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Article

Resource relocations in relation to dispersal in *Tetranychus ludeni* Zacher

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Abstract

Life history strategies of a species may affect its invasion success. Here, we used a haplodiploid pest, *Tetranychus ludeni* Zacher (Acari: Tetranychidae), which is native to Europe but now cosmopolitan, to investigate its life history strategies in relation to its dispersal tendency and distance. We tested whether and how dispersal influenced survival, lifetime fecundity, age-specific reproduction, and life table parameters of mated females. We show that mated females did not trade off their survival and lifetime reproductive output with dispersal but adjusted their resource allocations during different reproductive stages depending on whether and how far they dispersed. Long-distance dispersers invested more in dispersal in their early life while resident mites and short-distance dispersers invested more in reproduction during their early life. These resource allocation strategies may allow long-distance dispersers to explore the novel environment more effectively without compromising lifetime reproductive fitness, contributing to the invasion success of *T. ludeni*.

Key words: dispersers, fecundity, longevity, dispersal distance, resource allocation, spider mite

Introduction

Biological invasions have become more frequent in the recent decades due to the increase of international trade and travel, causing significant economic losses worldwide. Following introduction of exotic species to a new habitat by man, their dispersal plays a crucial role in population expansion (Clobert *et al.* 2009). Because dispersers' life history traits such as fecundity and survival can affect their population establishment at the invasion front and subsequent expansion (Duckworth & Badyaev 2007; Renault *et al.* 2018; Williams *et al.* 2019), understanding the reproductive performance of dispersers can provide knowledge for prediction and management of invasion risks.

Compared with residents, dispersers often have lower fecundity and higher mortality (Mole & Zera 1993; Bonte *et al.* 2012; Khuhro *et al.* 2014; Renault 2020; Nasu & Tokuda 2021), leading to slower population growth (Baguette & Schtickzelle 2006; Keenan & Cornell 2021). In addition, the cost of dispersal may increase with the distance a species moves, resulting in distance-specific resource trade-offs (Rousset & Gandon 2002; Baker & Rao 2004; Samietz & Köhler 2012; Serrano & Tella 2012), the magnitude of which can affect expansion speed. For example, dispersers in some species may allocate less resource to reproduction at their early life to facilitate dispersal (Roff 1984; Roff & Fairbairn 1991; Tanaka 1993; Innocent *et al.* 2010). Therefore, examining age-specific reproduction helps better understand the cost of dispersal and resource allocation strategies of dispersers.

Tetranychus ludeni Zacher (Acari: Tetranychidae) is a spider mite from Europe but has now invaded all continents except Antarctica (Bolland *et al.* 1998; CABI 2020), providing an opportunity to study the underlying mechanisms of its invasion success. It attacks over 300 plant species, including economically important crops such as bean, papaya, guava, eggplant, pumpkin, and apple (Bolland *et al.* 1998; Zhang 2003; Migeon *et al.* 2010). In spider mites, females usually disperse after mating (Mitchell 1973), especially when the population is crowded or when food is insufficient or poor in quality (Mcenroe 1969; Bitume *et al.* 2013). Although its flexible reproductive strategies (Zhou *et al.* 2018, 2021) and good adaptation to external environment (Zhang 2003; Gotoh *et al.* 2015; Ristyadi *et al.* 2019, 2021) may have helped *T. ludeni* establish in novel habitats, it is still unknown whether dispersers adjust their reproductive strategies to facilitate invasion success.

In the present study, we examined whether dispersal tendency and distance affected reproductive output, survival, age-specific reproduction, and life table parameters in *T. ludeni*. We allowed mites to disperse along a dispersal system, sampled residents and dispersers, followed up their daily reproduction and survival, and calculated their life table parameters. We hypothesized that compared with residents, dispersers should have lower lifetime fecundity, shorter longevity, and slower population growth.

Materials and Methods

Mite colony and experimental conditions

We collected *T. ludeni* adults on *Passiflora mollissima* Kunth (Malpighiales: Passifloraceae) in Palmerston North, New Zealand, and started and maintained the colony using 3- to 5-week-old common bean plants *Phaseolus vulgaris* L. (Fabales: Fabaceae) grown in pots. We used the first expanded leaves cut from 1- to 2-week-old plants grown in pots for all experiments. The colony was kept, and experiments carried out under environmental conditions of 25 ± 1 ºC, 40 ± 10% RH and 14:10 h (light:dark) photoperiod.

Preparation of mated females for experiments

To prepare male adults for mating, we transferred 50 female deutonymphs randomly selected from the colony onto a clean fresh leaf square (4 × 4 cm) on wet cotton wool in a Petri dish (9 cm in diameter × 1 cm in height) and allowed them to develop to virgin adult females and lay unfertilised eggs for three days. We then removed those adult females and allowed the eggs to develop to virgin male adults. We prepared three such dishes. We used 1- to 3-day-old virgin adult males to mate with females prepared below.

We randomly selected 50 adult females from the colony and transferred them onto a clean fresh leaf square (4 × 4 cm) on wet cotton wool in a Petri dish for egg laying for 24 hours. We then removed the female adults and allowed eggs to develop to the quiescent deutonymphal stage. We set up a total of 10 such dishes. We introduced 15–20 virgin males prepared above to female deutonymphs in each dish and allowed them to stay with the newly emerged females for 5 h, ensuring all females mated at or soon after emergence. We transferred 50 newly emerged (< 24 hours old), mated females from the above dishes onto a new leaf square (4 × 4 cm) in a dish. We prepared a total of 10 such leaf squares. We used 3-d-old, mated females for experiments because females of this age were most likely to disperse (unpublished data).

Experimental setup and data collection

We set up a dispersal system consisting of an array of 21 leaf squares (2 cm × 2 cm for the first leaf square and 2 cm × 1 cm for the rest) (Figure 1) placed on wet cotton wool in a tray (45 cm in length × 36 cm in width × 1.5 cm in height). To facilitate analysis of mite dispersal distance and subsequent reproductive fitness, we divided the array into three sections for data collection: (1)

resident leaf square (R)—the first leaf square where we released the mites; (2) median distance of dispersal (M)—leaf squares 2–11, and (3) long distance of dispersal (L)—leaf squares 12–21.

We transferred 50 3-d-old, mated females onto R leaf square and allowed them to settle for 40 minutes, after which time, all leaf squares were connected by Parafilm bridges (4.5 cm in length × 1.5 cm in width; Parafilm®, USA). Twenty-four hours after bridge connection, we sampled mites on R, M, and L leaf squares. We repeated the above procedure eight times. We sampled a total of 15, 20, and 13 mites from sections R, M, and L, respectively, for measurement of reproductive fitness in relation to dispersal distance: 15 mites from the 1st leaf square for section R; 1, 2, 3, 5, 6, 1 and 2 mites from the 2nd, 4th, 6th, 7th, 8th, 9th and 11th leaf squares, respectively, for section M, and 1, 2, 1, 5, 2, 1, and 1 mites from the 12th 13th, 15th, 16th, 17th, 19th and 21st leaf squares, respectively, for section L. We individually transferred sampled mites onto new leaf squares (1 × 1 cm) placed on wet cotton wool in Petri dishes, replaced leaf squares once every 24 hours until the mites died, and recorded their longevity. We counted the number of eggs laid on each leaf square, allowed them to develop to adult stage on the same leaf squares and recorded the number and sex of newly emerged adults.

Statistical analysis

We analyzed all data using SAS software (SAS 9.4, SAS Institute Inc., Cary, NC). To estimate how dispersal affected population growth, we calculated the life table parameters (Jervis *et al.* 2005) using the data on daily survival and daughter production of each female. The intrinsic rate of natural increase (r) was calculated by solving the Lotka-Euler equation: $\sum e^{-rx} l_x m_x = 1$, where x is the pivotal age, l_x is the proportion of females surviving to age x, and m_x is the number of daughters produced per female at age x. We also calculated the net reproductive rate ($R_0 = \sum l_x m_x$, daughters/female/generation), doubling time [$D_t = \log_e(2)/r$, days], and generation time [$T = \log_e(R_0)/r$, days]. We used the bootstrap method (Huang & Chi 2012; Yu *et al.* 2013) with 50,000 bootstrap samples to calculate the pseudo-values of a given parameter and employed the paired-bootstrap test (Efron & Tibshirani 1993; Mou *et al.* 2015; Reddy & Chi 2015) for multiple comparisons between any two dispersal distances (TTEST Procedure). The significance was determined according to the 95% t-based confidence limits (95% CLs), i.e., if 95% CLs > 0 or < 0, the mean difference between the two dispersal distances is significantly different ($P < 0.05$).

Data distribution was tested using Shapiro-Wilk test (UNIVARIATE Procedure). Data on female longevity were normally distributed and analyzed using ANOVA with Tukey test for multiple comparison (GLM procedure). Data on the number of eggs laid were not normally distributed and thus analyzed with non-parametric ANOVA followed by Bonferroni test for multiple comparison (GLM procedure).

We modified a Gaussian functional model (Archontoulis & Miguez 2015) to fit the daily number of eggs and daughters with two reproductive peaks: $y = p_1 * \exp\{-0.5*[(x - x_1)/w_1]^2\} + p_2 * \exp\{-0.5*[(x - x_2)/w_2]^2\}$, where p_1 and p_2 are the maximum y value of the first and second peaks, respectively; w_1 and w_2 are coefficients controlling the width of the first and second peaks, respectively; and x_1 (= 4) and x_2 are the age of mites at first and second peaks, respectively. We compared reproductive parameters of mites sampled in different sections (R, M, and L) and p_1 and p_2 within each section according to Julious (2004): if the 83.4% CLs do not overlap, then there is a significant difference.

Results

Resident (R) and dispersed females (M and L) laid similar number of eggs in their lifetime ($F_{2,45} = 1.06$, $P = 0.3566$) and had similar longevity ($F_{2,45} = 1.68$, $P = 0.1987$) (Figure 2). However, life table parameters changed with the distance females dispersed (Table 1): (1) the longer the dispersal distances were, the lower net reproductive rate (R_0) and intrinsic rate of increase (r) occurred, and (2) the opposite was the case for the generation time (T) and doubling time (D_t).

TABLE 1. The estimated mean (± SE) life table parameters at different dispersal distances in *T. ludeni*.

Distance	R_0	r	T	D_t
R	18.31 ± 0.30 a	0.1789 ± 0.0010 a	16.25 ± 0.06 c	3.88 ± 0.02 c
M	17.35 ± 0.18 b	0.1628 ± 0.0010 b	17.16 ± 0.08 b	4.17 ± 0.03 b
L	13.16 ± 0.36 c	0.1453 ± 0.0017 c	17.71 ± 0.09 a	4.78 ± 0.06 a
CLs $_{\text{(R vs M)}}$	0.2701~1.6599	0.0097~0.0154	-1.1138~-0.7141	-0.3623~-0.2264
CLs $_{\text{(R vs L)}}$	4.2272~6.0751	0.0295~0.0375	-1.6854~-1.2398	-1.0271~-0.7751
CLs $_{\text{(M vs L)}}$	3.4022~4.9701	0.0170~0.0249	-0.7897~-0.3076	-0.7336~-0.4799

Estimated values in columns followed by different letters are significantly different ($P < 0.05$). For each parameter, 95% CLs > 0 or < 0 indicates a significant difference between dispersal distances ($P < 0.05$).

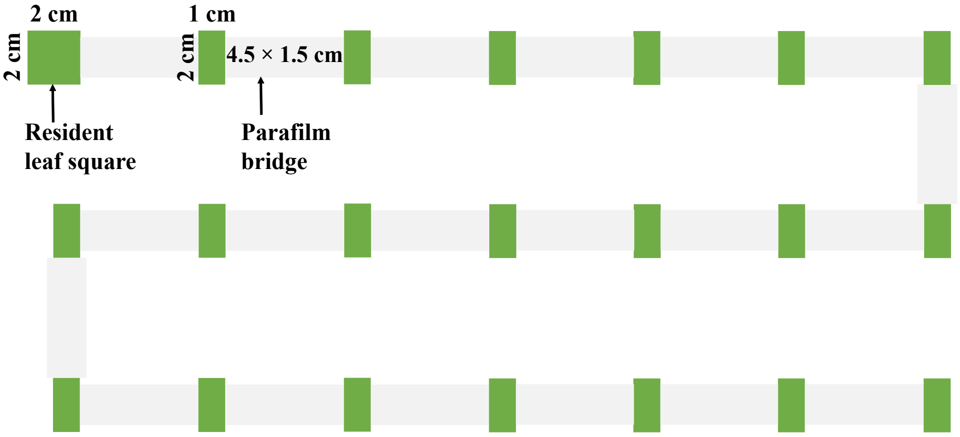

FIGURE 1. Dispersal system for experiments. The resident leaf square was used to introduce experimental mites. Parafilm bridges were placed on the top of leaf squares with approximately 1 mm overlapping to reduce the influence of water between leaf squares and bridges on mite dispersal.

Daily number of eggs and daughters produced had two peaks of similar shape regardless of dispersal distance, with one occurring immediately after their transfer to new leaf squares and the other taking place 5–7 days after their transfer (Figure 3). The first peak of daily fecundity and daughter production was significantly lower in L females than in R and M females (non-overlapping 83.4% CLs). The first peak was significantly higher than the second one in R and M females (non-overlapping 83.4% CLs) but the two peaks had similar height in L females (overlapping 83.4% CLs) (Figure 3).

Discussion

Theoretically, dispersal has energetic and survival costs (Bonte *et al.* 2012; Travis *et al.* 2012; Weigang & Kisdi 2015), often resulting in lower fecundity and higher mortality. However, our current study shows that females had similar lifetime fecundity and longevity regardless of whether and how far they dispersed (Figure 2). It is thus suggested that mated females may not trade off their lifetime fecundity and survival with dispersal in *T. ludeni*. There is also no evidence for trade-off between dispersal and fecundity in a damselfly (Therry *et al.* 2015). We argue that the lack of such trade-offs may contribute to invasion success observed in *T. ludeni* (Zhou *et al.* 2021).

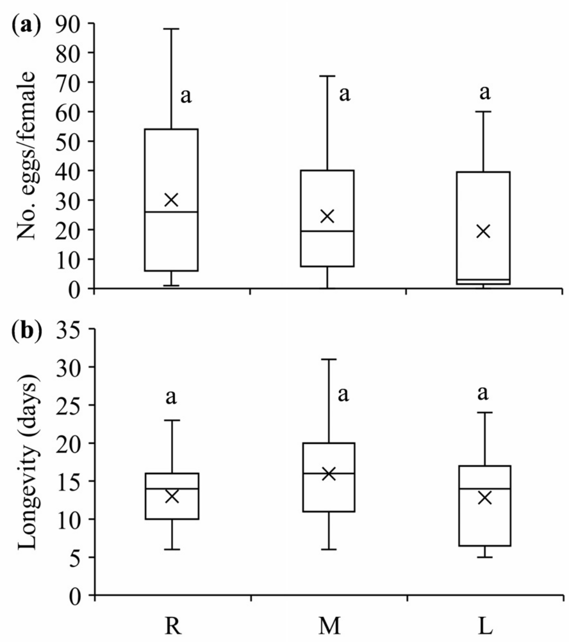

FIGURE 2. The total mean number of eggs laid per female (**a**) and longevity (**b**) of resident (R) and dispersed females (M and L) in *T. ludeni*. Each box plot shows the mean (×), median line, the upper and lower quartiles (the range where 25% of scores fall above and 25% fall below the median), and maximum '⊤' and minimum '⊥' scores. Boxes with the same letters are not significantly different ($P > 0.05$).

Our results indicate that dispersal tendency and distance had significant effects on life table parameters (Table 1). For example, dispersal significantly reduced the net reproductive rate (R_0) and intrinsic rate of increase (r) and increased the generation time (T) and doubling time (D_t). These findings suggest that the mites adjust their resource allocation to reproduction and movement depending on whether and how far they intend to disperse. In another word, although dispersed and resident mites had similar lifetime fecundity, dispersed mites spread their resources for reproduction in a wider range, prolonging generation time and population doubling time (Weerawansha *et al.* 2020). Similar phenomenon has also been reported in butterflies *Proclossiana eunomia* Esper, *Boloria aquilonaris* Stichel, *Euphydryas editha bayensis* Sternitsky, *E. aurinia* Rottemburg, and *Lopinga achine* Scopoli (Lepidoptera: Nymphalidae) (Baguette & Schtickzelle 2006).

As shown in Figure 3, mated *T. ludeni* females had two reproductive episodes in terms of daily number of eggs and daughters produced regardless of dispersal distance. However, females that dispersed a long distance (L) laid fewer eggs and produced fewer daughters than those that did not disperse (R) or only dispersed a median distance (M) during the first episode. These findings strongly suggest that L females allocate more resources for dispersal and reduce investment in reproduction in their early life (Zera & Denno 1997; Bonte *et al.* 2012). This kind of resource relocation has also been reported in other invertebrates (Roff 1984; Roff & Fairbairn 1991; Tanaka 1993). For example, in a haplodiploid insect *Melittobia australica* Girault (Hymenoptera: Eulophidae), dispersers have fewer number of eggs developed at emergence and produce fewer eggs in their first clutch than residents (Innocent *et al.* 2010).

When we compared the two reproductive peaks within mites that dispersed similar distances, we found that the second peaks in R and M females were significantly lower than the first ones while the two peaks had similar height in L females (Figure 3). Our results further suggest that in their early life R and M females invest more resources in reproduction than in dispersal while L females allocate more resources to dispersal than to reproduction. This strategy may allow L females to explore the novel environment more effectively and help invasion success (Sol *et al.* 2012; Sol & Maspons 2016) without compromising lifetime reproductive fitness.

In summary, we show that mated *T. ludeni* females do not trade off dispersal with their lifetime reproductive output and survival. Rather, they adjust their resource allocation depending on whether and how far they disperse, with long-distance dispersers investing more in dispersal in their early life while resident mites and short-distance dispersers investing more in reproduction in their early life. These strategies may facilitate invasion success of *T. ludeni*.

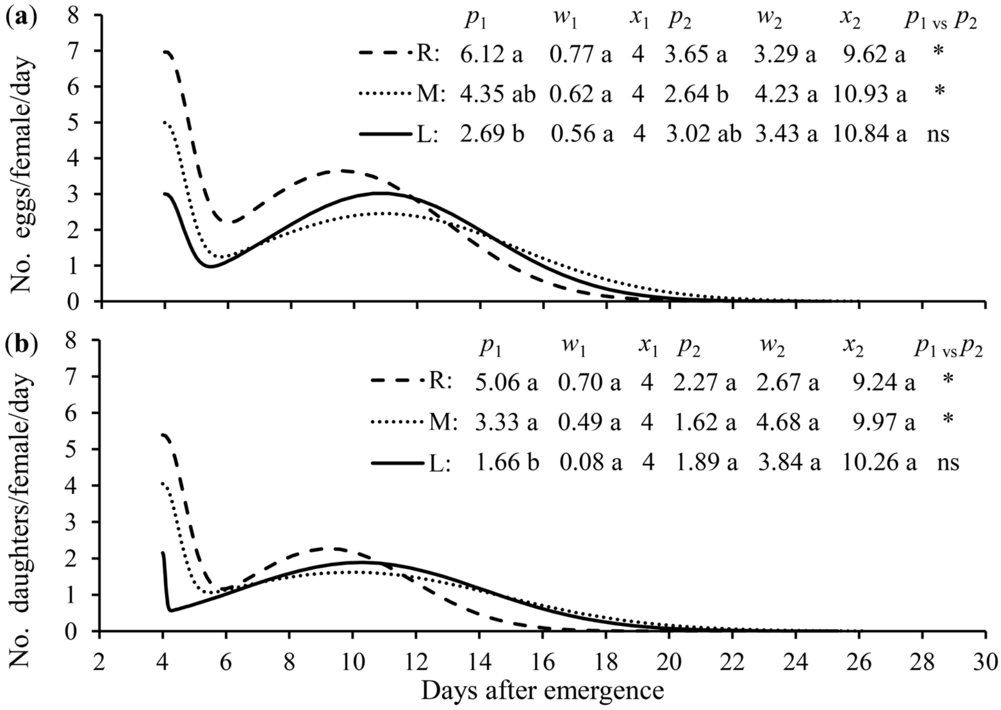

FIGURE 3. The estimated patterns of daily number of eggs (**a**) and daughters (**b**) produced by resident (R) and dispersed females (M and L) of *T. ludeni*. Raw data were fitted to the two-peak model for each parameter. Parameters with the same letters in column are not significantly different (overlapping 83.4% CLs, $P > 0.05$) between R, M, and L. '$p_{1\ \mathrm{vs}}\,p_2$' is the comparison in peak height between the first and second peaks within each line, where * indicates significantly different and 'ns' not significantly different.

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