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Article

Effect of foundress population density and size on reproduction and population growth of a haplodiploid mite

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Abstract

Tetranychus ludeni Zacher (Acari: Tetranychidae) is an invasive polyphagous haplodiploid pest mite of many vegetable crops in many parts of the world. This study investigated the effects of simultaneous variations in the local foundress population density and size on the reproduction and population growth of *T. ludeni*. We show that negative population-density and -size dependency limited the reproduction of foundresses, where the effects of population size on population growth overweighed that of population density. We further demonstrate that ovipositing females could accelerate population growth rate (intrinsic rate of increase, r_m) at higher population sizes by producing more daughters early during their lifespan, which can be an adaptive strategy to allow more daughters to complete development and disperse to reduce future food competition intensity. This study provided knowledge on population dynamics in response to foundress population density and size in general and *T. ludeni* population forecast and precise timing of pest management in particular.

Key words: *Tetranychus ludeni*, daughter production, disperse, resource competition, life table parameter

Introduction

The ability of organisms to increase their populations is crucial to their establishment in a new habitat especially for the invasive species. Local foundress population density and size are two important socio-environmental factors that regulate reproduction and population growth (Kunin 1997a; Danko *et al*. 2018). The former represents a function of spacing between neighbouring individuals in a finite area and the latter is the number of individuals in a local population (Kunin 1997a). In nature, resources are unevenly partitioned among individuals, and this inequality increases when resources become scarce with increasing population density and size (Krebs 1971; Łomnicki 1978; Rodenhouse *et al*. 1997; Leips & Travis 1999; Creighton 2005; Goubault *et al*. 2007). Therefore, it is fundamentally important to understand the nature and extent of population regulation by density- and size-dependent processes in population ecology (Levins 1979; Newton 1994, 1998; Ferrer & Donazar 1996; Rodenhouse *et al*. 1997; Penteriani *et al*. 2003).

It is widely reported that population growth is a decreasing function of population density (Harrison & Cappuccino 1995; Turchin 1995; Sibly *et al*. 2005), inducing a negative density-dependent reproduction associated with present and/or past population densities (Adler & Levins 1994; Sinervo *et al*. 2000; Rotem & Agrawal 2003; Meylan *et al*. 2007; Allen *et al*. 2008; Creighton 2005; Leips *et al*. 2009). The negative density-dependent reproduction could arise either through decreasing territory quality and resource scarcity which limit the individuals to low provisioning rates at high population densities (Andrewartha & Birch 1954; Pulliam & Danielson 1991; Dhondt *et al*. 1992; Ferrer & Donazar 1996; Rodenhouse *et al*. 1997; Both 1998; Kruger & Lindstrom 2001; Danko *et al*. 2018), or by adjusting the reproductive behaviours of individuals as a response to the varying density within the same habitat (Lack 1954; Both 1998; Fernandez *et al*. 1998). In a similar fashion the size of a population may also affect its dynamics, especially when conspecifics compete for resources (Krebs 1971; Rodenhouse *et al*. 1997; Leips & Travis 1999; Creighton 2005; Goubault *et al*. 2007) and when there is direct interference among individuals (Post *et al*. 1997). However, most studies on density-dependent reproduction are based on the relationship between the mean reproduction and population density (see Sinclair 1989), without knowing whether density is the only cause of such a relationship or the extent to which individuals respond to the varying density (Kempenaers & Dhondt 1992; Both 1998). It is necessary to understand the role of population size in reproduction (Harris 1984; Saunders *et al*. 1991) or whether and how population size could mediate density-dependent reproduction.

Nevertheless, the effect of varying population size on population growth has received less attention. This may be because the different notions of population density and size are often highly intercorrelated in most natural populations (Gaston 1994; Saether *et al*. 2002; Sibly *et al*. 2005) and are hard to be differentiated (Kunin 1997a). In practice, population density is sometimes used in place of population size when population size is low (Saether *et al*. 2002; Sibly *et al*. 2005) and the negative effects of population size are often considered as the results of the density-dependent regulatory process mediated by negative reactions between population density and growth (Murdoch 1994; Turchin 1999). However, local population density and size may have different effects on population dynamics (reviewed in Kareiva 1983; Kunin 1997b). Therefore, ignoring the role of local population size in population regulation may magnify the impact of local population density. Few studies have quantitatively examined how reproduction or population growth is related to the variations of animal population density and size (Saether *et al*. 2002, 2016), probably because the spacing between individuals constantly shifts as individuals are mobile (Kunin 1997a). To date, little is known about whether population density and size interact and regulate population dynamics in the same way and whether individuals will adjust their reproductive strategies in response to variations of these two factors.

In this study, we used *Tetranychus ludeni* Zacher (Acari: Tetranychidae) as the model species to investigate how foundress population density and size affected the reproductive performance and population growth by altering the population size of a given population density and *vice versa*. *T. ludeni* is an invasive haplodiploid spider mite native to Europe and now globally distributed (Bolland *et al*. 1998). It attacks many vegetable crops in the world (Bolland *et al*. 1998; Zhang 2003; Adango *et al*. 2006; Gotoh *et al*. 2015). The mite has a short life cycle (10 days at 27–28°C) (Moros & Aponte 1994; Da Silva 2002; Adango *et al*. 2006), long longevity (up to 28 days) and high reproductive potential (up to 112 eggs) (Adango *et al*. 2006). Tetranychid females usually mate at emergence and then disperse to establish new colonies with a female-biased sex ratio (Carey & Bradley 1982; Macke *et al*. 2011). These life history characteristics may encourage the outbreaks of mite populations in the fields or greenhouses.

Based on the knowledge outlined above, we designed a factorial experiment by altering the population density for each test population size and *vice versa*, and tested two hypotheses: (1) ovipositing females make earlier reproductive effort at high population densities and sizes, and (2) ovipositing females have higher reproductive output and population growth at low population densities and sizes. We recorded daily oviposition patterns and lifetime fecundity and daughter production at various population densities and sizes and computed life table parameters. Information generated in this study will contribute to knowledge on population dynamics in response to foundress population density and size in general and *T. ludeni* population forecast and management in particular.

Materials and Methods

Mite colony

A laboratory colony of *T. ludeni* was initiated 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.) (Zhou *et al*. 2018). We started our colony by transferring about 2,000 individuals from the initial colony onto 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). The colony was maintained, and experiments were carried out in a walk-in climate control room at 25 ± 1°C and 40–50% RH with a photoperiod of 16:8 hrs (L:D).

Experimental design and data collection

We set up nine treatments of three population sizes (1, 5 and 10 ovipositing females per leaf square) and three foundress population densities (0.7, 1 and 2 ovipositing females/cm^2), with 15–25 replicates for each treatment. To achieve the required population densities for the experiment, we altered the leaf area while keeping one of the three population size levels constant (Figure 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 on wet cotton in a Petri dish (9.5 cm diameter and 1.0 cm height) with a mesh-sealed hole (1 cm diameter) in the middle of the lid. Before the quiescent female deutonymph emerged (silvery in colour), we introduced a newly emerged male produced by a virgin female onto the arena and we removed the male immediately after mating terminated. For each replicate, we transferred mated female(s) of a desired density onto a test leaf square in a Petri dish mentioned above, allowed them to lay eggs for 24 hours. We then transferred them to a new leaf square of the same size once every 24 hours until their death. The number of eggs laid on each leaf square was recorded under a stereomicroscope (Leica MZ12, Germany). The larvae and nymphs were allowed to feed on the same leaf square for five days, after which time they were transferred onto another clean fresh leaf square of the same size where they developed to adults. The number of emerged daughters was also recorded.

The life table parameters (Jervis *et al*. 2005) were calculated for each treatment by using the above data on daily survival and reproduction of foundresses. The intrinsic rate of increase (r_m, daughters/foundress/day) was estimated by solving the Lotka-Euler equation, $\sum e^{-r_m x} l_x m_x = 1$, where x is the pivotal age, l_x is the proportion of the foundresses surviving to age x, and m_x is the number of daughters produced per foundress at age x. The pivotal age $x = x_0 + x_i$, where x_i is the age of ovipositing adults and x_0 the developmental time from egg to adulthood ranging from 10.3 to 11.5 days. Other life table parameters included the net reproductive rate ($R_0 = \sum l_x m_x$, daughters/foundress/generation), mean generation time [$T = \log_e(R_0)/r_m$, days], and doubling time [$Dt = \log_e(2)/r_m$, days]. For each treatment, a jackknife method (Caswell 2001) was used to estimate the life table parameters for each foundress and their means (± SE) for each treatment were calculated (Table S1).

Statistical analysis

All data were analysed using SAS software (SAS 9.4, SAS Institute Inc., Cary, NC). Rejection level of H_0 was set at $P < 0.05$. For each treatment, an asymptotic exponential model (Archontoulis & Miguez 2015) was applied to fit the daily cumulative number of eggs and daughters produced (y) (Figures 2 and 3):

$$y = a/\{1+\exp[-b(x-x_0)]\}, \quad \text{eq. 1}$$

where a is the maximum y value, x_0 is the inflection point at which the instantaneous growth rate is maximized, b is the constant growth rate of the curve. We developed a nonlinear regression model to fit data of daily number of eggs and daughters produced (y) (Figures 2 and 3):

$$y = a/\{1+[(x-x_0)/b]^2\}, \quad \text{eq. 2}$$

where a is the maximum y at age x_0, b is a constant rate controlling the width of the peak. For each model, the estimated parameters were compared between treatments according to the 95% confidence limits (CL), i.e., if the 95% CL overlapped, then there was no significant difference between treatments (Tables S2 and S3). NLIN Procedure was used for modelling.

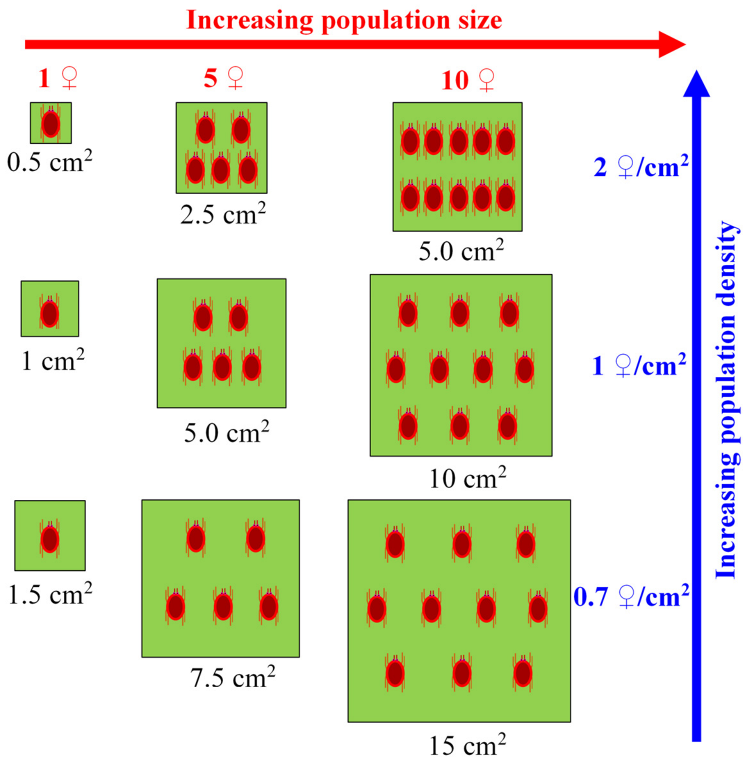

FIGURE 1. A diagram of factorial experimental design showing the population densities and sizes.

The life table parameters (y) were analysed by a generalized linear mixed model (GLIMMIX Procedure), with foundress population density and size and their interaction as fixed factors and replicate as a random factor (Figure 4):

$y = \exp(a + b\ \mathrm{PD} + c\ \mathrm{PS} + d\ \mathrm{PD}\times\mathrm{PS})$, eq. 3

where a is the intercept, and b, c and d are the estimated constants of population density (PD) and size (PS) and their interaction (PD×PS), respectively. To minimise the potential effect of decreasing population density and size with the progress of experiment, data recorded within 15 days of foundress lifespan were used for analyses in this study because > 85% of lifetime eggs were laid during this period.

Results

We detected a negative density-dependent production of eggs and daughters (a in eq. 1) at higher foundress population sizes of 5 and 10 but not at the low population size of one foundress (Figures 2 and 3, Table S2). However, the number of eggs and daughters accumulated significantly faster at high population sizes of 5 and 10 than at the population size of only one foundress (b in eq. 1), except at the highest population density and size (Figures 2 and 3, Table S2). The daily number of eggs and daughters produced peaked significantly earlier (< 6 days) at high population sizes of 5 and 10 than that (7.4–8.5 days) at the population size of only one foundress regardless of local population densities (x_0 in eq. 2), with a greater (a in eq. 2) and sharper peak (b in eq. 2) except at the highest population density and size (Figures 2 and 3, Table S3).

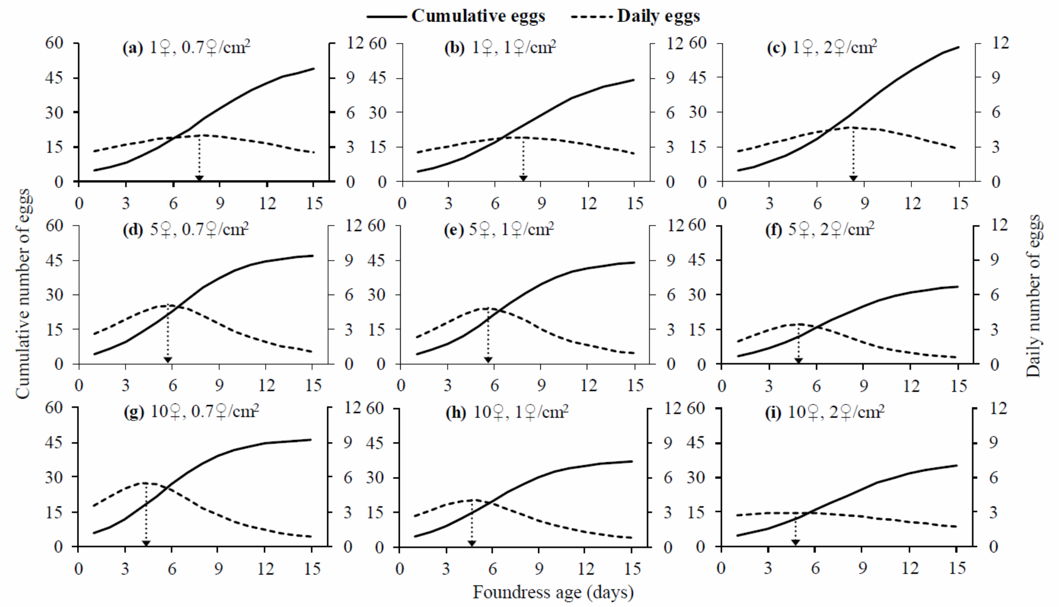

FIGURE 2. Cumulative and daily number of eggs laid by a foundress at different population densities (0.7, 1 and 2 ♀/cm^2) and sizes (1, 5 and 10 ♀). Cumulative number of eggs: $y = a/\{1+\exp[-b(x-x_0)]\}$; daily number of eggs: $y = a/\{1+[(x-x_0)/b]^2\}$. The arrows indicate the timing of peaks of eggs laid. The estimated parameters of models are listed in Tables S2 and S3.

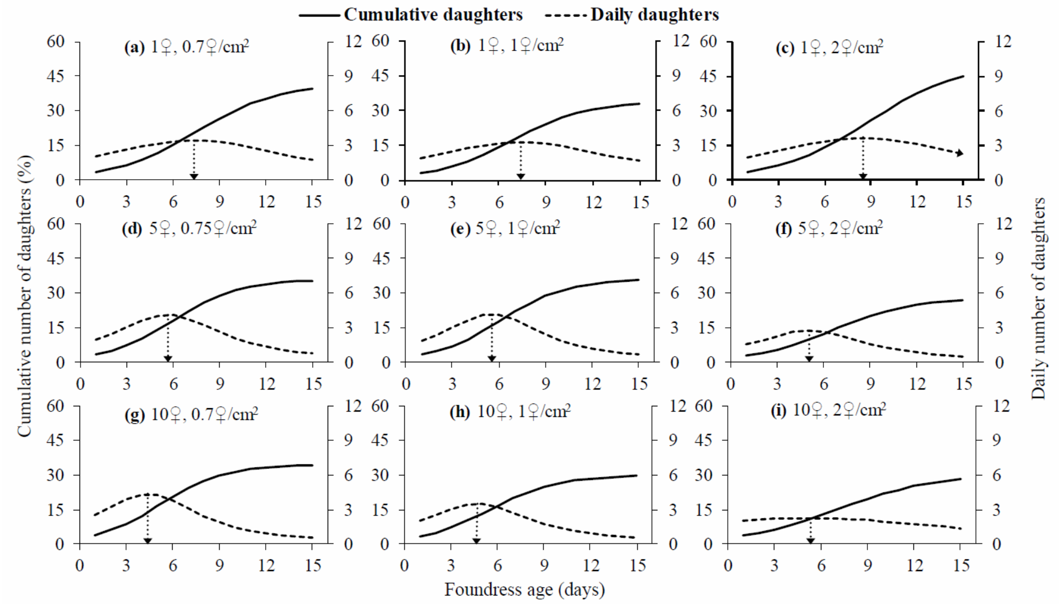

FIGURE 3. Cumulative and daily number of daughters produced by a foundress at different population densities (0.7, 1 and 2 ♀/cm^2) and sizes (1, 5 and 10 ♀). Cumulative number of daughters: $y = a/\{1+\exp[-b(x-x_0)]\}$; daily number of daughters: $y = a/\{1+[(x-x_0)/b]^2\}$. The arrows indicate the timing of peaks of daughters produced. The estimated parameters of models are listed in Tables S2 and S3.

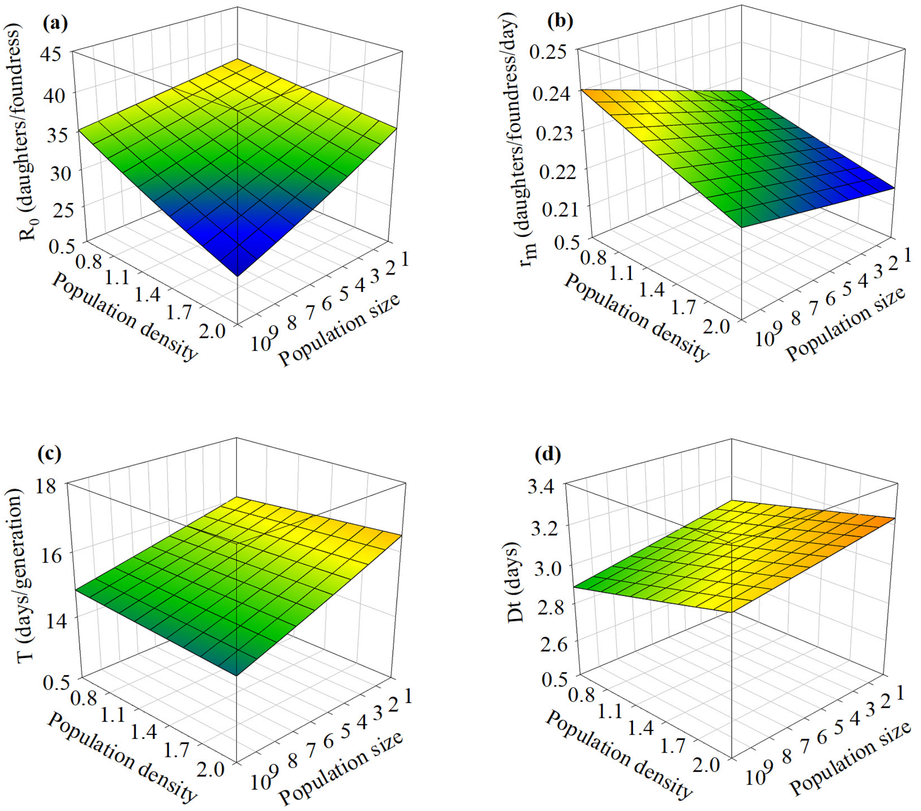

FIGURE 4. Effects of foundress population density (number of foundresses/cm^2) and population size (number of foundresses per leaf square) on life table parameters: (**a**) net reproductive rate (R_0), (**b**) intrinsic rate of increase (r_m), (**c**) generation time (T), and (**d**) doubling time (Dt). The estimated parameters of models are listed in Table S4.

Population density and size had no significant independent effect on the net reproductive rate (R_0) but their significant negative interaction resulted in a decrease of R_0 when both population density and size increased (Figure 4a, Table S4). Increase in population density caused a significant decrease of intrinsic rate of increase (r_m) whereas increasing population size incurred a significant increase of r_m (Figure 4b, Table S4). In contrast, increasing population density significantly prolonged the mean generation time (T) and doubling time (Dt) whereas increasing population size shortened these two parameters (Figure 4c–d, Table S4).

Discussion

In the present study, *T. ludeni* exhibited negative impacts of foundress population density and size on reproduction; however, the negative density-dependent reproduction was detected at higher population sizes of 5 and 10 foundresses but not at the low population size of one foundress, and foundresses at higher population sizes maximised their reproduction significantly faster and earlier during their lifespan, regardless of their local densities (Figures 2, 3 and 4a, Tables S2 and S3). The results have three implications. First, spider mites feed upon plant leaves by piercing cells and sucking cell contents, which will induce white or yellow spots or 'stipplings' and reduce the photosynthetic surface (Dhooria 2016). The overexploitation associated with quick cumulative excrement on host plants at high population densities may reduce the food availability and quality and thus offspring fitness. Furthermore, spider mites show scramble resource competition with a fast resource depletion when population density or size is high (Krips *et al.* 1998). Therefore, a decrease of reproduction under the elevated resource competition conditions can be considered as an adaptive strategy of ovipositing foundresses (De Roissart *et al.* 2016) to reduce the food resource competition of offspring with their mothers or among the offspring (Bonduriansky & Head 2007).

Second, the life history theory assumes that natural selection on organisms enables them to evolve optimal strategies, including the timing of reproduction and number of offspring produced, to maximize or optimize the reproductive fitness by allocating resources to a range of different demands throughout the lifespan (Stearns 1992; Roff 2002). A previous study reports that virgin females adjusted their resource allocations to yield larger sons that could produce more daughters at a higher rate, suggesting that *T. ludeni* has evolved the resource allocation strategy to compensate the loss of producing daughters for females at virgin stage through their sons' production of more daughters in the next generation (Zhou *et al.* 2018). Our results provide further evidence that foundresses maximising fecundity and producing more daughters during the early lifespan at higher population densities and sizes (Figures 2 and 3, Tables S2 and S3) could be a fitness advantage, as production of more daughters early enables more dispersing individuals to complete development, reducing future food competition intensity and elevating population growth (Osakabe *et al.* 2008; Yano 2008; Le Goff *et al.* 2010; Azandémè-Hounmalon *et al.* 2014).

Third, population density and size are usually intercorrelated in a population (Gaston 1994; Saether *et al.* 2002; Sibly *et al.* 2005) but are hard to be differentiated (Kunin 1997a). Previous studies have demonstrated the individual adjustment of reproductive behaviours in response to the varying density within a habitat (Lack 1954; Both 1998; Fernandez *et al.* 1998) rather than to the varying population size. In the present study, we differentiated the functions of population density and size and revealed that foundress population density and size interacted and affected the population dynamics in the same way (Figure 4a, Table S4); however, the negative density-dependent reproduction and early onset of reproductive peak occurred only when the population size was high. The results suggest that: (1) the individual adjustment of reproductive behaviours results from the increasing intensity of conspecific competition for resources (Krebs 1971; Rodenhouse *et al.* 1997; Leips & Travis 1999; Creighton 2005; Goubault *et al.* 2007) and direct interference among individuals (Post *et al.* 1997) at higher population sizes, and (2) the population size regulates population-density dependency and individual adjustment. Therefore, population size may have overweighed population density as a major socio-environmental factor regulating future population dynamics in *T. ludeni*.

The life table of a species summarises the life history characteristics such as survival, development, time of reproduction, and fecundity or female offspring production of individuals in a population (Jervis *et al.* 2005), reflecting the potential or capacity of population growth. Previous studies reveal that population density is a decreasing function of per capita growth (Harrison & Cappuccino 1995; Turchin 1995; Rotem & Agrawal 2003). We found that the simultaneous increase of population density and size reduced the net reproductive rate (R_0) (Figure 4a). According to the mathematical equations for life table parameter calculation (Jervis *et al.* 2005), decreasing net reproductive rate (R_0) will result in a smaller intrinsic rate of natural increase (r_m) and longer doubling time (Dt). However, our results only partially agreed with the notion because r_m was higher and Dt was shorter at lower population densities and higher population sizes (Figure 4b and d). These may be attributed to the faster rates of cumulative egg and daughter production and early onset of reproductive peak at higher population sizes (Figures 2 and 3, Tables S2 and S3). The higher r_m reduced the Dt, and higher r_m with relatively small R_0 shortened the mean generation time (T) (Figure 3c; Jervis *et al.* 2005).

In conclusion, results of this study demonstrate that: (1) both negative population density- and size-dependence may limit *T. ludeni* reproduction but the effect of population size overweighed that of population density, and (2) ovipositing females are capable to accelerate population growth at higher population sizes through producing more daughters early during their lifespan. Our findings that the population grows faster at low population densities and high population sizes could be used to forecast the future population size and decide the timing of pest control.

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References

Adango, E., Onzo, A., Hanna, R., Atachi, P. & James, B. (2006) Comparative demography of the spider mite, *Tetranychus ludeni*, on two host plants in West Africa. *Journal of Insect Science*, 6, 49.
https://doi.org/10.1673/031.006.4901

Adler, G.H. & Levins, R. (1994) The island syndrome in rodent populations. *Quarterly Review of Biology*, 69, 473–490.
https://doi.org/10.1086/418744

Allen, R.M., Buckley, Y.M. & Marshall, D.J. (2008) Offspring size plasticity in response to intraspecific competition: An adaptive maternal effect across life-history stages. *American Naturalist*, 171, 225–237.
https://doi.org/10.1086/524952

Andrewartha, H.G. & Birch, I.C. (1954) *The distribution and abundance of animals*. University of Chicago Press, Chicago.

Archontoulis, S.V. & Miguez, F.E. (2015) Nonlinear regression models and applications in agricultural research. *Agronomy Journal*, 107, 786–798.
https://doi.org/10.2134/agronj2012.0506

Azandémè-Hounmalon, G.Y., Fellous, S., Kreiter, S., Fiaboe, K.K.M., Subramanian, S., Kungu, M. & Martin, T. (2014) Dispersal behavior of *Tetranychus evansi* and *T. urticae* on tomato at several spatial scales and densities: implications for integrated pest management. *PLoS ONE*, 9(4), e95071.
https://doi.org/10.1371/journal.pone.0095071

Bolland, H.R., Gutierrez, J. & Flechtmann, C.H. (1998) World catalogue of the spider mite family (Acari: Tetranychidae). *Leiden, Brill.*
https://hdl.handle.net/11245/1.143245

Bonduriansky, R. & Head, M. (2007) Maternal and paternal condition effects on offspring phenotype in *Telostylinus angusticollis* (Diptera: Neriidae). *Evololution Biology*, 20, 2379–2388.
https://doi.org/10.1111/j.1420-9101.2007.01419.x

Both, C. (1998) Density dependence of clutch size: habitat heterogeneity or individual adjustment? *Journal of Animal Ecology*, 67, 659–666.
https://doi.org/10.1046/j.1365-2656.1998.00227.x

Carey, J.R. & Bradley, J.W. (1982) Developmental rates, vital schedules, sex ratios and life table for *Tetranychus urticae*, *T. turkestani* and *T. pacificus*. *Acarologia*, 23(4), 333–345.

Caswell, H. (2001) *Matrix population models: construction, analysis, and interpretation, 2nd edition*. Sunderland, Massachusetts, Sinauer Associates, 722 pp.

Creighton, J.C. (2005) Population density, body size, and phenotypic plasticity of brood size in a burying beetle. *Behavioural Ecology*, 16, 1031–1036.
https://doi.org/10.1093/beheco/ari084

Danko, A., Schaible, R., Pijanowska, J. & Danko, M.J. (2018) Population density shapes patterns of survival and reproduction in *Eleutheria dichotoma* (Hydrozoa: Anthoathecata). *Marine Biology*, 165(3), 48.
https://doi.org/10.1007/s00227-018-3309-z

Da Silva, C.A.D. (2002) Biology and thermal requirement of *Tetranychus ludeni* Zacher on cotton leaves. *Pesquisa Agropecuária Brasileira*, 37, 573–580.
https://doi.org/10.1590/S0100-204X2002000500001

De Roissart, A., Wybouw, N., Renault, D., Van Leeuwen, T. & Bonte, D. (2016) Life-history evolution in response to changes in metapopulation structure in an arthropod herbivore. *Functional Ecology*, 30, 1408–1417.
https://doi.org/10.1111/1365-2435.12612

Dhondt, A.A., Kempenaers, B. & Adriaensen, F. (1992) Density-dependent clutch size caused by habitat heterogeneity. *Journal of Animal Ecology*, 61, 643–648.
https://doi.org/10.2307/5619

Dhooria, M.S. (2016) *Fundamentals of applied acarology*. Singapore, Springer, 470 pp.

Fernandez, C., Azkona, P. & Donázar, J.A. (1998) Density-dependent effects on productivity in the Griffon Vulture *Gyps fulvus*: the role of interference and habitat heterogeneity. *Ibis*, 140, 64–69.
https://doi.org/10.1111/j.1474-919X.1998.tb04542.x

Ferrer, M. & Donazar, J.A. (1996) Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. *Ecology*, 77, 69–74.
https://doi.org/10.2307/2265655

Gaston, K.J. (1994) *Rarity*. London, Chapman and Hall, 224 pp.

Gotoh, T., Moriya, D. & Nachman, G. (2015) Development and reproduction of five *Tetranychus* species (Acari: Tetranychidae): do they all have the potential to become major pests? *Experimental and Applied Acarology*, 66, 453–479.
https://doi.org/10.1007/s10493-015-9919-y

Goubault, M., Mack, A.F.S. & Hardy, I.C.W. (2007) Encountering competitors reduces clutch size and increases offspring size in a parasitoid with female-female fighting. *Proceedings of the Royal Society B*: *Biological Sciences*, 274, 2571–2577.
https://doi.org/10.1098/rspb.2007.0867

Harris, L. (1984) *The fragmented forest: Island biogeographic theory and the preservation of biotic diversity*. Chicago, University of Chicago Press, 230 pp.

Harrison, S. & Cappuccino, N. (1995) Using density-manipulation experiments to study population regulation. *In*: Cappuccino, N. & Price, P. (Eds.), *Population dynamics: new approaches and synthesis*. San Diego, CA, Academic Press, pp 131–147.

Caswell, H. (2001) *Matrix population models: construction, analysis, and interpretation, 2nd edition*. Sinauer Associates, Sunderland, Massachusetts, pp. 63–160.

Kareiva, P. (1983) Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. *In*: Denno, R.F. & McClure, M.S. (Eds.), *Variable plants and herbivores in natural and managed systems*. Inc., New York, Academic Press, pp. 259–289.

Kempenaers, B. & Dhondt, A.A. (1992) Experimental test of an hypothesis explaining density-dependent clutch-size in tits *Parus* spp. *Ibis*, 134, 192–194.
https://doi.org/10.1111/j.1474-919X.1992.tb08397.x

Krebs, J.R. (1971) Territory and breeding density in the Great Tit, *Parus major* L. *Ecology*, 52, 2–22.
https://doi.org/10.2307/1934734

Krips, O.E., Witul, A., Willems, P.E.L. & Dicke, M. (1998) Intrinsic rate of population increase of the spider mite *Tetranychus urticae* on the ornamental crop gerbera: intraspecific variation in host plant and herbivore. *Entomologia Experimentalis et Applicata*, 89, 159–168.
https://doi.org/10.1046/j.1570-7458.1998.00395.x

Kruger, O. & Lindström, J. (2001) Habitat heterogeneity affects population growth in goshawk *Accipiter gentilis. Journal of Animal Ecology*, 70, 173–181.
https://doi.org/10.1111/j.1365-2656.2001.00481.x

Kunin, W.E. (1997a) Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *Journal of Ecology*, 85(2), 225–234.
https://doi.org/10.2307/2960653

Kunin, W.E. (1997b) Population biology and rarity: on the complexity of density-dependence in insect-plant interactions. *In*: Kunin, W.E. & Gaston, K.J. (Eds.), *The biology of rarity: causes and consequences of* *rare-common differences*. London, Chapman & Hall, pp. 150–173.

Lack, D. (1954) *The natural regulation of animal numbers*. New York, Oxford University Press, 343 pp.

Le Goff, G.J., Mailleux, A.C., Detrain, C., Deneubourg, J.L., Clotuche, G. & Hance T. (2010) Group effect on fertility, survival and silk production in the web spinner *Tetranychus urticae* (Acari: Tetranychidae) during colony foundation. *Behaviour*, 147, 1169–1184.
https://doi.org/10.1163/000579510X510980

Leips, J. & Travis, J. (1999) The comparative expression of life-history traits and its relationship to the numerical dynamics of four populations of the least killifish. *Journal of Animal Ecology*, 68, 595–616.
https://doi.org/10.1046/j.1365-2656.1999.00311.x

Leips, J., Richardson, J.M.L., Rodd, F.H. & Travis, J. (2009) Adaptive maternal adjustments of offspring size in response to conspecific density in two populations of the least killifish, *Heterandria formosa*. *Evolution*, 63, 1341–1347.
https://doi.org/10.1111/j.1558-5646.2009.00631.x

Levins, R. (1979) Coexistence in a variable environment. *American Naturalist*, 114, 765–783.
https://doi.org/10.1086/283527

Łomnicki, A. (1978) Individual differences between animals and natural regulation of their numbers. *Journal of Animal Ecology*, 47, 461–475.
https://doi.org/10.2307/3794

Macke, E., Magalhães, S., Bach, F. & Olivieri, I. (2011) Experimental evolution of reduced sex ratio adjustment under local mate competition. *Science*, 334, 1127–1129.
https://doi.org/10.1126/science.1212177

Meylan, S., Clobert, J. & Sinervo, B. (2007) Adaptive significance of maternal induction of density-dependent phenotypes. *Oikos*, 116, 650–661.
https://doi.org/10.1111/j.0030-1299.2007.15432.x

Moros, C.M. & Aponte, L.O. (1994) Biology and life table of *Tetranychus ludeni* Zacher on black bean *Phaseolus vulgaris* L. *Agronomia Tropical*, 44, 667–677.
https://doi.org/10.1590/S1984-46702009000100007

Murdoch, W.W. (1994) Population regulation in theory and practice. *Ecology*, 75, 271–287.
https://doi.org/10.2307/1939533

Newton, I. (1994) Experiments on the limitation of bird breeding densities: a review. *Ibis*, 136, 397–411.
https://doi.org/10.1111/j.1469-185X.1992.tb01017.x

Newton, I. (1998) *Population limitation in birds*. London, Academic Press, 597 pp.

Osakabe, M.H., Isobe, H., Kasai, A., Masuda, R. & Kubota, S. (2008) Aerodynamic advantages of upside-down take-off for aerial dispersal in *Tetranychus* spider mites. *Experimental and Applied Acarology*, 44, 165–183.
https://doi.org/10.1007/s10493-008-9141-2

Penteriani, V., Balbontin, J. & Ferrer, M. (2003) Simultaneous effects of age and territory quality on fecundity in Bonelli's eagle *Hieraaetus fasciatus*. *Ibis*, 145, e77–e82.
https://doi.org/10.1046/j.1474-919X.2003.00159.x

Post, J.R., Johannes, M.R.S. & Mcqueen, D.J. (1997) Evidence of density-dependent cohort splitting in age-0 yellow perch, *Perca flavescens*: potential behavioural mechanisms and population-level consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 867–875.
https://doi.org/10.1139/f96-335

Pulliam, H.R. & Danielson, B.J. (1991) Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist*, 137, 50–66.
https://doi.org/10.1086/285139

Rodenhouse, N.L., Sherry, T.W. & Holmes, R.T. (1997) Site-dependent regulation of population size: a new synthesis. *Ecology*, 78, 2025–2042.
https://doi.org/10.2307/2265942

Roff, D. (2002) *Life history evolution*. Sunderland, Massachusetts, Sinauer Associates, 527 pp.

Rotem, K.A. & Agrawal, A.A. (2003) Density dependent population growth of the two-spotted spider mite, *Tetranychus urticae*, on the host plant *Leonurus cardiaca*. *Oikos*, 103, 559–565.
https://doi.org/10.1034/j.1600-0706.2003.12531.x

Saether, B.-E., Engen, S. & Matthysen, E. (2002) Demographic characteristics and population dynamical patterns of solitary birds. *Science*, 295, 2070–2073.
https://doi.org/10.1126/science.1068766

Saether, B.-E., Visser, M.E., Groten, V., & Engen, S. (2016) Evidence for r- and K-selection in a wild bird population: A reciprocal link between ecology and evolution. *Proceedings of the Royal Society of London. Series B*: *Biological Sciences*, 283, 20152411.
https://doi.org/10.1098/rspb.2015.2411

Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, 5, 18–32.
https://doi.org/10.1111/j.1523-1739.1991.tb00384.x

Sibly, R.M., Barker, D., Denham, M.C., Hone, J. & Pagel, M. (2005) On the regulation of populations of mammals, birds, fish and insects. *Science*, 309, 607–610.
https://doi.org/10.1126/science.1110760

Sinclair, A.R.E. (1989) Population regulation in animals. *In*: Cherrett, J.M. (Eds.), *Ecological concepts: the contribution of ecology to an understanding of the natural world*. Oxford, UK, Blackwell Science, pp. 197–241.

Sinervo, B., Svensson, E. & Comendant, T. (2000) Density cycles and an offspring quantity and quality game driven by natural selection. *Nature*, 406, 985–988.
https://doi.org/10.1038/35023149

Stearns, S.C. (1992) *The evolution of life histories*. Oxford, Oxford University Press, xii + 249 pp.

Turchin, P. (1995) Population regulation: old arguments and a new synthesis. *In*: Cappuccino, P. & Price, P. (Eds.), *Population dynamics: new approaches and synthesis*. San Diego, CA, Academic Press, pp. 19–40.

Turchin, P. (1999) Population regulation: a synthetic view. *Oikos*, 84, 153–159.
https://doi.org/10.2307/3546876

Yano, S. (2008) Collective and solitary behaviors of two-spotted spider mite (Acari: Tetranychidae) are induced by trail following. *Annals of the Entomological Society of America*, 101(1), 247–252.
https://doi.org/10.1603/0013-8746(2008)101[247:CASBOT]2.0.CO;2

Zhang, Z-Q. (2003) *Mites of greenhouses: identification, biology and control.* Cambridge, UK, CABI publishing, 244 pp.

Zhou, P., He, X.Z. & Wang, Q. (2018) Sons from virgin mothers produce more daughters in a haplodiploid mite. *Systematic & Applied Acarology*, 23(9), 1869–1878.
https://doi.org/10.11158/saa.23.9.13

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TABLE S1. The estimated mean (± SE) lifetable parameters at different foundress population densities and sizes.

Parameter	Population density	Population size (♀)		
	(♀/cm^2)	1	5	10
R$_0$	0.7	45.16 ± 0.13	37.73 ± 0.08	36.99 ± 0.05
	1	29.36 ± 0.18	35.94 ± 0.10	31.14 ± 0.11
	2	42.12 ± 0.15	24.66 ± 0.09	33.74 ± 0.06
r$_m$	0.7	0.2274 ± 0.0008	0.2309 ± 0.0000	0.2408 ± 0.0000
	1	0.2091 ± 0.0007	0.2305 ± 0.0000	0.2303 ± 0.0000
	2	0.2208 ± 0.0000	0.2085 ± 0.0007	0.2210 ± 0.0000
T	0.7	16.76 ± 0.05	15.72 ± 0.01	15.00 ± 0.01
	1	16.16 ± 0.04	15.54 ± 0.01	14.93 ± 0.01
	2	16.94 ± 0.01	15.38 ± 0.04	15.92 ± 0.01
D$_t$	0.7	3.0485 ± 0.0110	3.0014 ± 0.0003	2.8788 ± 0.0002
	1	3.3149 ± 0.0108	3.0067 ± 0.0003	3.0099 ± 0.0005
	2	3.1394 ± 0.0004	3.3260 ± 0.0117	3.1365 ± 0.0003

TABLE S2. Statistical results of modelling of cumulative eggs and daughters produced over foundress' age at different population densities and sizes.

Size (n)	Density (♀/cm^2)	a	b	x_0	R^2	df	F	P
Cumulative eggs (Figure 2)								
1	0.7	52.74 b	0.35 b	7.81 ab	0.9064	3,347	1120.36	< 0.0001
	1	47.93 bc	0.34 b	7.75 ab	0.8436	3,179	321.73	< 0.0001
	2	65.79 a	0.33 b	8.83 a	0.9557	3,332	238.90	< 0.0001
5	0.7	47.73 bc	0.44 a	6.15 c	0.9513	3,369	2401.88	< 0.0001
	1	44.79 c	0.44 a	6.25 c	0.9477	3,345	2085.73	< 0.0001
	2	34.44 d	0.40 a	6.49 bc	0.8754	3,328	768.20	< 0.0001
10	0.7	46.59 bc	0.46 a	5.34 d	0.9784	3,342	5155.51	< 0.0001
	1	37.65 cd	0.42 a	5.71 cd	0.9303	3,294	1307.84	< 0.0001
	2	37.31 cd	0.34 b	6.93 bc	0.9756	3,311	4143.32	< 0.0001
Cumulative daughters (Figure 3)								
1	0.7	42.08 ab	0.38 ab	7.57 ab	0.8897	3,347	933.17	< 0.0001
	1	34.05 cd	0.42 ab	6.79 bc	0.8155	3,179	263.94	< 0.0001
	2	51.02 a	0.33 b	8.90 a	0.9456	3,331	1719.76	< 0.0001
5	0.7	35.93 c	0.47 a	5.99 cd	0.9366	3,369	1817.54	< 0.0001
	1	36.14 bc	0.46 a	6.13 c	0.9355	3,345	1658.99	< 0.0001
	2	27.76 d	0.40 ab	6.61 bc	0.8683	3,328	921.03	< 0.0001
10	0.7	34.61 c	0.48 a	5.24 d	0.9759	3,342	4608.25	< 0.0001
	1	29.98 d	0.45 a	5.55 cd	0.9232	3,294	1178.58	< 0.0001
	2	30.57 d	0.32 b	7.18 bc	0.9690	3,311	3251.40	< 0.0001

For each category, the increase rates of cumulation (*a*) with the same letter are not significantly difference ($P < 0.05$). Cumulative number: $y = a/\{1+\exp[-b(x-x_0)]\}$, where *a* is the maximum *y* value, x_0 is the inflection point at which the instantaneous growth rate is maximum, *b* is the constant growth rate.

TABLE S3. Statistical results of modelling of daily number of eggs and daughters produced over foundress' age at different population densities and sizes.

Size (n)	**Density (♀/cm^2)**	**a**	**x_0**	**b**	**R^2**	**df**	**F**	**P**
Daily eggs (Figure 2)								
1 ♀	0.7	3.96 cd	7.67 a	9.44 a	0.6614	3,356	231.82	< 0.0001
	1	3.80 cd	7.85 a	9.65 a	0.6297	3,187	106.00	< 0.0001
	2	4.64 bc	8.37 a	8.31 a	0.7588	3,314	357.53	< 0.0001
5 ♀	0.7	5.11 ab	5.74 b	4.78 b	0.8699	3,369	822.27	< 0.0001
	1	4.83 b	5.60 b	4.44 b	0.8448	3,352	638.91	< 0.0001
	2	3.44 de	4.91 c	4.48 b	0.7156	3,343	287.62	< 0.0001
10 ♀	0.7	5.50 a	4.38 c	4.51 b	0.8890	3,342	912.72	< 0.0001
	1	4.05 cd	4.64 c	5.03 b	0.8327	3,297	492.83	< 0.0001
	2	2.92 e	4.75 c	12.02 a	0.8117	3,312	448.33	< 0.0001
Daily daughters (Figure 3)								
1 ♀	0.7	3.45 c	7.36 a	7.69 a	0.6379	3,356	209.03	< 0.0001
	1	3.27 cd	7.41 a	7.58 a	0.6025	3,187	94.47	< 0.0001
	2	3.67 bc	8.49 a	8.14 a	0.7448	3,314	337.75	< 0.0001
5 ♀	0.7	4.08 ab	5.66 b	4.38 b	0.8422	3,369	656.44	< 0.0001
	1	4.14 ab	5.53 b	4.06 b	0.8229	3,352	545.13	< 0.0001
	2	2.71 d	5.09 bc	4.61 b	0.7144	3,343	286.01	< 0.0001
10 ♀	0.7	4.37 a	4.42 c	4.00 b	0.8796	3,342	833.04	< 0.0001
	1	3.49 c	4.67 c	4.39 b	0.8054	3,297	409.81	< 0.0001
	2	2.27 e	5.36 bc	12.06 a	0.8204	3,312	475.20	< 0.0001

For each category, the estimated timings of oviposition peak (x_0) with the same letter are not significantly difference ($P < 0.05$). Daily number of daughters: $y = a/\{1+[(x-x_0)/b]^2\}$, where a is the maximum y at age x_0, b is a constant rate (slope) controlling the steepness of the peak.

TABLE S4. Statistical results of modelling of life table parameters depending on foundress population density and size.

Parameter	Variable	Estimate	SE	$F_{(1,174)}$	P
R_0	Intercept	3.6552	0.0341		
	Density	- 0.0273	0.0249	1.20	0.2743
	Size	0.0005	0.0053	0.01	0.9202
	Density×Size	- 0.0172	0.0039	19.18	< 0.0001
r_m	Intercept	- 1.4763	0.0075		
	Density	- 0.0333	0.0055	37.01	< 0.0001
	Size	0.0074	0.0012	39.47	< 0.0001
	Density×Size	- 0.0014	0.0009	2.70	0.1021
T	Intercept	2.7764	0.0050		
	Density	0.0202	0.0037	30.71	< 0.0001
	Size	- 0.0072	0.0008	84.86	< 0.0001
	Density×Size	- 0.0034	0.0006	34.52	< 0.0001
D_t	Intercept	1.1092	0.0077		
	Density	0.0343	0.0056	37.19	< 0.0001
	Size	- 0.0074	0.0012	37.46	< 0.0001
	Density×Size	0.0014	0.0009	2.59	0.1093

Parameter = exp(a + b PD + c PS + d PD×PS), a is the intercept, and b, c and d are the estimated constants of population density (PD) and size (PS) and their interaction (PD×PS), respectively.