

Resource allocation strategies for survival and reproduction by an invasive pest in response to intermittent fasting

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Abstract

Intermittent fasting (IF) is a type of dietary restriction that involves fasting periods in intervals, which has been used as a strategy to improve health and extend longevity. Regular fasting is common during the process of biological invasions in nature. Yet, it is not clear how invasive animals adjust their resource allocations to survival and reproduction when periodical starvation occurs. Here, we used *Tetranychus ludeni*, a haplodiploid spider mite and an important invasive pest of horticultural crops around the world, to investigate the effects of IF on its life history strategies. We show that IF increased the longevity in females but not in males probably because of differences in resource storage, metabolic rate, and mating cost between sexes. In response to IF, females traded off fecundity and egg size but not the number of daughters for longevity gain, suggesting that *T. ludeni* females can adjust their life history strategies for population survival and growth during invasion process. Eggs produced by fasted females realized the same hatch rate and resultant young had the same survival rate as those by unfasted ones. In addition, IF had transgenerational maternal effects which prolonged offspring development period. We suggest that the longer immature developmental period can increase the body size of resulting adults, compensating egg size loss for offspring fitness. Our findings provide insight into resource allocations as responses to fasting, knowledge of which can be used for evaluation of pest invasions and for management of animal survival and reproduction by dietary regulations.

Key words: Acari, fasting, longevity, offspring performance, reproduction, Tetranychidae

Intermittent fasting is a type of dietary restriction that involves fasting periods in intervals (Catterson et al. 2018; Chambers 2019; Gunnars 2020). It may reduce oxidative damage by maintaining redox balance or elevating antioxidants (Angelier et al. 2015; Ensminger et al. 2021). As a result, it may benefit overall health and longevity of animals (Anson et al. 2003; Brandhorst et al. 2015; Lee and Longo 2016). So far, dietary restriction is probably the most reproducible and effective method to regulate aging and increase healthy lifespan in many species (Gribble et al. 2014; Lee and Longo 2016; Wang et al. 2017; Liang et al. 2018). However, effects of intermittent fasting on animal fitness may not always be consistent (Cerqueira et al. 2011; Dorighello et al. 2014; Longo and Mattson 2014). For instance, it extends the lifespan of mice if starting at the younger age but not at older age (Goodrick et al. 1990), prolongs the female longevity in a spider mite when practiced during the adult stage (Li and Zhang 2019), but shortens the female longevity in a predatory mite (Gotoh and Tsuchiya 2009). Furthermore, dietary restriction may also have transgenerational effects (Mautz et al. 2020; Dimofski et al. 2021; Ivimey-Cook et al. 2021).

The longevity discrepancy in response to fasting may be attributed to different reproductive modes (Li and Zhang 2019) and trade-offs among reproduction, growth, and somatic maintenance (Merry 2002; Kirkwood 2005) in different taxa. Under limited pool of energy available, organisms may change their resource allocation strategies to maintain the balance between different fitness functions such as activity, body size, reproduction, and survival (Stearns 1992; Bancroft and Margolies 1996; Martin et al. 2007). However, previous work on the effect of intermittent fasting focuses more on lifespan and less on reproduction (Li and Zhang 2019). Furthermore, most investigations use animals with sexual reproduction as study models, such as fruit flies, worms, and mice (Nakagawa et al. 2012). It is thus important to understand how the trade-offs between reproduction and other fitness functions occur in non-model organisms in response to dietary restriction (Gladyshev 2016; Li and Zhang 2019). Haplodiploid animals could be good models for investigating such trade-offs because both virgin and mated females can reproduce where the former give birth to haploid sons and the latter produce both diploid daughters and haploid sons (de la Filia et al. 2015; Lohse and Ross 2015).

Tetranychus ludeni Zacher (Acari: Tetranychidae) is a haplodiploid spider mite from Europe but has now invaded all continents except Antarctic (Migeon et al. 2010; CABI/EPPO 2011). It infests more than 300 plant species in 60 families, including many economically important crops such as bean, papaya, guava, eggplant, pumpkin, and apple (Bolland et al. 1998; Zhang 2003). Previous studies suggest that its invasion success may be facilitated by its flexible reproductive strategies (Zhou et al. 2020, 2021) and good adaptation to external environment (Zhang 2003; Gotoh et al. 2015; Ristyadi et al. 2019, 2021). Like many other invasive animals (Zhang et al. 2019; Papach et al. 2020), *T. ludeni* may encounter intermittent food shortages when senescence of their host plants occurs, food availability fluctuates or when they are carried by wind or transportation to new habitats. To date, little is known about how periodical food shortages affect life history traits in *T. ludeni* and whether this species has developed strategies for invasion success in response to periodical starvation.

In the present study, we investigated how intermittent fasting influenced both males and females in *T. ludeni*. We set up a series of intermittent fasting regimes during the adult stage and recorded their longevity, reproductive outputs, and offspring fitness. Based on the theoretical and empirical framework outlined above, we predict that intermittent fasting may have sex- and mating status-specific effects on *T. ludeni*, and such effects may be transgenerational. Our findings provide new insights into how these mites adjust their resource allocation strategies under different intermittent fasting conditions. This work also generates important knowledge for evaluation of their population dynamics under food stress environment during different invasion stages and information for management of animal survival and reproduction by dietary regulations.

Material and Methods

Breeding colony and experimental mite preparation

We established a breeding colony of *T. ludeni* from the field-collected adults on *Passiflora mollissima* (Kunth) (Malpighiales: Passifloraceae) in Palmerston North, New Zealand. We reared the colony on about 20 potted kidney bean plants (*Phaseolus vulgaris* L.), in the Massey University Entomology and IPM Laboratory, Palmerston North, New Zealand. We replaced 10 oldest plants with new ones fortnightly and transferred mites from the old plants to the new ones by cutting the leaves of old plants and placing them on the top of new ones. The mite colony was maintained, and experiments carried out at $25 \pm 1^\circ\text{C}$ temperature and 50–70% RH with a photoperiod of 16L:8D hours.

We randomly collected female deutonymphs from the colony and introduced them onto 10 fresh bean leaf squares (3 cm \times 3 cm, 30 individuals per leaf square), each being placed on a water-saturated cotton pad in a Petri dish (5.5 cm diameter \times 1.0 cm height). We allowed them to develop to virgin adult females for experiment. To obtain virgin adult males for experiment, we randomly collected 20 newly emerged virgin females prepared above, placed them on a leaf square (3 cm \times 3 cm), and allowed them to lay eggs for 24 hours. We prepared six such leaf squares. We allowed the eggs laid by virgin females on the leaf square (\approx 20–30 eggs) to develop to virgin male adults on the leaf square.

Effects of intermittent fasting on life history traits

To determine the effect of intermittent fasting on lifespan and reproduction in *T. ludeni*, we treated virgin and mated females and virgin and mated males with three intermittent fasting durations, i.e., 0 (control), 24, and 48 hours, resulting in 12 treatments (2 sexes \times 2 mating statuses \times 3 fasting durations). We set up maximum duration of fasting up to 48 hours as it has been recorded as the maximum duration of fasting that can be tolerated by *T. urticae* without causing extreme negative effects (Li and Zhang 2018). Each treatment had 25 replicates with one individual per replicate. Immediately after emergence we transferred a male and a female together (for mated mites) or an individual female or male (for virgin mites) onto a leaf square (2 cm \times 2 cm)

placed on a water-saturated cotton pad in a Petri dish (5.5 cm diameter × 1.0 cm height) using a soft paint brush. We let these mites feed for 24 h and then transferred them (mated and virgin) individually once a day onto a new leaf square (0-h fasting treatment) or a green plastic sheet (2 cm × 2 cm) (Colourhide, China) placed on a water-saturated cotton pad in a Petri dish. The daily mite transfer continued until death. Because mating occurs at emergence and multiple mating is common in spider mites (Puttaswamy and Channabasavanna 1979; Jose and Shah 1989; Oku 2009, 2014), 24-h pairing allowed us to obtain mated mites for experiments. We used the mites that stayed on plastic sheets for 24 and 48 h for treatments of 24-h and 48-h fasting, respectively. We treated the mites with three intermittent fasting periods from emergence to death using the following fasting sequence: 24-h feeding → 0-, 24- or 48-h fasting → 24-h feeding → 0-, 24- or 48-h fasting → 24-h feeding → 0-, 24- or 48-h fasting → continuous feeding until death. We set up the above fasting protocol because *T. ludeni* start laying eggs on the second day into adulthood and oviposition period lasts 7 to 12 days (Kaimal and Ramani 2011; Rode et al. 2018).

We checked the mites daily and recorded the pre-oviposition period (from an adult female emergence to its first egg being laid), oviposition period (from the first egg being laid to the last egg being laid by an adult female), daily fecundity (the number of eggs produced by a female per day), lifetime fecundity (total number of eggs produced by a female), and adult lifespan (from emergence to death). Immediately after we transferred the female from a leaf square or plastic sheet each day, we randomly selected two eggs laid by the female and measured their diameter under a digital camera (Olympus SC30, Japan) connected to the stereomicroscope (Leica MZ12, Germany) and a computer with adequate imaging software (CellSens® GS-ST-V1.7, Olympus, Japan) installed, without removing these eggs from the original leaf square/plastic sheet. We then calculated the egg size as: volume = $\frac{4}{3}\pi r^3$, where r is radius (= diameter/2). We allowed all eggs laid on each leaf square/plastic sheet to hatch. Upon hatching, we transferred neonate mites to a fresh leaf square and allowed them to feed on the leaf square for five days, and then transferred them to a new leaf square once every five days until they developed to adults. We recorded the egg hatch rate, adult emergence rate, number of daughters produced, and developmental period (from eggs to adults).

Data analysis

We analysed all data using SAS 9.4. Data on adult survival were compared using a Wilcoxon test (LIFETEST procedure). Data on the oviposition period, emergence rate of virgin females' offspring, fecundity of virgin females, numbers of daughters produced by mated females, arcsine-square-root transformed emergence rate of mated females' offspring and square-root transformed fecundity of mated females were normally distributed (Shapiro-Wilk test, UNIVARIATE procedure), and thus analysed using an analysis of variance (ANOVA, GLM procedure) with treatment as a fixed factor followed by Tukey's Studentized range test for multiple comparisons. Other data were not normally distributed even after transformation, and thus a generalized linear model with a Log function (GLIMMIX procedure) was applied to compare the difference in

preoviposition period, egg size, egg hatch rate, and offspring developmental period with treatment as a fixed factor. A *Gamma* distribution was applied for egg size and egg hatch rate and a *Poisson* distribution for preoviposition period and developmental time. For egg size and developmental period, mother's ID was used as a random factor. Multiple comparisons between treatments were performed using an adjust-Tukey test.

Results

Effect of intermittent fasting on adult survival and preoviposition and oviposition periods

Intermittent fasting of 48 h significantly prolonged female longevity (virgin female: $\chi^2_2 = 8.80$, $P = 0.0123$; mated female: $\chi^2_2 = 11.94$, $P = 0.0026$) (Figure 1A, B). Fasting had no significant impact on virgin male survival ($\chi^2_2 = 1.74$, $P = 0.4184$) (Figure 1C) but intermittent fasting of 48 h significantly reduced survival probability in mated males ($\chi^2_2 = 9.30$, $P = 0.0096$) (Figure 1D). Fasting significantly prolonged the preoviposition period ($F_{2,48} = 38.74$, $P < 0.0001$ for virgin females; $F_{2,61} = 4.42$, $P = 0.0162$ for mated females) (Figure 2A) but had no significant effect on oviposition period ($F_{2,48} = 0.06$, $P = 0.9402$ for virgin females; $F_{2,61} = 2.25$, $P = 0.1140$ for mated females) (Figure 2B).

Effect of intermittent fasting on lifetime fecundity, egg size and daughter production

Fasting had no significant impact on lifetime fecundity of virgin females ($F_{2,48} = 1.91$, $P = 0.1586$) but significantly reduced that of mated females ($F_{2,72} = 13.04$, $P < 0.0001$) (Figure 3A). Egg size significantly decreased when females were fasted for 24 and 48 h (virgin female: $F_{2,260} = 6.71$, $P = 0.0014$; mated female: $F_{2,358} = 7.69$, $P = 0.0005$) (Figure 3B). The number of daughters produced by mated females was not significantly different between treatments ($F_{2,33} = 1.72$, $P = 0.1951$) (Figure 3C).

Effect of intermittent fasting on offspring performance

Fasting during the adult stage of mothers did not significantly affect egg hatch rate [mated females: 71.56 ± 6.45 , 68.17 ± 6.96 and $65.98 \pm 8.30\%$ for 0, 24, and 48 h fasting, respectively ($F_{2,54} = 0.04$, $P = 0.9570$); virgin females: 69.52 ± 5.32 , 66.77 ± 6.04 and $46.28 \pm 11.19\%$ for 0, 24, and 48 h fasting, respectively ($F_{2,42} = 0.18$, $P = 0.8339$)] and adult emergence rate [mated females: 55.67 ± 20.96 , 24.04 ± 6.02 and $25.21 \pm 8.31\%$ for 0, 24, and 48 h fasting, respectively ($F_{2,54} = 1.90$, $P = 0.1597$); virgin females: 51.20 ± 7.06 , 48.83 ± 7.86 and $34.42 \pm 10.25\%$ for 0, 24, and 48 h fasting, respectively ($F_{2,42} = 0.93$, $P = 0.4011$)]. Compared to the control, sons from virgin mothers needed significantly longer developmental time after their mothers experienced fasting ($F_{2,81} = 3.98$, $P = 0.0224$) while fasting had no effect on developmental time of sons ($F_{2,4} = 0.05$, $P = 0.9524$) and daughters ($F_{2,96} = 1.19$, $P = 0.3072$) from mated mothers (Figure 4).

Discussion

Our results demonstrate that intermittent fasting (IF) during the first half of *T. ludeni* adult life increased female longevity by 15–39% regardless of mating status. Several studies have explored the possible mechanisms behind the IF-induced longevity extension in invertebrates. For example, Honjoh et al. (2009) and Kogure et al. (2017) suggest that this could result from gene expression changes, downregulating insulin-like peptides such as *ins-7* that may negatively regulate longevity in nematodes. In their study on fruit flies, Catterson et al. (2018) indicate that IF in early adult life can raise lipid content, improve gut health later in life, and increase longevity. Because regular starvation often occurs during invasion process (Zhang et al. 2019; Papach et al. 2020) and *T. ludeni* can reproduce through mother-son mating without inbreeding depression (Zhou et al. 2020, 2021), the increase of female longevity in response to IF may contribute to its invasion success.

However, the effect of IF on males was mating-status-specific, i.e., it shortened the longevity of mated males and had no impact on virgin males. Several factors could explain the observed patterns. First, *T. ludeni* females are much larger than males (Kaimal and Ramani 2011; Li and Zhang 2018) and should have more resources to lift lipid content in response to IF. Second, compared to females, males are more active (van Leeuwen et al. 2009; Li and Zhang 2018) with higher metabolic rates (Finiguerra et al. 2013), resulting in higher energy expenditure and reducing the longevity benefit (Shigenaga et al. 1994) from IF. Finally, mating is costly to males in terms of ejaculation (van Voorhies 1992; Shapiro et al. 1994; Olsson et al. 1997; Scharf et al. 2013), resulting in earlier death if mated males are also fasted. To date, it is unknown whether the haplodiploid nature of the spider mite also plays a role in the observed sex specific IF impact on longevity.

We show that IF prolonged preoviposition period in both virgin and mated *T. ludeni* females. Because diet during adulthood determines ovarian development and egg maturation in many species (Adams 2000; Danks 2000; Hahn et al. 2008; Mirth et al. 2019) and egg maturation occurs gradually during the adult stage in spider mites (Kawakami et al. 2009), fasting may delay this process, leading to longer preoviposition period. The IF-induced delay in reproduction may also contribute to the increase of female longevity. However, IF had no effect on oviposition period regardless of mating status, suggesting that females of this species strive to spread their egg laying for the same time frame to maximize the chance of population survival under different situations. Although IF reduced fecundity and egg size, it had no effect on the number of daughters produced. These findings suggest that females trade off fecundity and egg size but not daughter numbers for somatic survival when diet is restricted in their early life. Due to lack of inbreeding depression in *T. ludeni* (Zhou et al. 2020, 2021), maintaining production of similar number of daughters under the diet-restricted environment may be an important strategy for population survival and growth, facilitating invasion success.

Looking into the effect of mothers' experience on their offspring performance, we found that IF did not alter egg hatch rate and immature survival to adulthood, suggesting that smaller egg size induced by IF in mothers does not reduce egg viability and offspring endurance in *T. ludeni*. This seems to contradict previous findings in some other species where egg size determines offspring fitness (Carlberg 1991; Stewart et al. 1991;

Braby 1994; Fox 1994; Roff 2000; Macke et al. 2011; Koch and Meunier 2014; Warner and Lovern 2014). However, IF had transgenerational maternal effects on offspring developmental time, with sons from fasted virgin mothers needing longer time to develop to adults. We suggest that *T. ludeni* can compensate egg size loss for offspring fitness by extending developmental period which results in the same adult size as those from large eggs (Fox 1993; Fox and Dingle 1994). This may yet be another strategy this mite has developed to cope with food shortage. Further studies on this aspect are warranted to confirm the transgenerational effects on offspring reproductive outputs in *T. ludeni*.

In conclusion, IF increases female but not male longevity probably due to differences in resource storage, metabolic rate, and mating cost between sexes. In response to IF, females trade off fecundity and egg size but not daughter numbers for longevity gain, suggesting that *T. ludeni* females can adjust their life history strategies for population survival and growth during invasion process where food shortage is common. Eggs produced by fasted females achieve the same hatch rate and resulting young have the same survival rate as those by unfasted ones. Furthermore, IF also has transgenerational maternal effects which prolong offspring development period. We suggest that the longer immature developmental period can increase the body size of resulting adults, compensating egg size loss for offspring fitness. These resource allocation strategies of *T. ludeni* coupled with its adaptation to wide ranges of hosts (Gotoh et al. 2015) and temperatures (Gotoh et al. 2015; Ristyadi et al. 2019, 2021) may have facilitated its invasion success as these features can increase their survival in challenging environments. This work provides insight into resource allocations in response to fasting and useful knowledge for evaluation of pest invasions and management of animal survival and reproduction by dietary regulations.

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Authors' contribution

D.R., X.Z.H. and Q.W. conceived and designed the study; D.R. collected the data. All authors contributed to data analysis and manuscript preparation.

Conflict of Interest

The authors declare they have no conflict of interest.

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References

- Adams TS, 2000. Effect of diet and mating status on ovarian development in a predaceous stink bug *Perillus bioculatus* (Hemiptera: Pentatomidae). *Ann Entomol Soc Am* **93**:529–535.
- Angelier F, Wingfield JC, Parenteau C, Pellé M, Chastel O, 2015. Does short-term fasting lead to stressed-out parents? A study of incubation commitment and the hormonal stress responses and recoveries in snow petrels. *Horm Behav* **67**:28–37.
- Anson RM, Guo Z, de Cabo R, Iyun T, Rios M et al., 2003. Intermittent fasting dissociates beneficial effects of dietary restriction on glucose metabolism and neuronal resistance to injury from calorie intake. *Proc Natl Acad Sci* **100**:6216–6220.
- Bancroft JS, Margolies DC, 1996. Allocating time between feeding, resting and moving by the two-spotted spider mite *Tetranychus urticae* and its predator *Phytoseiulus persimilis*. *Exp Appl Acarol* **20**:391–404.
- Bolland HR, Gutierrez J, Flechtman, CH, 1998. *World Catalogue of the Spider Mite Family (Acari: Tetranychidae)*, The Netherlands: Brill.
- Braby MF, 1994. The significance of egg size variation in butterflies in relation to hostplant quality. *Oikos* **71**:119–129.
- Brandhorst S, Choi IY, Wei M, Cheng CW, Sedrakyan S et al., 2015. A periodic diet that mimics fasting promotes multi-system regeneration, enhanced cognitive performance, and healthspan. *Cell Metab* **22**:86–99.
- CABI/EPPO, 2011. *Tetranychus ludeni*. [Distribution map]. In: *Distribution Maps of Plant Pests* (pp. Map 758). Wallingford: CABI. <https://www.cabi.org/ISC/abstract/20113409546>. Accessed on 3 June 2022
- Carlberg U, 1991. Egg-size variation in *Extatosoma tiaratum* (MacLeay) and its effect on survival and fitness of newly hatched nymphs (Insecta: Phasmida). *Biolo Zentralbl* **1102**:163–173.
- Catterson JH, Khericha M, Dyson MC, Vincent AJ, Callard R et al., 2018. Short-term, intermittent fasting induces long-lasting gut health and tor-independent lifespan extension. *Curr Biol* **28**:1714–1724.
- Cerqueira FM, da Cunha FM, Caldeira da Silva CC, Chausse B, Romano RL, Garcia CC et al., 2011. Long-term intermittent feeding, but not caloric restriction, leads to redox imbalance, insulin receptor nitration, and glucose intolerance. *Free Radic Biol Med* **51**:1454–1460.
- Chambers JR, 2019. *The Intermittent Fasting*. Pan Macmillan, Australia.
- Danks HV, 2000. Measuring and reporting life-cycle duration in insects and arachnids. *Eur J Entomol* **97**:285–303.
- Dimofski P, Meyre D, Dreumont N, Leininger-Muller B, 2021. Consequences of paternal nutrition on offspring health and disease. *Nutrients* **13**:2818.
- de la Filia AG, Bain SA, Ross L, 2015. Haplodiploidy and the reproductive ecology of arthropods. *Curr Opin Insect Sci* **9**:36–43.
- Dorighello GG, Rovani JC, Luhman CJ, Paim BA, Raposo HF et al., 2014. Food restriction by intermittent fasting induces diabetes and obesity and aggravates spontaneous atherosclerosis development in hypercholesterolaemic mice. *Br J Nutr* **111**:979–986.

- Ensminger DC, Salvador-Pascual A, Arango BG, Allen KN, Vázquez-Medina JP, 2021. Fasting ameliorates oxidative stress: A review of physiological strategies across life history even in wild vertebrates. *Comp Biochem Physiol A Mol Integr Physiol* **256**:110929.
- Finiguerra MB, Dam HG, Avery DE, Burris Z, 2013. Sex-specific tolerance to starvation in the copepod *Acartia tonsa*. *J Exp Mar Biol Ecol* **446**:17–21.
- Fox CW, 1993. The influence of maternal age and mating frequency on egg size and offspring performance in *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Oecologia* **96**:139–146.
- Fox CW, 1994. The influence of egg size on offspring performance in the seed beetle *Callosobruchus maculatus*. *Oikos* **71**:321–325.
- Fox CW, Dingle H, 1994. Dietary mediation of maternal age effects on offspring performance in a seed beetle (Coleoptera: Bruchidae). *Funct Ecol* **8**:600–606.
- Gladyshev VN, 2016. Aging: Progressive decline in fitness due to the rising deleteriousness adjusted by genetic, environmental, and stochastic processes. *Aging Cell* **15**:594–602.
- Goodrick CL, Ingram DK, Reynolds MA, Freeman JR, Cider N, 1990. Effects of intermittent feeding upon body weight and lifespan in inbred mice: Interaction of genotype and age. *Mech Ageing Dev* **55**:69–87.
- 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? *Exp Appl Acarol* **66**:453–479.
- Gotoh T, Tsuchiya A, 2009. Food scarcity reduces female longevity of *Neoseiulus californicus* (Acari: Phytoseiidae). *Exp Appl Acarol* **47**:249–256.
- Gribble KE, Kaido O, Jarvis G, Welch DBM, 2014. Patterns of intraspecific variability in the response to caloric restriction. *Exp Gerontol* **51**:28–37.
- Gunnars K, 2020. *Intermittent Fasting 101 - the Ultimate Beginner's Guide*. San Francisco: Healthline Media, <https://www.healthline.com/nutrition/intermittent-fasting-guide#benefits>. Accessed on 3 June 2022.
- Hahn DA, James LN, Milne KR, Hatle JD, 2008. Life-history plasticity after attaining a dietary threshold for reproduction is associated with protein storage in flesh flies. *Funct Ecol* **22**:1081–1090.
- Honjoh S, Yamamoto T, Uno M, Nishida E, 2009. Signaling through RHEB-1 mediates intermittent fasting-induced longevity in *C-elegans*. *Nature* **457**:726–731.
- Ivimey-Cook ER, Sales K, Carlsson H, Immler S, Chapman T et al., 2021. Transgenerational fitness effects of lifespan extension by dietary restriction in *Caenorhabditis elegans*. *Proc Roy Soc B Biol Sci* **288**:20210701.
- Jose VT, Shah AH, 1989. Bionomics of the spider mite, *Tetranychus macferlanei* injurious to cotton in Gujarat, India. In: Channabasavanna GP, Viraktamath CA eds. *Progress in Acarology*. Brill Archive, 23–28.
- Kaimal SG, Ramani N, 2011. Biology of *Tetranychus ludeni* Zacher (Acari: Tetranychidae) a pest of velvet bean. *Indian J Fundam Appl Life Sci* **16**:1–6.
- Kawakami Y, Goto SG, Ito K, Numata H, 2009. Suppression of ovarian development and vitellogenin gene expression in the adult diapause of the two-spotted spider mite *Tetranychus urticae*. *J Insect Physiol* **55**:70–77.
- Kirkwood TB, 2005. Understanding the odd science of aging. *Cell* **120**:437–447.
- Koch LK, Meunier J, 2014. Mother and offspring fitness in an insect with maternal care: phenotypic trade-offs between egg number, egg mass and egg care. *BMC Evol Biol* **14**:1–9.

- Kogure A, Uno M, Ikeda T, Nishida E, 2017. The microRNA machinery regulates fasting-induced changes in gene expression and longevity in *Caenorhabditis elegans*. *J Biol Chem* **292**:11300–11309.
- Lee C, Longo V, 2016. Dietary restriction with and without caloric restriction for healthy aging [version 1; peer review: 3 approved]. *F1000Research* **5**:117. <https://doi.org/10.12688/f1000research.7136.1>
- Li G-Y, Zhang Z-Q, 2018. Does size matter? Fecundity and longevity of spider mites *Tetranychus urticae* in relation to mating and food availability. *Syst Appl Acarol* **23**:1796–1808.
- Li G-Y, Zhang Z-Q, 2019. The sex- and duration-dependent effects of intermittent fasting on lifespan and reproduction of spider mite *Tetranychus urticae*. *Front Zool* **16**:10.
- Liang Y, Liu C, Lu M, Dong Q, Wang Z et al., 2018. Calorie restriction is the most reasonable anti-ageing intervention: A meta-analysis of survival curves. *Sci Rep* **8**:1–9.
- Lohse K, Ross L, 2015. What haplodiploids can teach us about hybridization and speciation. *Mol Ecol* **24**:5075–5077.
- Longo VD, Mattson MP, 2014. Fasting: Molecular mechanisms and clinical applications. *Cell Metab* **19**:181–192.
- Macke E, Magalhães S, Do-Thi Khanh H, Luciano A, Frantz A, Facon B, Olivieri I, 2011. Sex allocation in haplodiploids is mediated by egg size: Evidence in the spider mite *Tetranychus urticae* Koch. *Proc Biol Sci* **278**:1054–1063. <https://doi.org/10.1098/rspb.2010.1706>
- Martin B, Pearson M, Kebejian L, Golden E, Keselman A et al., 2007. Sex-dependent metabolic, neuroendocrine, and cognitive responses to dietary energy restriction and excess. *Endocrinology* **148**:4318–4333.
- Mautz BS, Lind MI, Maklakov AA. 2020. Dietary restriction improves fitness of aging parents but reduces fitness of their offspring in nematodes. *J Gerontol A Biol Sci Med Sci* **75**:843–848.
- Merry BJ, 2002. Molecular mechanisms linking calorie restriction and longevity. *Int J Biochem Cell Biol* **34**:1340–1354.
- Migeon A, Nouguié E, Dorkeld F, 2010. Spider mites web: A comprehensive database for the Tetranychidae. In: Sabelis M, Bruin J eds. *Trends in Acarology*. Dordrecht: Springer, 557–560.
- Mirth CK, Alves AN, Piper MD, 2019. Turning food into eggs: Insights from nutritional biology and developmental physiology of *Drosophila*. *Curr Opin Insect Sci* **31**:49–57.
- Nakagawa S, Lagisz M, Hector KL, Spencer HG, 2012. Comparative and meta-analytic insights into life extension via dietary restriction. *Aging Cell* **11**:401–409.
- Oku K, 2009. Males of the two-spotted spider mite attempt to copulate with mated females: Effects of double mating on fitness of either sex. *Exp Appl Acarol* **50**:107–113.
- Oku K, 2014. Sexual selection and mating behavior in spider mites of the genus tetranychus (Acari: Tetranychidae). *Appl Entomol Zool* **49**:1–9.
- Olsson M, Madsen T, Shine R, 1997. Is sperm really so cheap? Costs of reproduction in male adders *Vipera berus*. *Proc R Soc Lond B Biol Sci* **264**:455–459.
- Papach A, Williams GR, Neumann P, 2020. Evolution of starvation resistance in an invasive insect species *Aethina tumida* (Coleoptera: Nitidulidae). *Ecol Evol* **10**:9003–9010.
- Puttaswamy C, Channabasavanna GP, 1979. Life history of *Tetranychus ludeni* (Acari: Tetranychidae) under field conditions. *Indian J Acarol* **4**:41–48.

- Ristyadi D, He XZ, Wang Q, 2019. Dynamics of life history traits in *Tetranychus ludeni* Zacher in response to fluctuating temperatures. *Syst Appl Acarol* **24**:2272–2277.
- Ristyadi D, He XZ, Wang Q, 2021. Response to thermal environment in *Tetranychus ludeni* Zacher (Acari: Tetranychidae). *Syst Appl Acarol* **26**:942–953.
- Rode PDA, Toldi M, Reichert MB, Johann L, Ferla NJ, 2018. Development of *Tetranychus ludeni* (Acari: Tetranychidae) on transgenic soybean cultivars. *Phytoparasitica* **46**:137–141.
- Roff D, 2000. Trade-offs between growth and reproduction: An analysis of the quantitative genetic evidence. *J Evol Biol* **13**:434–445.
- Scharf I, Peter F, Martin OY, 2013. Reproductive trade-offs and direct costs for males in Arthropods. *Evol Biol* **40**:169–184.
- Shapiro DY, Marconato A, Yoshikawa T, 1994. Sperm economy in a coral reef fish, *Thalassoma bifasciatum*. *Ecology* **75**:1334–1344.
- Shigenaga MK, Hagen TM, Ames BN, 1994. Oxidative damage and mitochondrial decay in aging. *Proc Natl Acad Sci* **91**:10771–10778.
- Stearns SC, 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Stewart LA, Hemptinne JL, Dixon AFG, 1991. Reproductive tactics of ladybird beetles: Relationships between egg size, ovariole number and developmental time. *Funct Ecol* **5**:380–385.
- van Leeuwen T, Vontas J, Tsagkarakou A, Tirry L, 2009. Mechanism of acaricide resistance in two-spotted spider mite *Tetranychus urticae*. In: Horowitz AR, Ishaaya I eds. *Biorational Control of Arthropod Pests Application and Resistance Management*. Netherlands: Springer, 347–393.
- van Voorhies WA, 1992. Production of sperm reduces nematode lifespan. *Nature* **360**:456–458.
- Wang X, Du XY, Zhou Y, Wang S, Su F, Zhang SC, 2017. Intermittent food restriction initiated late in life prolongs lifespan and retards the onset of age-related markers in the annual fish *Nothobranchius guentheri*. *Biogerontol* **18**:383–396.
- Warner DA, Lovern MB, 2014. The maternal environment affects offspring viability via an indirect effect of yolk investment on offspring size. *Physiol Biochem Zool* **87**:276–287.
- Zhang D-W, Xiao Z-J, Zeng B-P, Li K, Tang Y-L, 2019. Insect behavior and physiological adaptation mechanisms under starvation stress. *Front Physiol* **10**:1–8.
- Zhang, Z-Q, 2003. *Mites of Greenhouses: Identification, Biology and Control*, CABI Publishing, United Kingdom.
- Zhou P, He XZ, Chen C, Wang Q, 2020. No evidence for inbreeding depression and inbreeding avoidance in a haplodiploid mite *Tetranychus ludeni* Zacher. *Syst Appl Acarol* **25**:1723–1728.
- Zhou P, He XZ, Chen C, Wang Q, 2021. Reproductive strategies that may facilitate invasion success: Evidence from a spider mite. *J Econ Entomol* **114**:632–637.

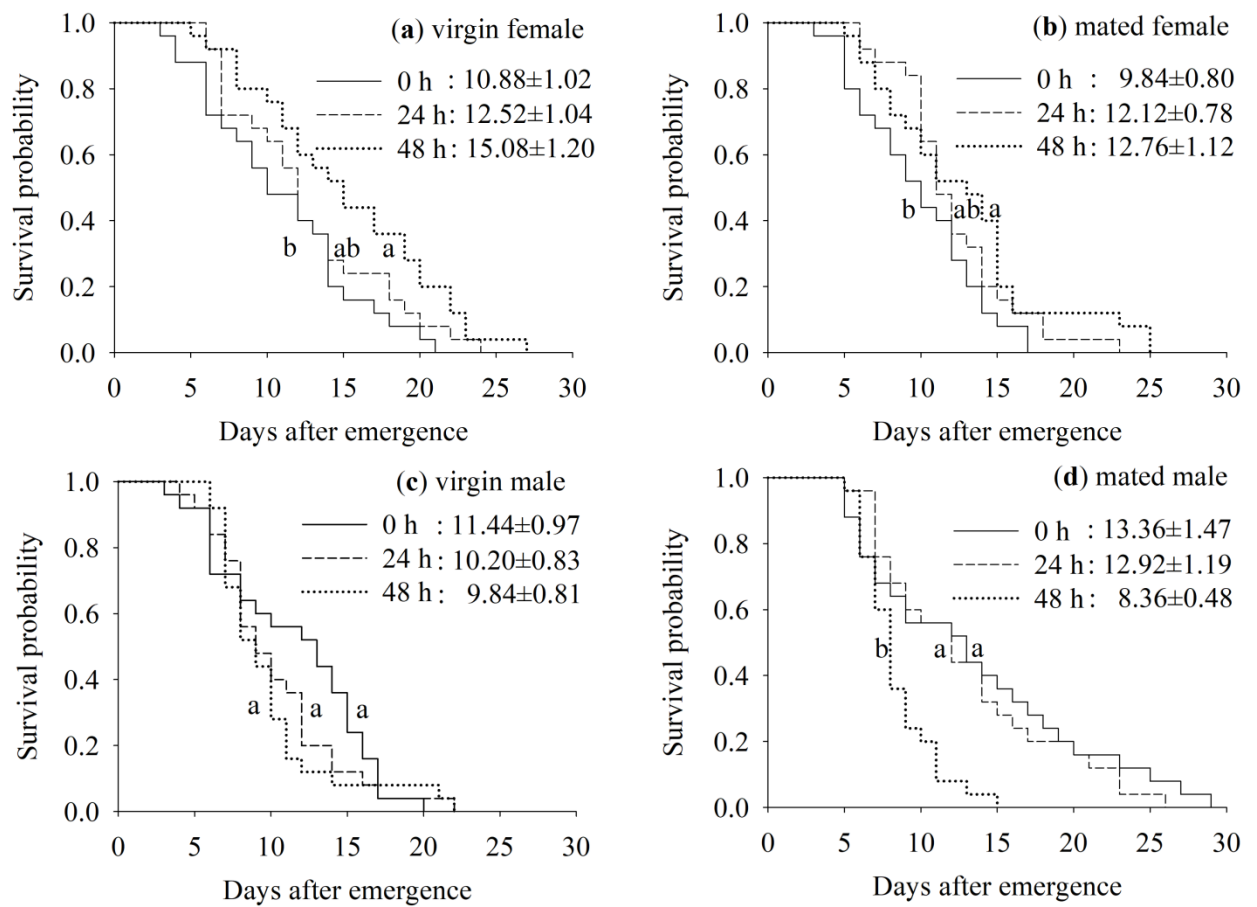


Figure 1. Survival probability of virgin females (A), mated females (B), virgin males (C) and mated males (D) fasted for different durations in *T. ludeni*. Lines with the same letters are not significantly different ($P > 0.05$). The mean (\pm SE) longevity (days) is given for each treatment.

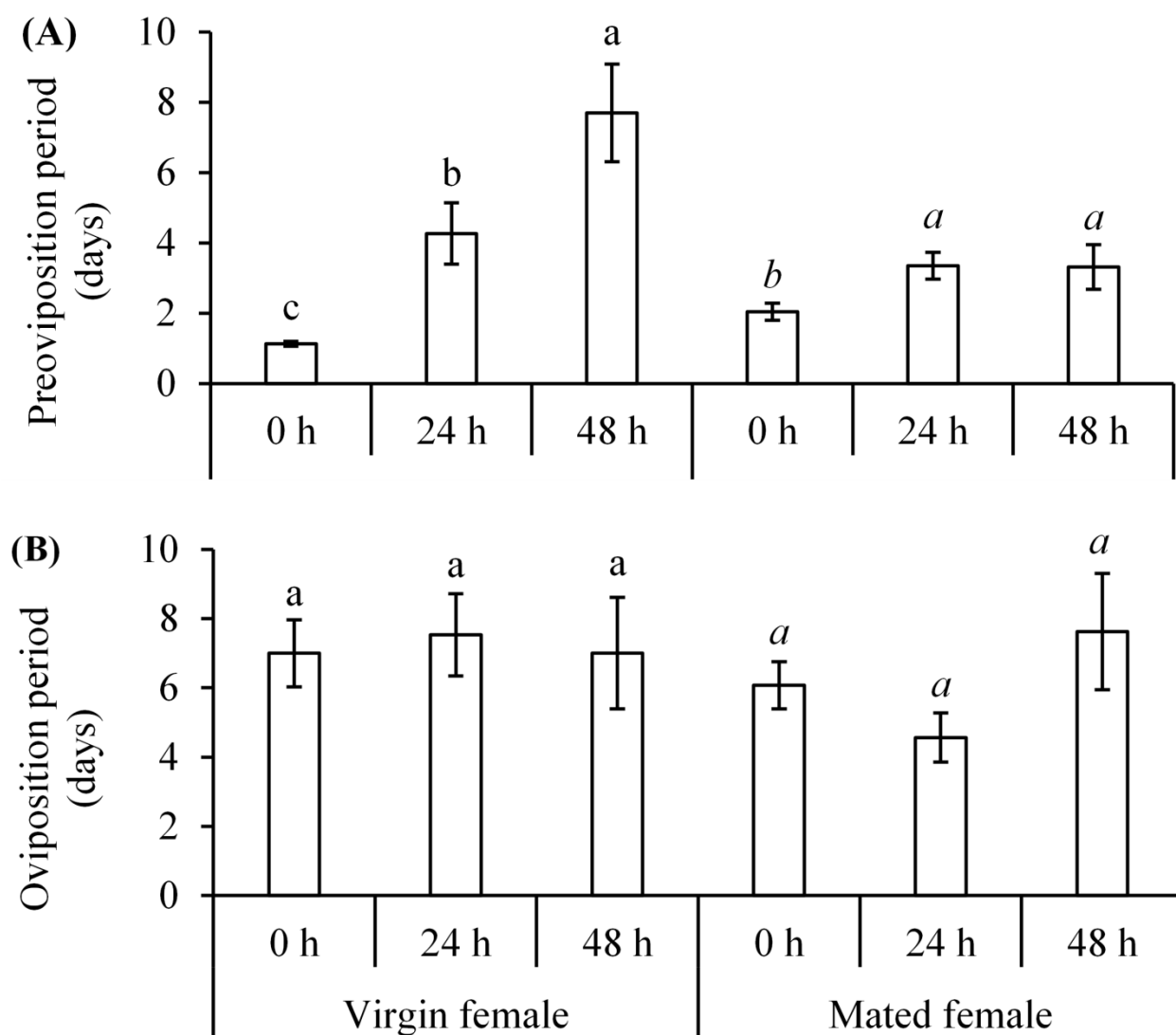


Figure 2. Mean (± SE) preoviposition (A) and oviposition period (B) of virgin and mated females fasted for different durations in *T. ludeni*. Columns with the same letters (small case for virgin females, small italic case for mated females) are not significantly different ($P > 0.05$)

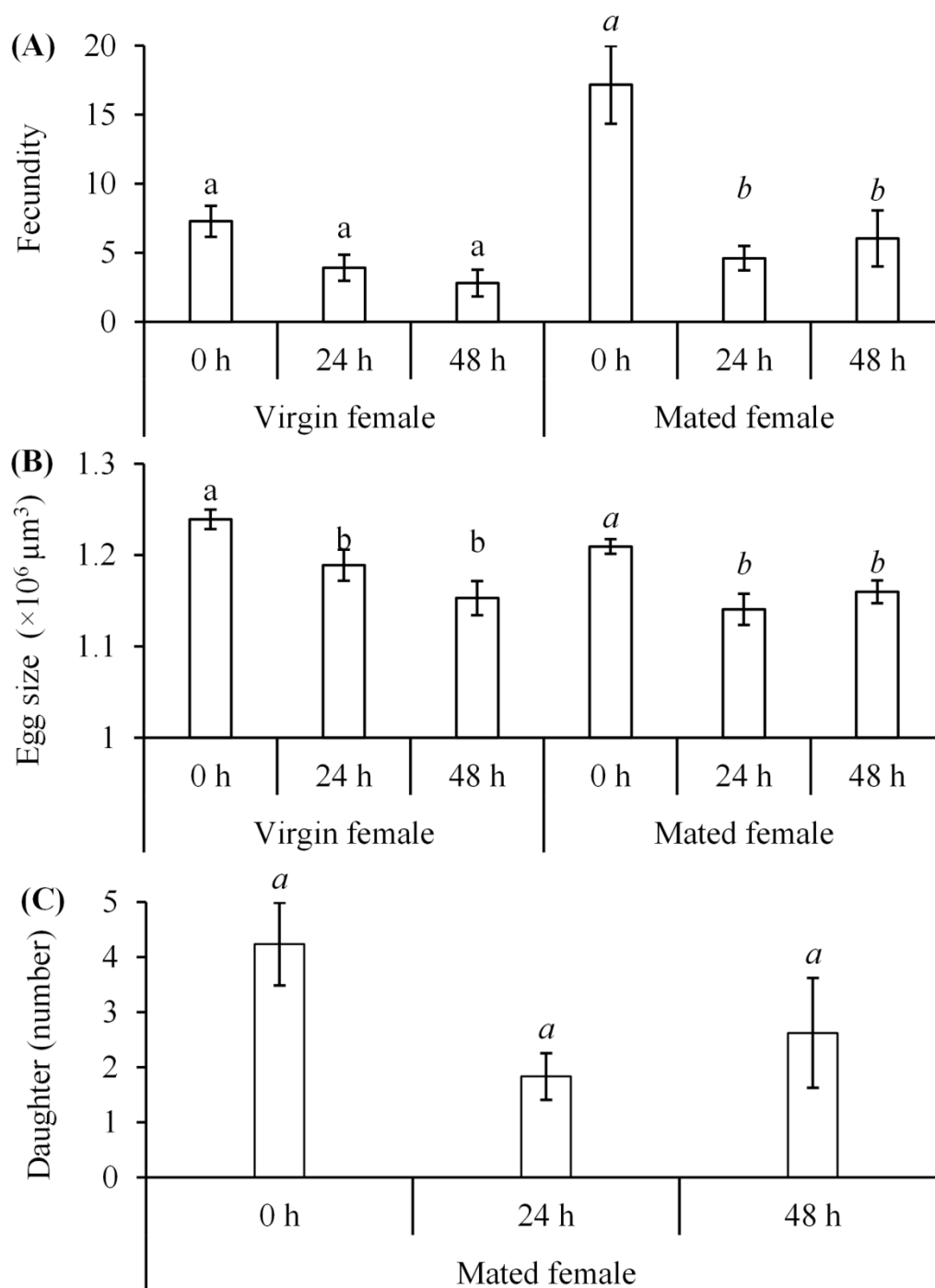


Figure 3. Mean (\pm SE) lifetime fecundity (A) and egg size (B) of virgin and mated females, and number of daughters (C) produced by mated females fasted for different durations in *T. ludeni*. Columns with the same letters (small case for virgin females, small italic case for mated females) are not significantly different ($P > 0.05$)

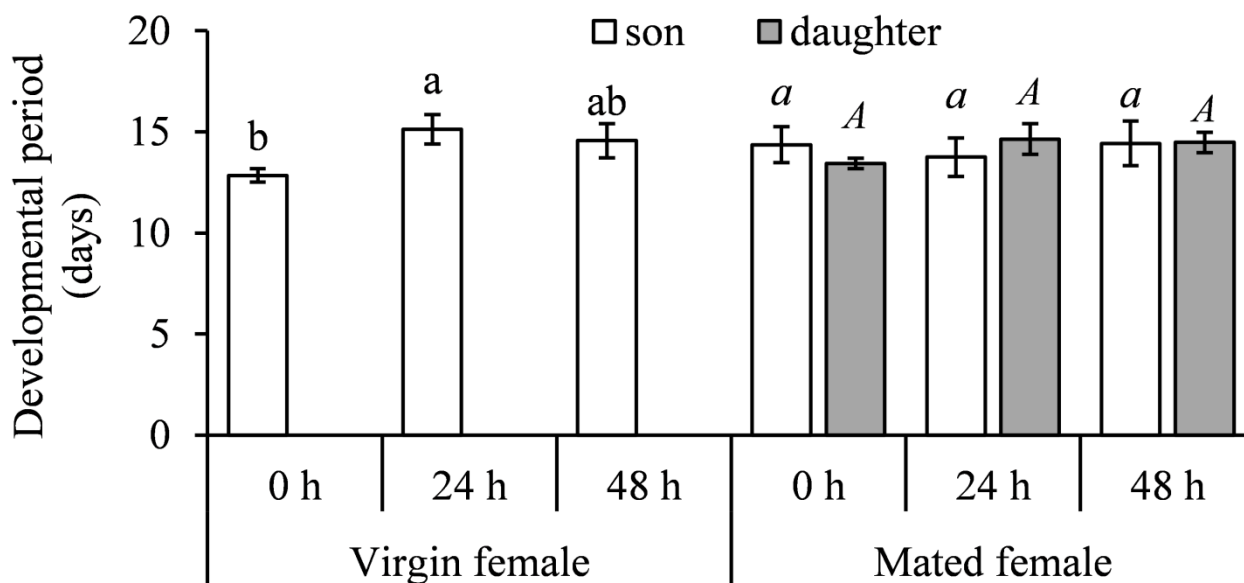


Figure 4. Mean (\pm SE) developmental time of offspring of virgin and mated females fasted for different durations in *T. ludeni*. For sons produced by virgin or mated females, columns with the same letters (small case for virgin females, small italic case for mated females) are not significantly different ($P > 0.05$); for daughters produced by mated females, columns with the same capital letters in italic are not significantly different ($P > 0.05$)