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Article

Adjustment of fecundity and sex ratio in response to social environments in a haplodiploid mite

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Abstract

Animals can adjust reproductive strategies in favour of corporation or competition in response to local population size and density, the two key factors of social environments. However, previous studies usually focus on either population size or density but ignore their interactions. Using a haplodiploid spider mite, *Tetranychus ludeni Zacher*, we carried out a factorial experiment in the laboratory to examine how ovipositing females adjust their fecundity and offspring sex ratio during their early reproductive life under various population size and density. We reveal that females laid significantly more eggs with increasing population size and significantly fewer eggs with increasing population density. This suggests that large populations favour cooperation between individuals and dense populations increase competition. We demonstrate a significant negative interaction of population size and density that resulted in significantly fewer eggs laid in the large and dense populations. Furthermore, we show that females significantly skewed the offspring sex ratio towards female-biased in small populations to reduce the local mate competition among their sons. However, population density incurred no significant impact on offspring sex ratio, while the significant positive interaction of population size and density significantly increased the proportion of female offspring in the large and dense populations, which will minimise food or space competition as females usually disperse after mating at crowded conditions. These results also suggest that population density affecting sex allocation in *T. ludeni* is intercorrelated with population size. This study provides evidence that animals can manipulate their reproductive output and adjust offspring sex ratio in response to various social environments, and the interactions of different socio-environmental factors may play significant roles.

Key words: population size, population density, interaction, spider mite, *Tetranychus ludeni*, reproduction, sex allocation

Introduction

Animals in patchy habitats often face intraspecific competitions (Iritani *et al.* 2020; Ausband & Mitchell 2021; Li & Zhang 2021) and adjust their reproductive strategies in response to social environments (Lihoreau & Rivault 2008; Ruan & Wu 2008; Krams *et al.* 2009; Schausberger *et al.* 2017; Conroy & Roff 2018; Crocker & Hunter 2018; Li & Zhang 2021). The number of individuals in a local population(population size) and the number of individuals per unit area in a habitat (population density) are two key socio-environmental forces that drive population regulations (Estevez *et al.* 2007; West 2009; Sprenger *et al.* 2011; Weerawansha *et al.* 2020; Ausband & Mitchell 2021). Fluctuations in population size and density alter the resources available for local individuals so that they must change their fecundity and offspring sex ratio accordingly to adapt (Wauters & Lens 1995; Estevez *et al*. 2007; Webber & Wal 2018; Burant *et al.* 2020; Weerawansha *et al*. 2020). However, in the field populations, the effect of population density is difficult to be disentangled from that of population size and *vice versa* due to their strong inter-relationship (Amsalem & Hefetz 2011). Few studies have distinguished the distinct effects of animal population density and size on reproduction and determined whether population density and size interact and how their interactions will alter an animal's reproductive strategies.

Larger population size and higher density often result in lower reproductive performance because of the intense competition for resources and increasing behavioural interference (Estevez *et al*. 2007; Wong *et al*. 2013; Li & Zhang 2021). For example, the spider mite *Tetranychus urticae* Koch has lower fecundity in a larger group with a higher density (Li & Zhang 2021). However, when the population density remains constant, females of the same species in larger groups lay more eggs than those in the smaller ones (Le Goff *et al*. 2010). Similar findings are also reported in many other group-living species (Avilés & Turino 1998; Prokopy & Reynolds 1998; Estevez *et al*. 2007; Salomon & Lubin 2007; Lihoreau & Rivault 2008; Krams *et al*. 2009). This phenomenon may be attributed to the fact that group living helps access to food and mates, protect against predators, and increase available time for forage and feeding efficiency (Ranta *et al*. 1993; Dyer 2000; Mori & Saito 2006; Sato & Saito 2006; Estevez *et al*. 2007; Vanthournout *et al*. 2016). To date, how female animals adjust their fecundity in response to variations of both population size and density is still not clear.

Mothers can also alter their offspring sex ratio in response to social environments (Hamilton 1967; Trivers & Willard 1973; Taylor & Bulmer 1980; Charnov 1982; West *et al*. 2005; West 2009; Iritani *et al*. 2020). For example, when the population density is high where food resources are limited, mothers should skew the offspring sex ratio towards the dispersing sex to reduce resource competition among siblings or close relatives (Clark 1978; Silk 1983; Mari *et al*. 2008; Hjernquist *et al*. 2009; Visser *et al*. 2014; Song *et al*. 2016). However, when food resources are sufficient in a small population, mothers should favor a female-biased offspring sex ratio to reduce the competition for mates between sons (Hamilton 1967; Sato & Saito 2006; Macke *et al*. 2012, 2014). So far, empirical studies on sex allocation have focused on offspring sex ratio regulation in response to either the population size or density (Charnov 1982; West *et al*. 2005; West 2009), ignoring the impact of potential interactions and relative importance of the population size and density.

Spider mites (Acari: Tetranychidae) are a group of haplodiploid invertebrates where mated females produce both male and female offspring and virgin ones give birth to male offspring only (Oku 2010; Zhou *et al*. 2018). They live in groups of patchy habitats and may have developed strategies to maximize their fitness under different population sizes and densit. In the present study, we used the spider mite *Tetranychus ludeni* Zacher as a model species to investigate how ovipositing females adjust their fecundity and sex ratio in response to the variation of social environments. To distinguish the different effects of population density and size and their interaction, we carried out a series of factorial experiments by allowing both population size and density to vary and recorded the number of eggs laid and proportion of female offspring. Information generated from this study provides insights into the mechanisms behind adjustment of fecundity and sex ratio in response to the various social environments.

Materials and Methods

Mite colony

A breeding colony of *T. ludeni* was raised from adults collected on *Passiflora mollissima* (Kunth) in Palmerston North, New Zealand in September 2017, and reared on 3- to 5-week-old kidney bean plants (*Phaseolus vulgaris* L.). We maintained the colony on the bean plants in an aluminium-frame cage (30 cm length × 30 cm width × 65 cm height) covered with 200-mesh nylon gauze with a zip door (20 cm width × 55 cm height) at 25 ± 1°C and 40–50% RH with a photoperiod of 16:8 hours (light:dark). We carried out the experiment in a walk-in climate control room under the above environmental conditions and used the first expanded leaves of 1- to 2-week-old bean plants for experiments.

Experimental design and data collection

To test how population size and density affected the reproduction of *T. ludeni*, we conducted a factorial experiment by allowing both population size and density to vary at three levels, with nine treatments: three population sizes (1, 5 and 10 mated females) × three population densities (0.7, 1 and 2 mated females/cm^2), with 15–25 replicates for each treatment (Table 1). To obtain mated females, we randomly collected the quiescent female deutonymphs from the colony and individually introduced them onto a 1-cm^2 leaf square placed upside down on a wet cotton pad in a Petri dish (9.5 cm diameter × 1.0 cm height) with a mesh-sealed hole (1 cm diameter) in the middle of the lid. Before the female emerged (silvery in colour), we introduced a newly emerged male adult produced by a virgin female onto the arena. We removed the male immediately after copulation ended.

TABLE 1. A factorial design showing the leaf area, and population size and density for the experiment.

Leaf area (cm^2)	Population size (♀)	Population density (♀/cm^2)	Replicate (n)
1.5	1	0.7	25
1	1	1	19
0.5	1	2	24
7.5	5	0.7	25
5	5	1	22
2.5	5	2	16
15	10	0.7	18
10	10	1	17
5	10	2	21

For each replicate, we transferred mated female(s) (< 1 hour old) of a desired population size and density onto a leaf square of desired size (Table 1) in a Petri dish mentioned above and allowed them to lay eggs for 24 hours. We then transferred the mate females to a new leaf square of the same size once every 24 hours and the process was repeated until they died. We recorded the number of eggs laid on each leaf square. We allowed the larvae hatching from the resulting eggs to live on the same leaf square for five days and subsequently transferred them onto another fresh leaf square of the same size where they developed to adulthood. The sex of the resulting offspring was then recorded once the adults emerged. The mites start laying eggs about a day after mating (unpublished data). We only used data recorded during the first five days of oviposition period for analysis because of the death of many females beyond day 5 of oviposition, which would change the social environment.

Statistical analysis

We analysed the data using SAS software (SAS 9.4, SAS Institute Inc., Cary, NC). Rejection level of H_0 was set at $P < 0.05$. Data on the daily number of eggs laid and proportion of female offspring were not normally distributed (Shapiro-Wilk test, UNIVARIATE procedure), we thus analysed these data using a generalized linear mixed model (GLIMMIX Procedure), with population size (PS) and density (PD) and their interactions (PS×PD) as the fixed factors and female age as a random factor. We ran a two-factor model to test the effects of PS and PD first, and then a three-factor model to test whether the PS×PD changed the effects of PS and PD.

Results

Effect of social environments on fecundity

When we tested the effect of population size (PS) and density (PD) simultaneously, we found that the females laid significantly more eggs with increasing PS ($F_{1,843}$= 21.20, $P < 0.0001$) and significantly fewer eggs with increasing PD ($F_{1,843}$= 17.19, $P < 0.0001$) (Figure 1a). Our analysis of the impact of PS×PD interactions on fecundity shows that when PS and PD were low, mothers laid significantly more eggs with the increase of both PS and PD ($F_{1,842}$= 59.86, $P < 0.0001$ for PS; $F_{1,842}$ = 7.09, $P = 0.0079$ for PD), but when PS and PD were high, females produced significantly fewer eggs with the increase of both PS and PD ($F_{1,842}$ = 40.8, $P < 0.0001$) (Figure 1b).

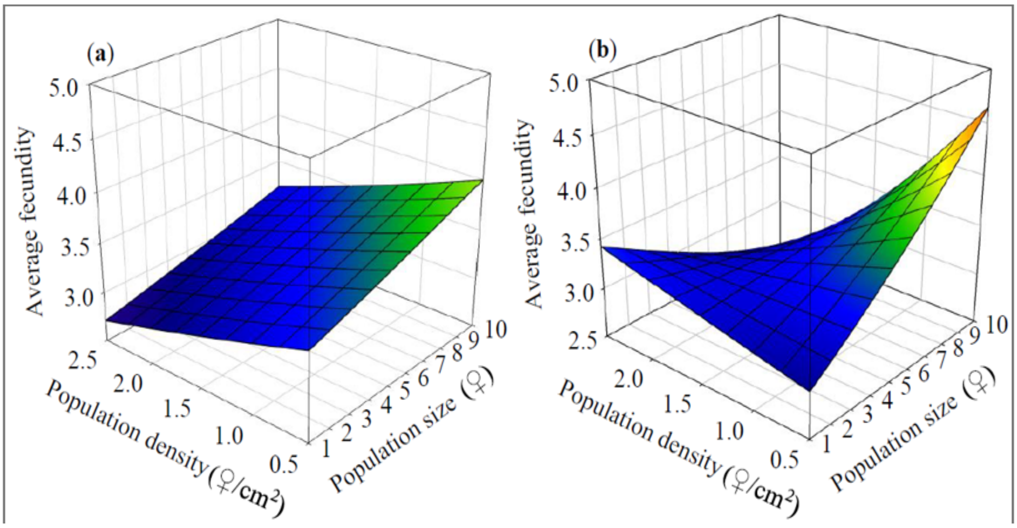

FIGURE 1. Effect of population size (PS, number of females per leaf square), density (PD, number of females/cm^2) and their interactions (PS×PD) on average fecundity of the first five days: (**a**) two-factor model, eggs = exp (1.2514 + 0.0189 PS - 0.1092 PD), and (**b**) three-factor model, eggs = exp (0.9737 + 0.0726 PS + 0.1181 PD - 0.0445 PS×PD).

Effect of social environments on sex allocation

Our results indicate that when only PS and PD were included in the two-factor model, increasing PS significantly reduced the proportion of female offspring produced ($F_{1,804}$= 14.40, $P = 0.0002$) but PD incurred no significant impact on sex allocation ($F_{1,804}$ = 1.94, $P = 0.1637$) (Figure 2a). In the three-factor model, we found that PS×PD interaction significantly increased the proportion of female offspring at higher PS and PD ($F_{1,803}$ = 10.61, $P = 0.0012$) but did not significantly alter the effects of PS and PD on sex allocation ($F_{1,803}$ = 20.80, $P < 0.0001$ for PS; $F_{1,803}$ = 3.57, $P = 0.0592$ for PD) (Figure 2b).

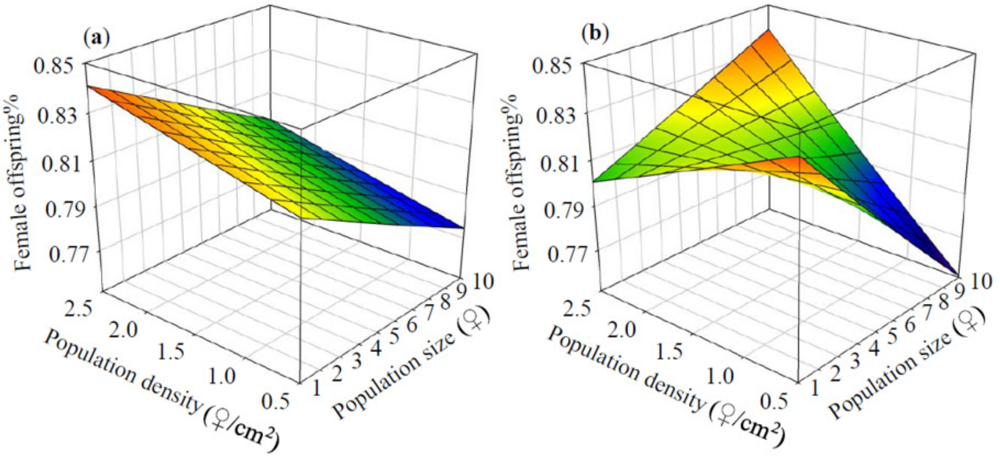

FIGURE 2. Effect of population size (PS, number of females per leaf square), density (PD, number of females/ cm^2) and their interactions (PS×PD) on average sex ratio of the first five days: (**a**) two-factor model, female offspring% = exp (- 0.2021 - 0.0061 PS + 0.0140 PD), and (**b**) three-factor model, female offspring% = exp (- 0.1449 - 0.0168 PS - 0.0331 PD + 0.0088 PS×PD).

Discussion

Animals are believed to have evolved strategies to maximise their reproductive fitness in varied social environments (Estevez *et al*. 2007; Iritani *et al*. 2020; Weerawansha *et al*. 2020; Ausband & Mitchell 2021; Li & Zhang 2021). Similar to other species (e.g., Wardhaugh & Didham 2005; Khan *et al*. 2018; Li & Zhang 2021), *T. ludeni* females reduced their fecundity with the increase of population density (Figure 1a) because individuals at crowded conditions usually have a higher level of behavioural interferences or aggressions (Estevez *et al*. 2007; Wong *et al*. 2013; Li & Zhang 2021) and intense food competition (Wertheim *et al*. 2005; Burant *et al*. 2020). Spider mite populations can grow rapidly due to short lifecycles and high fecundity (Shih *et al*. 1976; Tuan *et al*. 2016) but their exponential population growth can end abruptly due to overexploitation of the host plants (Krips *et al*. 1998). Therefore, fecundity reduction at dense environments may be a flexible strategy of *T. ludeni* females to reduce the intensity of food competition and minimise the possibility of local population extinction.

However, when population size increased, the fecundity significantly increased in *T. ludeni* (Figure 1a). This may be attributed to cooperative nature of spider mites, i.e., aggregating and constructing common silk webs under the leaves, which protect them and their offspring from environmental hazards (Davis 1952; McMurtry *et al*. 1970; Ashley 2003; Mori & Saito 2005; Le Goff *et al*. 2010). Therefore, group living may increase access to food and time for forage and feeding (Ranta *et al*. 1993; Dyer 2000; Mori & Saito 2006; Sato & Saito 2006; Estevez *et al*. 2007; Vanthournout *et al*. 2016), and in turn promote reproduction. Similarly, many studies also report that the presence of conspecific eggs may stimulate female reproduction, for example, in the tobacco budworm *Helicoverpa virescens* (F.) (Navasero & Ramaswamy 1993), cactus bug *Chelinidea vittiger aequoris* McAtee (Fletcher & Miller 2008), and white butterfly *Pieris napi* L. (Raitanen *et al*. 2014).

In the present study, we found a significant interaction between population density and size, which altered the reproductive behaviour of *T. ludeni* (Figure 1b). First, fecundity significantly increased with the increase of population size when the population density was low, or with the increase of population density when the population size was small. Second, fecundity significantly decreased in large and dense populations. These results have two implications: (1) cooperation enhances spider mite reproduction when the population size is small and the population density is low, where the benefits of cooperation exceed the costs of food competition among the ovipositing females; and (2) the costs of food competition outweigh the benefits of cooperation if the populations are large and dense. These findings suggest that group-living females of *T. ludeni* can determine whether they corporate in reproduction or compete for resources under different social environments.

Sex allocation is one of the main life history traits that manipulate resource competition in a local population (Hamilton 1967; Clark 1978; West *et al.* 2005; West 2009). We demonstrated that *T. ludeni* mothers favoured a female-biased offspring sex ratio in a small population (Figure 2a) or in a small population with low density (Figure 2b). These results agree to the theoretical prediction of local mate competition (Hamilton 1967) and empirical studies on spider mites (Sato & Saito 2006; Macke *et al.* 2012, 2014), i.e., when mothers oviposit in a small group where their sons compete for mates, they will produce more daughters, reducing the local mate competition.

However, the population density did not significantly affect offspring sex ratio regardless of whether its interaction with population size was accounted for analysis or not, while the significant positive effect of interaction resulted in an increase of female-biased sex ratio in large and dense populations (Figure 2). We suggest that the effect of population density on sex allocation in *T. ludeni* is intercorrelated with that of population size. In a large and dense population, *T. ludeni* females produce more daughters that will disperse from the dense environments to form new colonies, reducing the competition for food or space (Clark 1978; Silk 1983; Mari *et al.* 2008; Hjernquist *et al.* 2009; Visser *et al.* 2014; Song *et al.* 2016). In addition, the mechanism of sex allocation adjustment in *T. ludeni* may have shifted from reducing mate competition in small and sparse populations to reducing competition for food or space in large and dense populations. Therefore, treating population density and size as independent factors in statistical models may generate misleading conclusions.

In conclusion, the present study provides evidence that *T. ludeni* females can immediately manipulate their reproductive output and adjust offspring sex ratio in response to social environments during their early reproductive period. We reveal that ovipositing mothers may have cooperated in a large population with low density or in a small population with high density to increase their reproduction. However, mothers may reduce their reproduction in a large and dense population due to the intense food or space competition. Furthermore, mothers can increase production of daughters in small populations with low density and large populations with high density to minimise mate and food/space competition, respectively. We propose that including interaction of population size and density in the statistical model is essential to generate accurate conclusions of the impacts of social environments on animal reproductive adjustments.

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