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**Article**

# Sons from virgin mothers produce more daughters in a haplodiploid mite

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## Abstract

Population size can be very small in the newly invaded/introduced site or front edge of population expansion where mates are difficult to find. This scenario can lead to extinction of a local population in many animal species. However, when it happens to a haplodiploid animal, individual virgin females may adjust their strategies to produce sons of greater reproductive success such as higher mating success and fertility, which may help increase the chance of establishment. Here we investigated how maternal mating status affected sons' reproductive success in a haplodiploid spider mite, *Tetranychus ludeni* Zacher, a cosmopolitan pest of many crops. We show that virgin females laid significantly larger eggs than mated females, giving rise to larger deutonymphs and adults, but mating status of mothers had no influence on mating success and longevity of their sons. We provide the first empirical evidence in a haplodiploid mite that virgin mothers adjusted their resource allocations to yield sons that produced more daughters at a higher rate.

**Key words:** Spider mite, female mating status, male mating success, male reproductive success

## Introduction

In haplodiploid arthropods, mated females may lay unfertilised haploid eggs giving rise to sons and fertilised diploid eggs leading to daughters while virgin females can only produce haploid sons (Filia *et al*. 2015). When population size is small, it is likely that females are not able to find mates and produce daughters. This scenario may be particularly common in new environment such as recently invaded site or front edge of population expansion (Engen *et al*. 2003). Therefore, females may have developed strategies to adjust their resource allocations in response to the situation. So far, whether and how virgin females adjust their resource allocations and whether and how such adjustment influences their sons' reproductive success are poorly understood in haplodiploid animals.

Several authors have investigated the effect of maternal mating status on offspring performance in a haplodiploid mite, *Tetranychus urticae* Koch. In one study, sons produced by virgin females appear to be able to find their mates more quickly than males produced by mated females (Ohzora & Yano 2008). In another study, however, maternal mating status does not affect mate-searching behaviour of males (Oku & van den Beuken 2017). Macke *et al*. (2011, 2012) report that male eggs laid by virgin females are usually larger than male eggs produced by mated females. Although the effect of maternal mating status is not examined, larger males are found to be more likely to win male-male competition for mates (Potter *et al*. 1976) and better resist against attempted interference during mating (Enders 1993). However, it is not clear whether maternal mating status has any influence on sons' reproductive outputs in any haplodiploid mite species, knowledge of which is important for the better understanding of invasive potential of these animals.

*Tetranychus ludeni* Zacher is native to Europe and now globally distributed (Bolland *et al*. 1998; CABI 2011). It appears to be better adapted to hot weather and have a more subtropical distribution than the cosmopolitan congeneric *T. urticae* (Martin 2000; Gotoh *et al*. 2015). This species is a serious pest of bean, eggplant, hibiscus, pumpkin and other cucurbitaceous plants in warm regions and a common pest on greenhouse plants in temperate areas (Zhang 2003). It has denser webbing than *T. urticae*, which is believed to make its biological control by predatory mites less effective (Martin 2000; Zhang 2002). However, compared to *T. urticae*, *T. ludeni* has been much less studied. For example, nothing is known about the effect of mothers' mating status on traits of their sons in *T. ludeni*.

In the present study, we carried out a series of experiments to examine how maternal mating status affected sons' body size, mating success, longevity, and reproductive outputs in *T. ludeni*. Based on the knowledge outlined above, we proposed and tested three hypotheses: (1) virgin females produce larger eggs than mated females and larger eggs develop to larger adults; (2) sons from virgin females (SVF) have better mating success than sons from mated females (SMF), and (3) SVF have higher reproductive output and greater longevity than SMF.


**Materials and Methods**

*Mite colony*

A colony of *T. ludeni* was established from adults collected on *Passiflora mollissima* (Kunth) in September 2017 in Palmerston North, New Zealand, and reared on kidney bean plants (*Phaseolus vulgaris* L.). Three to 5-week-old bean plants were used for maintaining the colony, and the first expanded leaves of 1 to 2-week-old plants were used for experiments. The colony was maintained and the potted plants grown in two separate environmental rooms at 25 ± 1 ℃, 40 ± 10% RH and 14:10 h (L:D) in the Massey University Entomology and IPM Laboratory, Palmerston North, New Zealand. Experiments were carried out in the third environmental room with the same environmental conditions. Mites were reared on kidney bean plants for three generations before experiments.


*Experimental mites*

To obtain sons from virgin females (SVF) and mated females (SMF), we randomly selected 60 female and 45 male deutonymphs from the colony and transferred them onto small leaf squares (1.0 × 1.0 cm), one mite on each square in a Petri dish (9.5 cm diameter and 1.0 cm height), and allowed them to become quiescent deutonymphs (QD) and emerge. Leaf squares were placed on the wetted cotton wool. The Petri dish was covered with a lid which had a 1-cm-diameter hole covered with metal mesh (aperture size = 0.25 mm) in the centre.

We kept 15 1-d-old virgin females individually in their Petri dishes to produce SVF. To obtain SMF we individually paired 45 1-d-old virgin females with 45 1-d-old virgin males for 24 hours and then removed the males. Because virgin *T. ludeni* females lay reddish eggs whereas mated females lay translucent eggs, we examined the colour of all eggs laid by the females exposed to males for 2 days following removal of males. Females that laid translucent eggs were considered as mated and used for producing SMF and the remaining were discarded. On the third day, we transferred virgin and mated females individually onto new leaf squares, one mite on each leaf square, and allowed them to oviposit for 24 hours, after which time, we transferred them onto new leaf squares. This procedure was repeated for 3–10 days depending on the desired number of mites required for experiments. We transferred eggs from virgin and mated females individually onto new leaf squares, one egg on each square in a Petri dish, and allowed them to develop to deutonymphs or adults. All dishes were numbered so that eggs and resultant adults were matched.

*Body size and mating success of SVF and SMF*

To investigate the size and size distribution of eggs from females of different mating status (Figure 1), we measured 51 eggs laid by virgin females and 247 eggs (including both fertilised and unfertilised eggs) laid by mated females. We measured many more eggs from mated females because the sex ratio of offspring produced by mated female *T. ludeni* was highly female-biased (Gotoh *et al*. 2015). Egg size (total area from top view) was determined using a digital camera (Olympus SC30, Japan) connected to a stereomicroscope (Leica MZ12, Germany) and a computer with adequate imaging software (CellSens® GS-ST-V1.7, Olympus, Japan) installed. Measured eggs were individually transferred onto new leaf squares (1.0 × 1.0 cm) using a fine brush and raised in Petri dishes. On the fifth day, each larva or nymph was provided with a new leaf square of the same size to avoid leaf quality deterioration. Eggs that successfully developed to QDs were used to determine the difference in size of male eggs laid by virgin (n = 31) and mated females (n = 24) (Table 1). QDs of 27 SVF and 20 SMF were photographed and their size (total area from top view) measured using the above device. After emergence, 26 1-d-old SVF and 19 1-d-old SMF adults were photographed and their size measured again as above.

**TABLE 1.** Size ($\times 10^4\,\mu m^2$) of SVF and SMF.

|  | Egg | Quiescent deutonymph | Adult |
| --- | --- | --- | --- |
| SVF | 1.3519 ± 0.0158 a | 3.1048 ± 0.0483 a | 2.9674 ± 0.0373 a |
| SMF | 1.1385 ± 0.0280 b | 2.8625 ± 0.0551 b | 2.7544 ± 0.0520 b |
| $F_{(df)}$ | 49.84 $_{(1,53)}$ | 10.95 $_{(1,45)}$ | 11.66 $_{(1,43)}$ |
| P | < 0.0001 | 0.0018 | 0.0013 |

Means (± SE) with the same letter in each column are not significantly different (P > 0.05).

To determine whether the mating success of SVF and SMF was different, we randomly selected female deutonymphs from experimental mites as described in the previous section. Mites were individually transferred onto leaf squares (1.0 × 1.0 cm), one mite on each square in a Petri dish. About 20 hours after transfer, the QD females turned silvery and were ready for test. For each replicate, we randomly selected a 1-d-old SVF and a 1-d-old SMF from the experimental mites and randomly marked one of them on his rear dorsal using blue baking colour (Hansells, Queen New Zealand Pty. Ltd) before releasing them to a QD female on a leaf square in a Petri dish. We recorded their behaviours using the device mentioned above for 10 minutes after the female emerged. A total of 68 replicates were recorded. Because the first released males might be more likely to locate, guard and mate with the QD females independent of the mating status of their mothers, we carried out a second set of release regime: we transferred a 1-d-old SVF and a 1-d-old SMF onto a leaf square about 2 hours before the introduction of the QD female. Other experimental procedures were the same as the above test. Fifty-one replicates were performed.

*Reproductive success of SVF and SMF*

This experiment was designed to determine the reproductive success of SVF and SMF. To provide sufficient female adults for experiments, we randomly collected 300 female deutonymphs from the colony each day and transferred them onto leaf squares (5 × 5 cm) with 50 mites on each square for development into adults. On the first day of experiments, we provided a 1-d-old SVF or SMF with 10 1-d-old virgin females on a leaf square (2 × 2 cm) in a Petri dish for 24 hours. The next day, the male (2-d-old) was transferred onto a new leaf square of the same size with 10 1-d-old virgin adult females for 24 hours. This procedure was repeated until the male died.

After the male had been transferred onto a new leaf square, the females were allowed to oviposit on their leaf square for 5 days, and then transferred onto a new leaf square of the same size. This procedure was repeated until all females died. All eggs laid by these females were allowed to develop to deutonymphs. For each test male, the longevity, fertile period (period during which the male could fertilise eggs, verified by the production of at least one daughter) and total number of daughters produced were recorded. Fifteen SVF and 15 SMF were tested.

*Statistical analysis*

All analyses were done using SAS 9.4 with a rejection level set at $\alpha < 0.05$. Male mating success (Figure 2) was analysed using a Chi-square test (FREQ procedure). A Wilcoxon test (LIFETEST procedure) was used to compare the survival probability of SVF and SMF. A goodness-of-fit test (Shapiro-Wilk test; UNIVARIATE procedure) was used to test the distribution of data when mean comparison was performed. Data on the mean size of male eggs, QDs and adults (Table 1) and the fertile period and number of daughters (Figure 3) were normally distributed and thus analysed using an analysis of variance (ANOVA, GLM procedure) followed by Tukey's Studentized range test. However, data on mean size of eggs laid by virgin females and mated females (both fertilised and unfertilised eggs) were not normally distributed, and thus analysed using a non-parametric ANOVA (GLM procedure). The size distributions of those eggs were compared by a Kolmogorov-Smirnov Test (NPAR1WAY procedure) (Figure 1).

We also developed a Power curve model (NLIN procedure) to fit the data on accumulation of insemination potential (number of daughters produced by SVF or SMF; Figure 4): accumulative daughters $= a + b \, (1 - c^{\text{age}})$, where $a$ is the model constant, $b$ is the maximum number of daughters produced during males' lifetime reflecting the maximum potential of sperm transferred, and $c$ is the constant increasing rate of daughters produced per day, and $a > 1$, $b > 1$, and $1 > c > 0$. The estimated parameters are significantly different from 0 if the 95% confidence limits (CL) do not include 0 (both upper and lower CL $> 0$ or $< 0$) (Julious 2001). Julious' (2004) methods were used to compare parameters in Table 2, where there is no significant difference for a given parameter if the 83.4% CL overlap. The coefficient of determination ($R^2$) for Power curve model was calculated as: $1 - ($residual sum of square/corrected total sum of square) (Tahriri *et al*. 2007).

**TABLE 2.** Comparison of estimated parameters of Power curve model between SVF and SMF*.

| Parameter | Male | Estimate | SE | 83.4% CL | |
|---|---|---|---|---|---|
| | | | | lower | upper |
| *a* | SVF | 134.10 | 60.25 | 50.42 | 217.90 |
| | SMF | 119.80 | 46.64 | 54.97 | 184.60 |
| *b* | SVF | 1688.90 | 80.31 | 1573.20 | 1804.70 |
| | SMF | 1056.80 | 65.19 | 966.20 | 1147.50 |
| *c* | SVF | 0.90 | 0.01 | 0.88 | 0.92 |
| | SMF | 0.89 | 0.02 | 0.86 | 0.92 |

* *a*, the model constant; *b*, the maximum number of daughters produced; and *c*, the constant daily increasing rate of accumulative daughters produced. All estimated parameters are significant at $P < 0.05$ level (95% CL $> 0$).

**Results**

Body size and mating success of SVF and SMF

Our results show that eggs laid by virgin females were significantly larger (mean $\pm$ SE = 1.3262 $\pm$ 0.0147, $\times 10^4 \, \mu m^2$) than those by mated females (1.2601 $\pm$ 0.0063, $\times 10^4 \, \mu m^2$) ($F_{1,296} = 19.52$, P <

0.0001), and the size distributions of eggs from virgin and mated females were significantly different (D = 0.3172, P < 0.0001; Figure 1). SVF of all stages from eggs to adults were significantly larger than SMF (Table 1). However, SVF and SMF had similar mating success regardless of which sex was introduced into the arena first (Chi-square test: $x_1^2$ = 0.15, P = 0.7008 when males were introduced first; $x_1^2$ = 0.02, P = 0.8759 when QD females were introduced first) (Figure 2).

Reproductive success of SVF and SMF

The fertile period was not significantly different between SVF and SMF ($F_{1,28}$ = 1.76, P = 0.1958; Figure 3A). SVF produced significantly more daughters (mean total ± SE = 1,407 ± 108) than SMF (mean total ± SE = 855 ± 78) ($F_{1,28}$ = 17.29, P = 0.0003; Figure 3B). Further analyses show that the estimated maximum number (*b*) of daughters produced was significantly greater in SVF than in SMF (83.4% CL did not overlap; Table 2), contributing to the faster accumulation of daughters produced (Figure 4). However, the longevity was not significantly different between SVF (17.73 ± 1.54 days) and SMF (18.07 ± 1.89 days) ($x_1^2$ = 0.13, P = 0.7182).



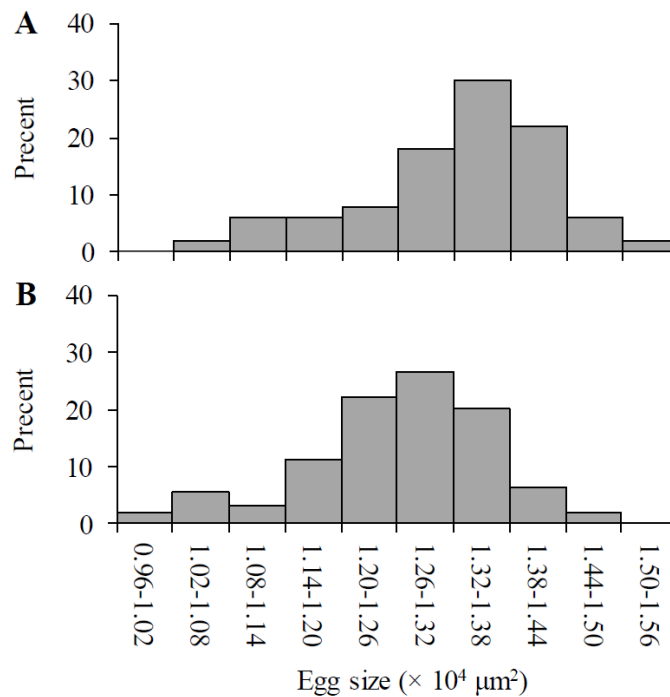**FIGURE 1.** Size distribution of eggs laid by (A) virgin females (n = 51) and (B) mated females (n = 247).
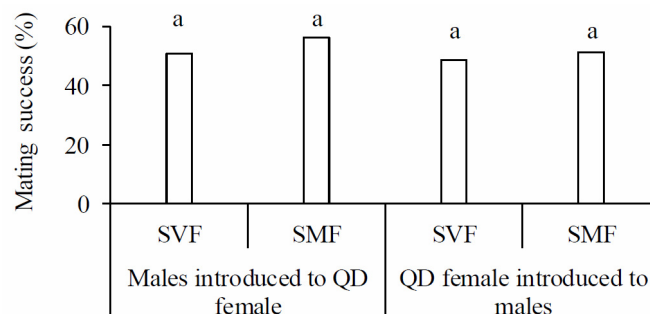


**FIGURE 2.** Mating success of SVF and SMF. Columns with the same letters in each case are not significantly different (Chi-square test: P > 0.05).
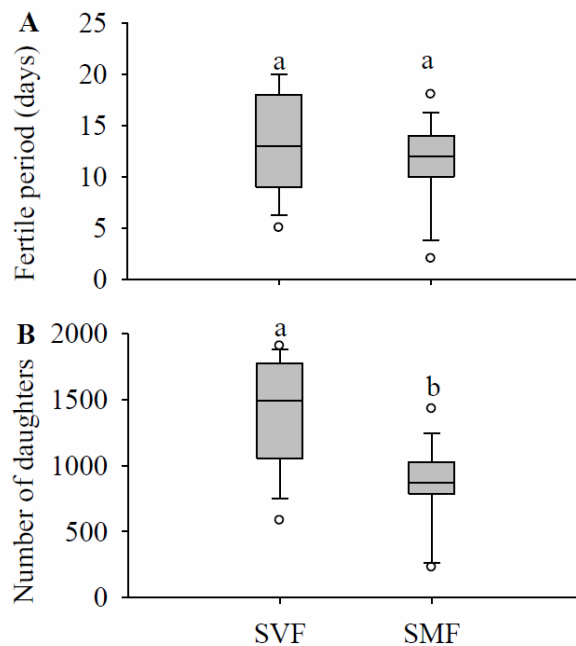
**FIGURE 3.** Fertile period (A) and daughters produced (B) in SVF and SMF. Columns with the same letters are not significantly different (ANOVA: P > 0.05).
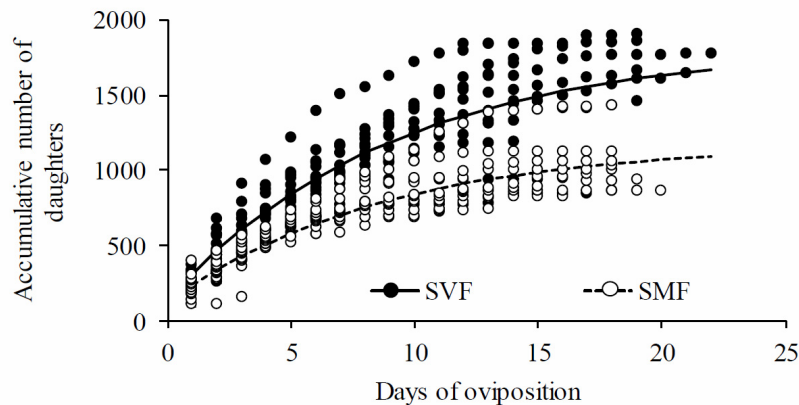


**FIGURE 4.** Lifetime reproductive potential of SVF and SMF. SVF: accumulative daughters = 134.10 + $1688.90(1 - 0.90^{age})$ ($R^2 = 0.9639$, $F_{2,230} = 360.29$, $P < 0.0001$); SMF: accumulative daughters = 119.80 + $1056.80(1 - 0.89^{age})$ ($R^2 = 0.9544$, $F_{2,206} = 232.61$, $P < 0.0001$).

## Discussion

Numerous studies have reported the positive relationships between egg size and offspring fitness across taxa including mites (e.g., Macke *et al*. 2011), insects (e.g., Azevedo *et al*. 1997; Fox 1994, 2000; Fox & Czesak 2000; Torres-Vila & Rodriguez-Molina 2002; Fischer *et al*. 2002, 2003), fish (e.g., Hutchings 1991; Maruyama *et al*. 2003; Tamada & Iwata 2005), and birds (e.g., Price 1998; Ferrari *et al*. 2006). However, prior to the current study, little was known about strategic resource allocations to their sons by mothers of different mating status and the consequences of such strategies in a haplodiploid animal.

In *T. urticae*, virgin mothers produce significantly larger sons than mated mothers; however, mean egg size and egg size distribution are similar regardless of maternal mating status when both fertilised and unfertilised eggs are included in the analysis, suggesting that the differential egg size allocation takes place prior to fertilisation (Macke *et al*. 2011). As a result, the fact that virgin females produce larger sons is not a resource allocation strategy in response to maternal mating status in that species. However, when both fertilised and unfertilised eggs were incorporated in our analysis, we demonstrate that virgin females laid significantly larger eggs than mated females, and the size distributions of eggs from virgin and mated females were significantly different (Figure 1). Our findings indicate that the egg size difference between virgin and mated *T. ludeni* females is indeed a result of strategic resource allocation in response to maternal mating status, with more resources being allocated to their sons when females do not have the chance to produce daughters.

When we compare male offspring produced by mothers of different mating status, we show that virgin *T. ludeni* females laid significantly larger male eggs than mated females, and the resultant larger male eggs developed to larger deutonymphs and adults (Table 1). In principle, larger males have advantages in male-male competition (Andersson 1994; Emlen 2008; Hunt *et al*. 2009; Suzaki *et al*. 2013; Shelly 2018). Ohzora and Yano (2008) reveal that although size is not measured, sons from virgin mothers disperse faster and start guarding females sooner than those from mated mothers in *T. urticae*, suggesting that the former may have better mating success than the latter. However, our data from the two mate competition tests do not support this notion because larger SVF and smaller SMF had the same mating success when they were allowed to compete for a female (Figure 2). In an experiment on *T. urticae* with a design similar to ours, Oku and van den Beuken (2017) did not find any difference in mate-searching behaviour between SVF and SMF. These suggest that maternal mating status affects neither mating success nor mate-searching behaviour of their sons.

When we tested the lifetime fecundity of SVF and SMF, we found that SVF produced significantly more daughters than SMF (Figure 3B). Furthermore, compared to SMF, SVF contributed to a significantly faster increase of daughter population growth (Table 2, Figure 4). These data strongly suggest that when a female has no chance to mate, she produces sons that can yield more daughters at a higher speed. This strategy compensates the loss of producing daughters for virgin females through their sons' production of more daughters at a faster rate in the next generation. As a result, SVF may be able to found a colony faster as compared to SMF. The resource allocation strategy taken by virgin *T. ludeni* females and its consequences reported above may be attributed to the notion that large males generally have more sperm available for copulation (Wiernasz *et al*. 2001; Locatello *et al*. 2008; Anthes *et al*. 2014; O'Dea *et al*. 2014; Sturm 2014) and replenish their sperm reserves faster (O'Dea *et al*. 2014) than small males because testis size usually increases with body size (Gage 1994; Simmons 2012).

Mating may be costly to males, including expenditure on sperm and seminal fluid production (Voorhies 1992; Pitnick 1996), mate access (Barnes & Partridge 2003; Metzler *et al*. 2016), and immune defence against sexually transmitted pathogens (Schwenke *et al*. 2016), which could reduce resources for somatic maintenance (Vinogradov 1998). As a result, mating may cut males' future survival (Roff 1992; Stearns 1992; Cichoń 2001; Roff & Fairbairn 2007). Because SVF sire more eggs than SMF, the former are expected to spend more resources for reproduction and to live shorter lives. However, both SVF and SMF had similar longevity, suggesting that survival of *T. ludeni* males is not dependent on their reproductive expenditure or their mothers' mating status.

In conclusion, this study provides the first empirical evidence that the virgin females strategically allocate more resources to their sons, which can produce more daughters at a higher rate, in a haplodiploid mite. In a newly invaded scenario where population is small and females are more likely to be virgin, this feature may increase the chance for the species to become established.

## Acknowledgements

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