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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 (IF) 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 IF 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 IF focuses more on lifespan and less on reproduction (Goodrick et al. 1983; Mattson and Wan 2005; Hwangbo et al. 2020). 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 IF influenced both males and females in *T. ludeni*. We set up a series of IF 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 IF 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 IF 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 ± 1 °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 × 3 cm, 30 individuals per leaf square), each being placed on a water-saturated cotton pad in a Petri dish (5.5 cm diameter × 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 × 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 (≈20–30 eggs) to develop to virgin male adults on the leaf square.

Effects of IF on life history traits

To determine the effect of IF on lifespan and reproduction in *T. ludeni*, we treated virgin and mated females and virgin and mated males with three IF durations, i.e., 0 (control), 24, and 48 hours, resulting in 12 treatments (2 sexes × 2 mating statuses × 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 × 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 IF 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 = $4/3\pi r^3$, 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 5 days, and then transferred them to a new leaf square once every 5 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 analyzed 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 analyzed 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 *Poison* 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 IF on adult survival and preoviposition and oviposition periods

IF of 48 h significantly prolonged female longevity (virgin female: $x_2^2 = 8.80, P = 0.0123$; mated female : $x_2^2 = 11.94$, $P = 0.0026$) (Figure 1A, B). Fasting had no significant impact on virgin male survival ($x_2^2 = 1.74, P = 0.4184$) (Figure 1C) but IF of 48 h significantly reduced survival probability in mated males ($x_2^2 = 9.30, P = 0.0096$) (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 IF 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 IF 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: $69.52 \pm 5.32, 66.77 \pm 6.04$ 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: $55.67 \pm 20.96, 24.04 \pm 6.02$ 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 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
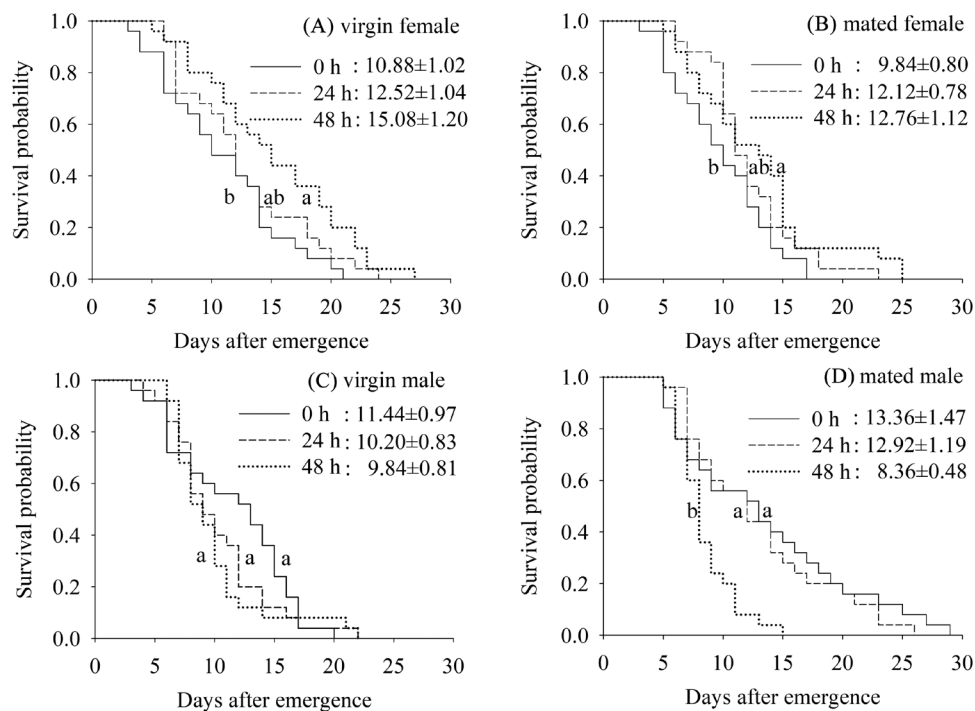

Figure 1. Survival probability of virgin females (**A**), mated females (**B**), virgin males (**C**) and mated males (**D**) fasted for different durations in *T. ludeni*. Lines with the same letters are not significantly different (*P* > 0.05). The mean (± *SE*) longevity (days) is given for each treatment.
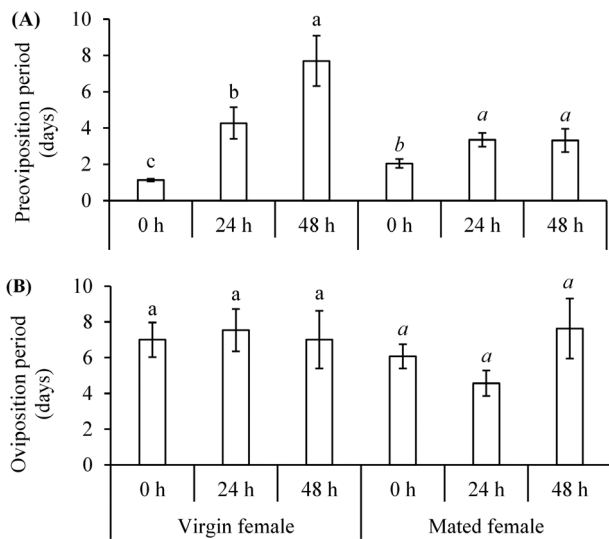
Figure 2. Mean (± *SE*) preoviposition (**A**) and oviposition period (**B**) of virgin and mated females fasted for different durations in *T. ludeni*. Columns with the same letters (small case for virgin females, small italic case for mated females) are not significantly different (*P* > 0.05).

Figure 3. Mean (± *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).
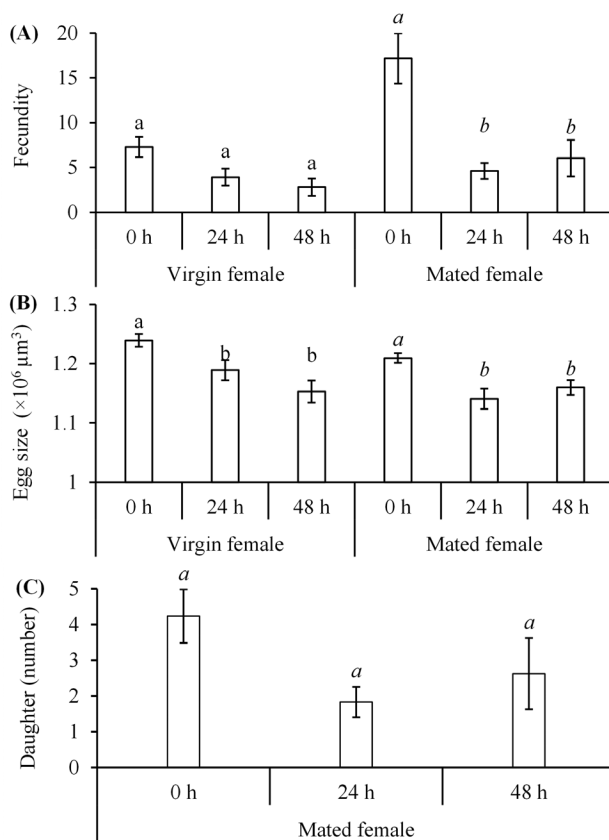
that IF in early adult life can raise lipid content, improve gut health later in life, and increase longevity. Because regular starvation often occurs during invasion process (Zhang et al. 2019; Papach et al. 2020) and *T. ludeni* can reproduce
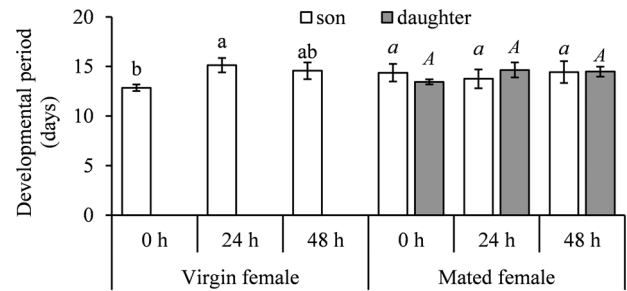

Figure 4. Mean (± *SE*) developmental time of offspring of virgin and mated females fasted for different durations in *T. ludeni*. For sons produced by virgin or mated females, columns with the same letters (small case for virgin females, small italic case for mated females) are not significantly different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

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.

Acknowledgements

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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