cohabited with their partners were more responsive to starvation and lived for shorter periods than the virgin males. There was no clear evidence that the variation in body size was related to starvation tolerance for either sex. When offered with food, small males significantly outlived the large females. Within each sex, no correlation was found between body size and lifespan. The lifetime fecundity appeared to increase with body size, but the positive relationship was not significant for mated females on starvation.

Sex-specific tolerance to starvation

In the short-term test without any food replenishment, we demonstrated that there was a remarkable sex difference in starvation tolerance: female spider mites could withstand much longer starvation than males could and had a much higher survival rate. Similar results were also shown in a copepod (*Acartia tonsa*), whose males had a lower survival than females in the absence of food (Finiguerra *et al.* 2013). This sex-specific starvation response can be attributed to their difference in energy reservation. In a previous study with fruit fly *D. melanogaster*, it was shown that the content of body lipid and starvation tolerance are positively associated with each other, and female fruit flies had a higher amount of body lipid than the males did (Chippindale *et al.* 1996), which is consistent with the size-efficient hypothesis (Threlkeld 1976; Tessier *et al.* 1983). This sex difference in energy storage may also occur in mites as well as copepods and thus contribute to the sex-specific starvation tolerance.

The females under starvation might be able to shift energy between soma maintenance and reproduction, as indicated by two main pieces of evidence. On the one hand, females mite significantly reduced their reproductive rates on the first day of starvation. When they fed, they were supposed to produce 6~7 eggs on average (Li & Zhang unpublished data), but in this study the starved female laid only 1.3 eggs averagely. It is possible that starved females retain or absorb the egg when they encounter tight energy budget so that they can re-allocate the resource from reproduction to survival, just as in other arthropods (Montserrat & Magalhães 2007; Boivin & Ellers 2016). On the other hand, the females eased their reproduction on the second day of starvation, suggesting that they shifted energy for egg production to their own survival under adverse conditions.

Another possible explanation for the sex difference in response to starvation is their behavioural difference in the adult stage. Male mites are generally active in searching for females in order to sire more offspring, while female mites are less active and spend most of the time resting. This was supported by the evidence that many more male than female mites were trapped in water. In addition,

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the mated males showed lower survival rates than virgins. The higher energy expenditure results in an early onset of energy exhaustion and eventually death.

Body size and longevity

The body size of *T. urticae* varied substantially with food availability, and those females that were fed were much larger than starved females. However, the difference in body size has no clear association with their longevity and starvation tolerance, suggesting that body size is not a critical contributor to the starvation resistance and longevity of spider mite under our lab conditions. This result agrees with a number of studies that used invertebrates as models to explore size-longevity relationship at within-species level, and which found body size or mass is not a reliable/accurate predictor of survival. For example, in a recent study with female *Drosophila melanogaster*, longevity is not significantly affected by body size (Travers *et al.* 2015). The non-significant relationship between longevity and body size was also frequently reported in other model organisms such as *C. elegans* and non-model organisms, including the beetle *Callosobruchus maculatus* (for female only Fox *et al.* 2004), parasitoid *Cephalonomia stephanoderis* Betrem (Lauzière 2014), stinkbug predator *Podisus rostralis* (Zanuncio *et al.* 2002), mosquito *Aedos triseriatus* (Landry *et al.* 1988), and goldspotted oak borer *Agrilus auroguttatus* (Lopez & Hoddle 2014). This report may suggest that within species the morphology variation in body size is not adequate to result in lifespan changes. The interspecific positive relationship between body size and longevity was based on the oxidative stress theory of ageing. It states that small animals have a relatively higher mass-specific metabolic rate than large species, giving rise to severer oxidative damage and shorter longevity. However, because metabolic rate is not in proportion to body size within species, there is no reason to expect that oxidative damage should relate to body size (Khazaeli *et al.* 2004). It is therefore likely that within species, the range of body size and the metabolic rate variation are not the decisive factors affecting longevity.

Body size and female fecundity

The body size of the female was found to be positively associated with their fecundity, particularly for virgin females, but the mated females on starvation were an exception as they produced very few eggs even when they lived for a few days. This is not surprising, given that natural selection favours large females that have more energy and nutrient reserve for egg production, meaning they have a fecundity advantage over smaller females. The difference in the relationship across treatments may suggest that other factors such as food and mating status also affect fecundity. In this study, when mated females were deprived of food they produced very few eggs because starvation made them save energy for survival. It seems that the association between body size and fecundity collapsed because of starvation or food level. This was also supported by research with *Agrilus auroguttatus,* in which the females with unknown feeding history collected from the field showed that lifetime oviposition was not correlated with any body size indicators, including elytron length, elytron width, or tibia length (Lopez & Hoddle 2014); earlier field research by Branson (2008) and Gotthard *et al.* (2007) also failed to find positive association between body size and reproductive traits.

In insects and many other animals, high stress resistance to environmental factors can enhance survival probability. Consequently, in some studies stress resistance was deemed an indicator of organisms' great fitness (Johnson *et al.* 2002; Lithgow & Walker 2002; Rea *et al.* 2005). This notion was supported by some researchers, who claimed that selected lines of long-lived animals always have better performance when experiencing stress, including starvation and high temperature or *vice versa* (Zwaan *et al.* 1995; Norry & Loeschcke 2003; Stazione *et al.* 2017), although it is not always the case. Our study finds no evidence that the females highly tolerant to starvation lived longer than

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males. Surprisingly, the females were shown to have a relatively shorter lifespan than the starvation-sensitive males, irrespective of their mating status. The inversed association between starvation tolerance and longevity between male and female was principally due to their difference in reproductive investment across food conditions. The female showed dramatic increase in reproductive output when food was available, while the reproductive investment of the male may not vary between food treatments. This assumption, however, has not yet been justified in this study owing to the lack of an appropriate method for measuring the reproductive efforts in male spider mites. To test this assumption, we propose employing other model organisms, such as cricket (*Gryllus spp*), whose reproductive investment of the male can be easily checked, the reproductive efforts can be measured in calling efforts by electronic monitoring device (e.g.: Zajitschek *et al.* 2009, Archer *et al.* 2012; Rapkin *et al.* 2018).

Conclusion

Although the longevity difference between species from mammals and birds can be well explained by their body size in accordance with the rate of living theory, the relationship between body size and life history fitness within-species for the small invertebrates should be interpreted with caution. This study, as well as many previous reports, has provided insights that many other factors, including mating status (Himuro & Fujisaki 2010), genetic background (Khazaeli *et al.* 2005), and diet and temperature (Chen *et al.* 2005; Norry & Loeschcke 2002), can more dramatically affect the association between life history traits. This is particularly important when these environmental factors may be a major source of variation of body size and lifespan or both at the same time. Therefore, the within-species association between body size and longevity will not be fully understood until further research is conducted into various environmental conditions.

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