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RESEARCH

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Effects of rainfall on parasitism and survival of *Telenomus remus*, an egg parasitoid of fall armyworm

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Abstract

Telenomus remus is an egg parasitoid of *Spodoptera* species, including the major agricultural pest *Spodoptera frugiperda*. Climatic factors are closely related to the development and population dynamics of such parasitoids. However, the effects of rainfall on the biological performance of this wasp have not be studied. Here, we modeled the effects of different intensities of rainfall (control: 0, light rain: 5.0, moderate rain: 10.2, and torrential rain: 42.8 mm/h; falling over a 30 min period) on the parasitism rate, developmental time, and survival of *T. remus* on eggs of *S. frugiperda*. We assessed the effect of rainfall exposure on both *T. remus* adults and on parasitized *S. frugiperda* eggs. Simulated rainfall resulted in a notable decline in the number of hosts parasitized by *T. remus* adults for up to 12 h following rainfall, but the parasitism rate returned to normal within one day after rain ceased. Torrential rain reduced immediate (within 24 h) survival of adults of *T. remus* females, but there was no subsequent effect on adult survival after rain ceased. When parasitized host eggs were exposed to rain events, some eggs were dislodged. Moderate or torrential intensity rainfall dislodged 12 and 44% of *S. frugiperda* eggs from maize leaves. For *T. remus* eggs exposed to rain that were not dislodged, the probability of reaching adulthood and successfully emerging was negatively correlated with rainfall intensity. However, for all levels of rainfall intensity, the survival of eggs that were not dislodged was greater than those that were dislodged. These findings suggest farmers should avoid releasing natural enemies when rainfall occurs or is forecast, and they should make supplemental releases after unanticipated rainfall occurs immediately after releases.

Keywords Egg parasitic wasps, Fall armyworm, Simulated rainfall, Life history, Biological control

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Introduction

Fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is a major agricultural pest native to the tropical and subtropical parts of the Americas (Sparks 1979; Tay et al. 2023). This pest has also invaded many other regions, including sub-Saharan Africa, parts of Asia, and southern Australia (Kenis et al. 2023). FAW is a polyphagous herbivore whose larvae feed > 353 plant species in 76 families (Montezano et al. 2018; Guo et al. 2018), including maize, sorghum, wheat, rice, cotton, and other cash crops (Oliveira et al. 2014; Barros et al. 2018; Wu et al. 2021). The financial burden of FAW control is considerable: the Food and Agriculture Organization (FAO) estimates that Brazil alone spends approximately $600 million annually to manage the pest (Wild 2017), while production losses of US$9.4 billion due to FAW occur annually in Africa (Eshen et al. 2021). Currently, management of FAW is difficult because of its strong migratory ability, high physiological and behavioral plasticity, and rapid rate of development of resistance to insecticides (Jing et al. 2021).

Integrated pest management (IPM) is a more holistic, coordinated, and systematic approach to maintaining pest population densities below economic thresholds, while reducing the number of chemical applications (Stenberg 2017). Biological control based on natural enemies is an important component of IPM that can be sustainable, cost-effective, and environmentally friendly (Bale et al. 2008; Giles et al. 2017). *Telenomus remus* (Nixon) (Hymenoptera: Scelionidae) is an egg parasitoid that attacks several species of noctuid moths, including *S. frugiperda* (Colmenarez et al. 2022) that helps limit populations of this pest (Lyu et al. 2023). Egg parasitoids of noctuid pests have been used in biological control programs in India, the United States, New Zealand, Venezuela, and Colombia, and these efforts have resulted in field parasitism rates of 43–90% after augmentative releases (Gutierrez-Martinez et al. 2012; Kenis et al. 2019; Colmenarez et al. 2022; Fortes et al. 2023).

Climatic factors, such as rainfall, can affect the biological performance of such parasitoids on their target pests and change the resulting level of field efficacy (Gherlenda et al. 2016; Abram et al. 2019; Zang et al. 2021). Rainfall can directly (mechanical impacts) or indirectly (changes in soil and atmospheric temperature and humidity, host plant status, natural enemy-host interactions) affect insect feeding, survival, development, reproduction, and migration (Weissflog et al. 2018; Rahman et al. 2019; Andrade et al. 2020; Aguirrebengoa et al. 2020; Wainwright et al. 2023). For example, indoor simulated rainfall can wash eggs or larvae of *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) or *S. frugiperda* off their hosts and reduce egg hatch and larval survival rates (Kobori and Amano 2003; Wan et al. 2023). Also, rainfall-mediated soil moisture levels have been shown to affect pupation, emergence, and reproduction of species such as *Bactrocera tryoni* (Froggatt) (Diptera: Drosophilidae) (Hulthen and Clarke 2006) and *S. frugiperda* (Yan et al. 2022). Correlations between rainfall events and natural enemy parasitism rates and pest population levels have also been recorded in outdoor experiments (Karban et al. 2017; Agboyi et al. 2021; Grande et al. 2021). For example, parasitism by *T. remus* in a release area reach only 33% during a period of torrential rain compared to 72–100% in less rainy periods (Agboyi et al. 2021). Nevertheless, few studies have examined the impact of rain on either levels of parasitism or life history traits of parasitic wasps.

In this study, we investigated the effects of varying intensities of rainfall (control: 0 mm/h, light rain: 5.0 mm/h, moderate rain: 10.2 mm/h, and torrential rain: 42.8 mm/h) on parasitism, development, and survival of *T. remus* reared on *S. frugiperda.* Specifically, we measured the impact of rain on *T. remus* adults, and we examined impacts of rain on parasitized *S. frugiperda* eggs. Also, here we report findings of complementary studies on the probability of *S. frugiperda* eggs (parasitized by *T. remus*) being dislodged by rain and on the survival of such fallen parasitized eggs. Our results should aid in developing more effective natural enemy release strategies.

Materials and methods

Host insects and the parasitoid

Larvae from a wild population of *S. frugiperda* (maize strain) were collected from maize plants in Danzhou, Hainan, China, in July 2020 (Yan et al. 2021). Larvae were reared on fresh maize leaves in plastic boxes (20 × 15 × 8 cm, with a screened lid) under laboratory conditions (26 ± 1 °C, 75 ± 5% rh, L:D 12:12 photoperiod). Leaves were replaced and dead insects removed daily. Newly emerged adults were sexed and transferred into a gauze cage (20 × 20 × 20 cm) with fresh maize leaves for oviposition and tissue paper soaked in a 10% honey solution as a supplementary food source. The resulting eggs were used to rear the next generation. The colony was held under laboratory conditions for three generations before being used in our experiments.

A colony of the parasitoid *T. remus* was established from *S. frugiperda* eggs collected in maize fields where *S. frugiperda* was present in 2020. A subsample of the parasitoids reared from these eggs was preserved in 100% ethanol and stored at − 80 °C in the Environment and Plant Protection Institute, Chinese Academy of Tropical Agricultural Sciences, Danzhou, China. Taxonomists from the Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, China conducted the morphological identification, confirming the parasitoids in the sample as *T. remus.* Adult parasitoids obtained from this process were allowed to reproduce in a climatic chamber under the same conditions as above by supplying enough *S. frugiperda* eggs (five times as many eggs as parasitic wasps) in glass test tubes (0.6 cm diameter × 4 cm length) plugged with sterile cotton soaked in a 15% (w/v) honey solution. After every 24 h, the parasitized *S. frugiperda* eggs were placed in another tube and replaced with another set of individuals. *Telenomus remus* population used for our experiments had been reared for over three generations on *S. frugiperda*.

Rainfall simulation

Precipitation is defined as the depth of the water layer (mm) that falls to the ground in a given period, and 1 mm of precipitation is equivalent to an increase of 0.1 mL of water per 1 cm^2 of ground (Cai and Xu 2023). Light rainfall is defined as daily rainfall of less than 10 mm, moderate rainfall as 10 to 24.9 mm, and torrential rainfall as 25 to 49.9 mm (Cai and Xu 2023). The simulated rainfall system consists of a steel bracket (height = 2 m) plus the other instruments, which were purchased from Shandong Renke Measurement and Control Technology Co., Ltd., China). These items included a water supply pipe (15 m), a rotary nozzle, a water pressure control valve, a rain gauge, and a temperature and humidity recorder (Rahman et al. 2019). The nozzle was mounted 2 m above the ground, and the rain gauge mouth was 70 cm above the ground. Using this set up, we quantified rainfall intensity at different water pressures under air-conditioned laboratory conditions (26 ± 1 °C, 55% r.h., L:D 12:12 photoperiod) using an application time of 30 min. Our four treatments were (1) the control (0 mm/h), (2) light rain (5.0 mm/h), (3) moderate rain (10.2 mm/h), and (4) torrential rain (42.8 mm/h). During each simulated rain event, we recorded changes in the temperature and humidity in test environment, and we found that the temperature dropped ca 2 °C (26 to 24 °C) and the humidity rose by about 10% (55% to 65%) after the torrential rainfall. Temperature and relative humidity returned to their pre-rainfall levels by 30 min after the end of the rain event. We simulated this variable temperature (humidity) pattern using a climate chamber and found that it had no significant effect on parasitism, development, or survival of the parasitoid. We therefore excluded the indirect effects of rainfall (temperature and humidity changes due to rain). Our experiments only considered the physically disruptive effect of rainfall.

Exp. #1. Number of host eggs parasitized per female up to two time points (12 and 24 h) after rain

To assess the impact of exposure of adult parasitoids to a bout of rain (in the four treatments described above), *S. frugiperda* egg masses (24 h-old, with egg counts ranging from 83 to 107) were placed in centrifuge tubes, together with a control or rain-exposed mated female parasitoid (24-h old). Host eggs were removed 12 or 24 h afterwards from contact with the parasitoid. Five days later, the numbers of parasitized host eggs (recognized due to darkening of host egg) were counted under an ultra-field microscope.

Effect of simulated rainfall on survival of parental adult parasitoid

Immediate mortality To measure the amount of immediate mortality caused by various levels of rainfall, we transferred one pair of mated *T. remus* (24 h-old, one female: one male) with a mechanical aspirator into a polytetrafluoroethylene (PTFE) centrifuge tube (3 cm diameter × 11 cm length), the bottom of which had been replaced with a screen mesh to allow drainage of applied rainfall. Subsequently, the parasitoid wasps in the tubes were subjected to the four simulated rainfall treatments as described above (rainfall bouts lasting 30 min). The tilt angle of the centrifuge tube was adjusted to ensure that the rainfall entered the test tube in parallel (Chen et al. 2019; Rahman et al. 2019). The adult parasitoids in the test did not fly out of the tube due to the impact of the rainfall during the experimental period. During the period of simulated rain application, the control treatment experienced the same environment as the torrential rainfall treatment, but without the presence of rainfall (Chen et al. 2019; Rahman et al. 2019). There were ten replicates for each treatment.

Longevity among survivors of initial mortality Twenty female parasitoids that had survived the immediate effects of rain (being alive 24 h after application of rain), were immediately placed individually in centrifuge tubes where they were fed with 15% honey water. The longevity of those wasps was then tracked until all wasps died.

Effects on F1 progeny of rain-exposure of parental adult parasitoids

For the egg masses in Exp. #1 that were removed after 24 h with parental, rain-exposed parasitoids, we determined (1) the number of F1 parasitoids that emerged, (2) the sex ratio (as percentage female in F1 generation), and (3) the developmental time of the immature stage (from parasitism to the emergence of F1 adult parasitoids). The mean number of emerged individuals in each egg mass was consider one replicate, and the survival rate of the immature parasitoid stage (from oviposition to the emergence of F1 adults) was calculated as # F1 adult emerged / no. of parasitized *S. frugiperda* eggs.

Exp. #2. Effects of rainfall on retention rate of parasitized eggs and on traits of immature parasitoids not dislodged by rain

The purpose of Exp. #2 was to measure the impacts of rain on parasitoid progeny, first as numbers directly dislodged from maize leaves by rain and second as changes in life history traits of progeny of dislodged vs intact eggs. To that end, well-grown, uniformly tall (around 50 cm) maize plants at the nodulation stage (6-leaf stage) were transplanted into pots (25 cm diameter × 20 cm height) that were placed in screen cages (1 m height × 40 cm width × 50 cm length, with zippered tops). Moths were added to cages to allow for deposition of egg masses on leaves of maize plants. Then, egg masses (monolayer, 87–110 eggs) on maize leaves were selected for the experiment. Eggs in the masses were counted under a stereomicroscope (Nikon SMZ1500) and then placed in centrifuge tubes with their maize leaves. A pair of mated *T. remus* parasitoids was introduced into each tube, and then 24 h later, parasitoids were removed, and the egg masses were fixed to the adaxial surface of the leaves on the maize plants using a stapler to ensure that the heights of all egg masses on their maize plants were the same. One egg mass was placed on each maize plant, and ten replicates were set up for each of the four simulated rainfall treatments. The potted maize plants were repositioned so that each entire egg mass would be exposed to the rainfall and then the simulated rainfall was applied for 30 min (Chen et al. 2019; Rahman et al. 2019). The rainfall-treated egg masses were placed under a stereomicroscope, and the numbers of non-dislodged eggs were counted. Then, the non-dislodged eggs were transferred to centrifuge tubes and held for emergence of *T. remus* offspring. For these emerged parasitoids, we determined the sex ratio (as the percentage of females), the survival rate of immature parasitoids, and the developmental time of immature parasitoids (oviposition to adult emergence), all for non-dislodged eggs.

Also, the number of *T. remus* individuals emerging inside the screen cages (from dislodged eggs) and the developmental times and survival rates of parasitoids in host eggs dislodged by rain were recorded (the latter as the number of days from rain event to parasitoid emergence).

Statistical analysis

Statistical analyses were conducted in SPSS (IBM SPSS Statistics for Windows, Version 26.0, IBM Corp., Armonk, NY, USA). Data were tested for normality using the Shapiro–Wilk test, homogeneity of variances was assessed with Levene's Test, and some outliers were removed before further statistical analysis. When necessary, data were arcsine-transformed or log-transformed with a log base of 10 to follow a normal or near-normal distribution. One-way ANOVA was used to determine the effect of rainfall intensity on the number of parasitized eggs, the percentage of parasitized eggs, the number of emerged offspring, immature parasitoid developmental time, survival of immature parasitoids and female adults, egg retention rate, and sex ratio, followed by Tukey method for post hoc comparisons ($\alpha = 0.05$). The Kruskal–Wallis test with a Bonferroni adjusted post hoc ($\alpha = 0.05$) was used to analyze the differences in the number of emerged individuals (from dislodged eggs) between rainfall intensities. Two-way ANOVA was used to determine the interaction of rainfall intensity and location of egg masses (retained vs. dislodged eggs) on the *T. remus* parasitoids' immature stage survival (after an arcsine transformation) and immature stage duration, followed by the Tukey method for post hoc comparisons ($\alpha = 0.05$). Because of the extremely low number of dislodged eggs in the light rain treatment, only data from moderate and torrential rainfall intensities were analyzed.

Results

Exp. #1. Number of host eggs parasitized per female up to two time points (0–12 and 0–24 h) after rain

At the 12 h time point (0–12 h), the number of *S. frugiperda* eggs parasitized per female *T. remus* was negatively correlated with rainfall intensity. At the 12 h time point (0–12 h) after exposure to all tTree rainfall intensities, the numbers of host eggs parasitized per wasp were all significantly lower than that in the no-rain control (27.6 individuals) ($F = 70.003$, $df = 3$, $P < 0.001$) (Fig. 1A), with the lowest value being after torrential rainfall (7.6 individuals).

At the 24 h time point (0–24 h) only wasps subject to the torrential rainfall treatment laid significantly fewer eggs than the control ($F = 52.853$, $df = 3$, $P < 0.001$) (Fig. 1B).

Effect of simulated rainfall on survival of parental adult parasitoid

Rainfall significantly affected the survival of parental adult parasitoid wasps (from Exp. #1) during the first 24-h after exposure to rain ($F = 44.315$, $df = 3$, $P < 0.001$) (Fig. 2A), with significant reductions in survival under moderate rain (89% survival vs 100% in control) and then torrential rain (63% survival). However, the overall longevity of these parental generation females that survived the first 24 h after rainfall was not significantly different from the control ($F = 1.732$, $df = 3$, $P = 0.164$) (Fig. 2B).

Effects on F1 progeny of rain-exposure of parental adult parasitoids

Exposure of parental adult parasitoids in Exp. #1 to simulated rain, summed over all rain levels, had no subsequent significant effect on the developmental time of the resulting immature F1 parasitoids ($F = 2.631$, $df = 3$, $P = 0.065$) (Fig. 3A), except for the treatment in which parental adults were subject to torrential rainfall. The F1 offspring of the torrential rain group had a slight, but significant, increase in the developmental time of the immature stages (egg to adult emergence) compared to

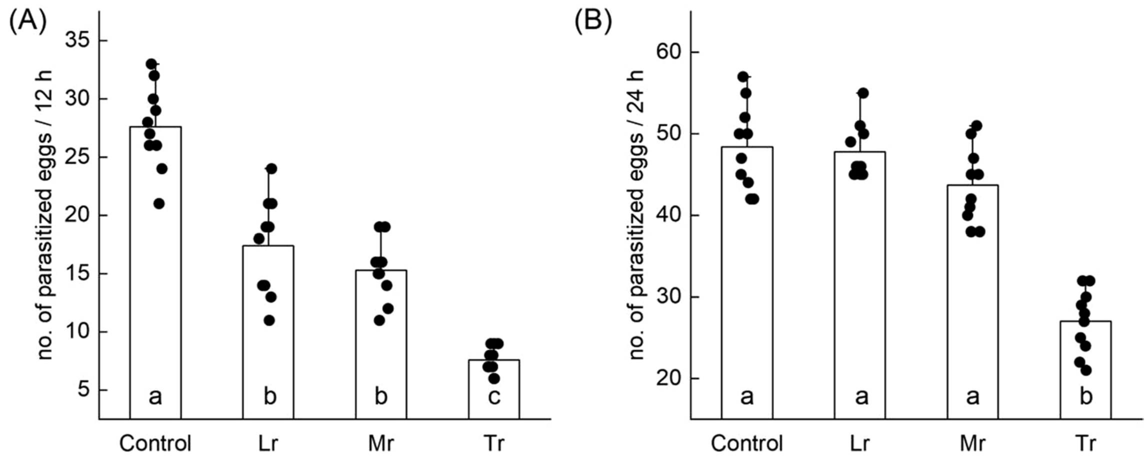

Fig. 1 The number of host eggs parasitized per female *T. remus* within 12 h (**A**) or 24 h (**B**) after a 30 min exposure to rainfall of various intensities: control = no rainfall (0 mm/h), Lr = light rain (5.0 mm/h), Mr = moderate rain (10.2 mm/h), and Tr = torrential rain (42.8 mm/h),. Different lowercase letters indicate significant differences between rainfall treatments (P < 0.05, one-way ANOVA followed by Tukey method for post hoc test)

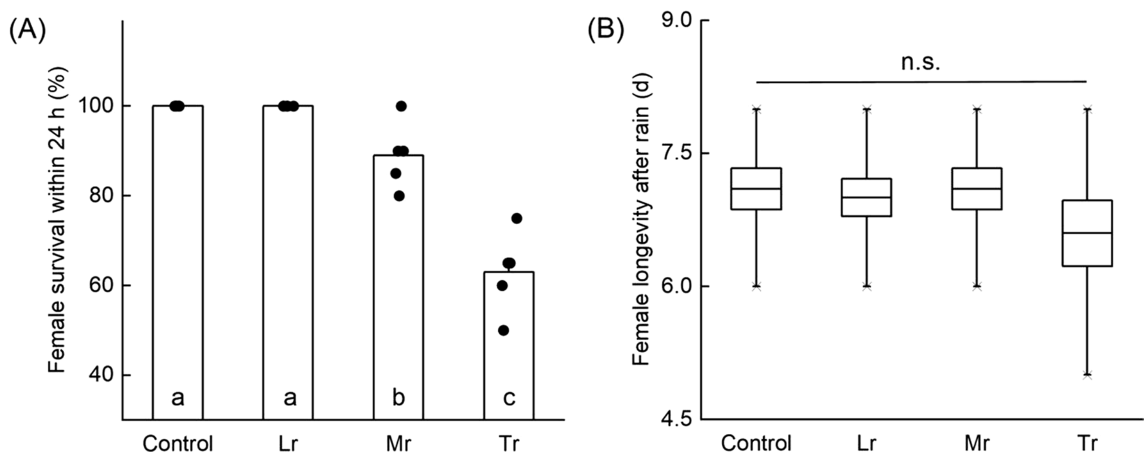

Fig. 2 Adult parasitoid survival within 24 h of exposure to rain (**A**) and subsequent total longevity (**B**) of female *T. remus* adults after exposure to rainfall of various intensities: control = no rainfall (0 mm/h), Lr = light rain (5.0 mm/h), Mr = moderate rain (10.2 mm/h), and Tr = torrential rain (42.8 mm/h). Different letters indicate significant differences between rainfall treatments (P < 0.05, one-way ANOVA followed by Tukey method for post hoc test)

the control (Fig. 3A). However, the number of emerged offspring was more strongly affected (F = 48.792, *df* = 3, P < 0.001) (Fig. 3B), which occurred because torrential rainfall suppressed the oviposition by female parasitoids during the rainfall event. This conclusion rests on the observation that immature parasitoid survival of the offspring (87.5% on average) itself was not significantly affected by exposure to rainfall of the adults during the oviposition bout (F = 0.518, *df* = 3, P = 0.672) (Fig. 3C). Also, there was no effect of exposure of adults to rain during the oviposition bout on the sex ratio of the resulting offspring compared to the control, with all groups having a strongly female-biased ratio (≈ 75.7%) (F = 0.209, *df* = 3, P = 0.889) (Fig. 3D).

Exp. #2. Effects of rainfall on retention rate of parasitized eggs and on traits of immature parasitoids not dislodged by rain

Retention rates of parasitized host eggs declined with increased rainfall intensity due to egg dislodgment by rain (F = 372.668, *df* = 3, P < 0.001), with Lr, Mr, and Tr treatments losing 2.1%, 13.0%, and 43.8% of the eggs to dislodgement by rain (Fig. 4A).

For parasitized eggs that were not dislodged by rain, neither the developmental time of immature parasitoids (egg-adult) (F = 1.376, *df* = 3, P = 0.266) (Fig. 4B) nor the progeny sex ratio (F = 0.405, *df* = 3, P = 0.750) (Fig. 4C) were affected by different rainfall intensities. For the non-dislodged parasitized eggs, the survival of

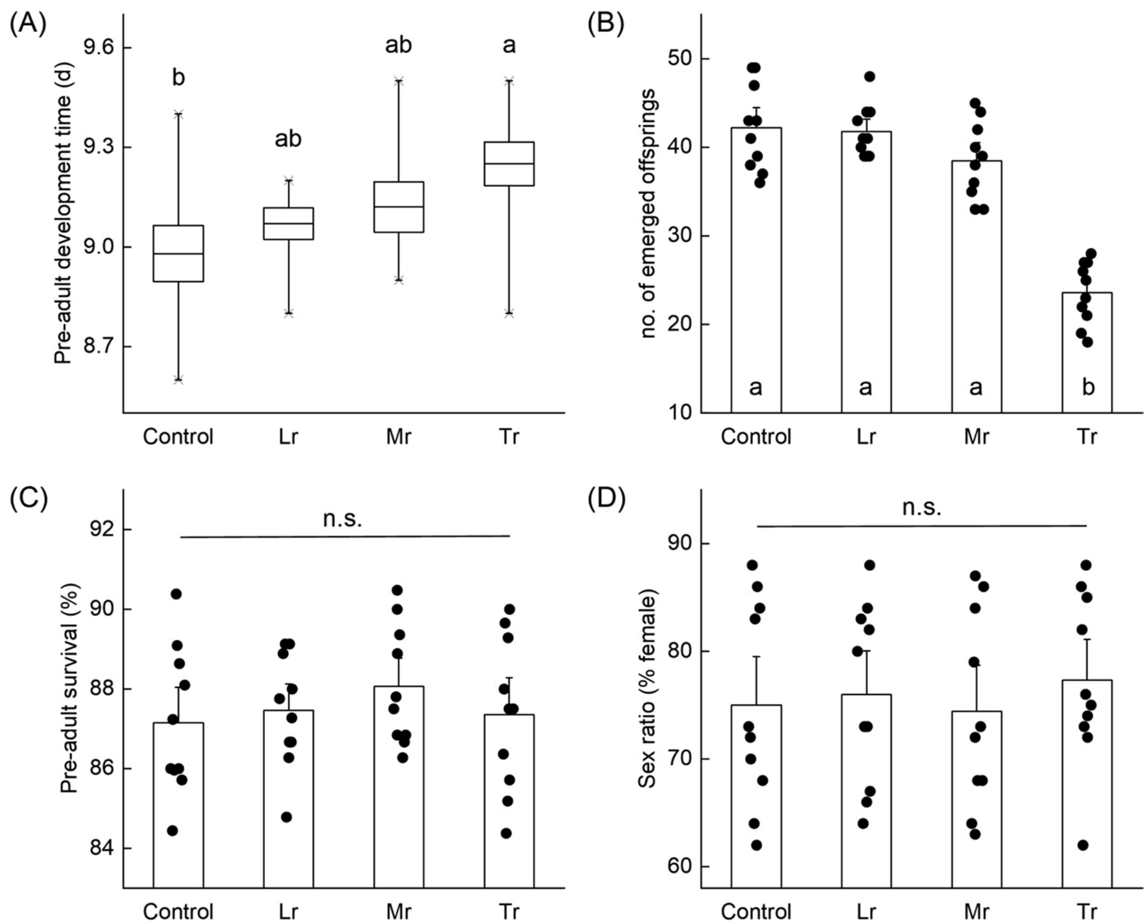

Fig. 3 Effects of rainfall exposure of adults during the parasitization bout on traits of resulting offspring: i.e., developmental duration (**A**), number of emerged F1 adults (**B**), F1 immature survival (**C**), and F1 sex ratio (**D**), where control = no rainfall (0 mm/h), Lr = light rain (5.0 mm/h), Mr = moderate rain (10.2 mm/h), and Tr = torrential rain (42.8 mm/h). Different lowercase letters indicate significant differences between rainfall treatments (P < 0.05, one-way ANOVA followed by Tukey method for post hoc test)

the immature parasitoid stage (parasitization to adult emergence) was significantly and negatively correlated with rainfall intensity (F = 364.469, *df* = 3, P < 0.001) (Fig. 4D), with torrential rainfall reducing survival to only 34.3% compared to 87.2% in the controls.

The developmental time of immature parasitoids in host eggs was not significantly affected by rainfall intensity or egg location (retained on host plant vs. dislodged by rain) (Table 1) (Fig. 5A). In contrast, survival of immature parasitoids in host eggs was significantly affected by both rainfall intensity, egg location, and their interaction (Table 1). Independent of rainfall intensity, the survival of immature parasitoids in retained host eggs (moderate rainfall = 73.0%; torrential rainfall = 34.3%) was significantly higher than that of eggs dislodged by rain, when compared at the same level of rainfall (moderate rainfall = 29.2%; torrential rainfall = 22.0%) (Fig. 5B). For parasitoid eggs retained on the host plant, the number of emerged *T. remus* F1 individuals decreased with increasing intensity of rainfall (F = 199.004, *df* = 3, P < 0.001) (Fig. 5C). In contrast, the number of F1 parasitoids emerging from dislodged eggs was positively related to rainfall intensity (H = 17.671, *df* = 3, P < 0.001) (Fig. 5D).

Discussion

We observed that after simulated rainfall, *T. remus* adults remained inactive for several hours, possibly drying their wings or regaining body temperature (Dickerson et al. 2012). During these hours, wasps did not attack hosts. Similarly, rainfall interrupted feeding in larvae of both *P. xylostella* and *Pieris brassicae* (Linnaeus) (Lepidoptera: Pieridae), and non-feeding persisted for a while even after rain ended (Chen et al. 2019). This period of inactivity may explain the reduction in parasitism in the first 12 h after rainfall for *T. remus.* Thereafter, this parasitoid regained normal activity under light and moderate rainfall intensities, such that parasitism over the first 24 h

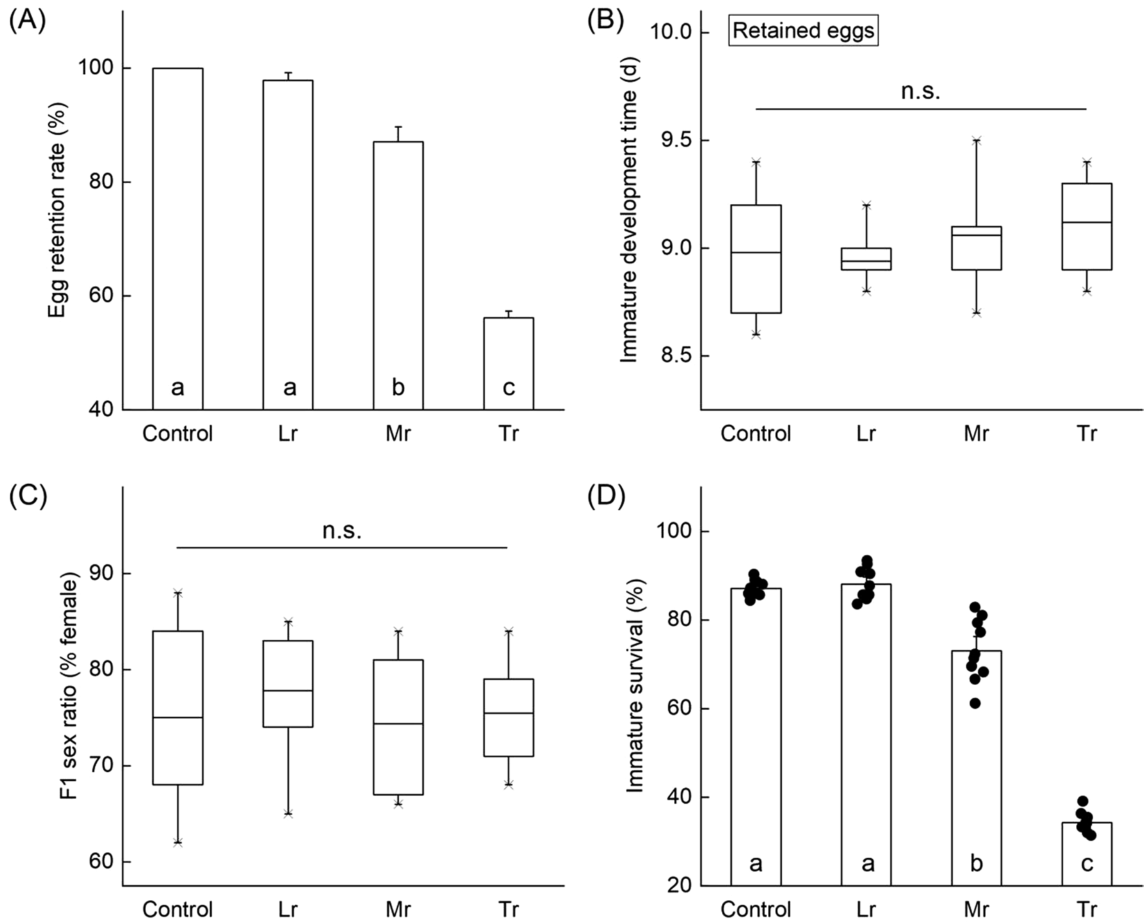

Fig. 4 Effects of rainfall on the rate of host-egg retention (i.e., eggs not dislodged by rain) (**A**), and well as the immature stage developmental duration (**B**), F1 sex ratio (**C**), and F1 immature survival rate (**D**) of parasitoids from non-dislodged eggs, where control = no rainfall (0 mm/h), Lr = light rain (5.0 mm/h), Mr = moderate rain (10.2 mm/h), and Tr = torrential rain (42.8 mm/h). Different lowercase letters indicate significant differences between rainfall treatments ($p < 0.05$, one-way ANOVA followed by Tukey method for post hoc test)

Table 1 Analysis of effects of rainfall intensity and egg location (retained on leaf vs dislodged) on the survival of immature parasitioids in host eggs and on developmental times of immature stages of *T. remus*

	Source	χ^2	*df*	P-value
Immature stagesurvival	Rainfall intensity	105.14	1	< 0.001
	location of eggs	173.78	1	< 0.001
	Rainfall * location	92.80	1	< 0.001
Immature stage developmental time	Rainfall intensity	0.83	1	0.362
	location of eggs	0.03	1	0.862
	Rainfall * location	0.05	1	0.821

after rain was not significantly different from the control. However, parasitism after torrential rainfall was reduced in both the 12 h and 24 h time points (post rain). This impact of torrential rain may be due to a damage to the wasp's wings, abdomen, and other body parts (Dickerson et al. 2012) or may have been due to effects on wasp detection or localization of hosts (Fink and Wolfgang 1995).

Mortality of *T. remus* adults occurred exclusively under moderate or torrential rainfall. Before rain treatments, parasitoids rested on the walls and bottom of the centrifuge tubes, and this distribution was not affected by light rainfall. In contrast, the moderate and torrential rainfall caused wasps to be concentrated at the bottom of the tubes, likely knocked down by the impact of the rain. The momentum transfer of such rainfall may have broken the surface tension of the parasitoid wasps' bodies (Dickerson et al. 2012). Also, water did not drain quickly out of the scintillation tubes used, potentially subjecting wasps to a risk of drowning in the water collected in the bottom of the tubes (Jones et al. 2018). However, over half (≈ 63%) of the parasitoid wasps survived even after experiencing the highest intensity rainfall for up to 30 min. Dickerson et al. (2012) showed that adults of *Anopheles*

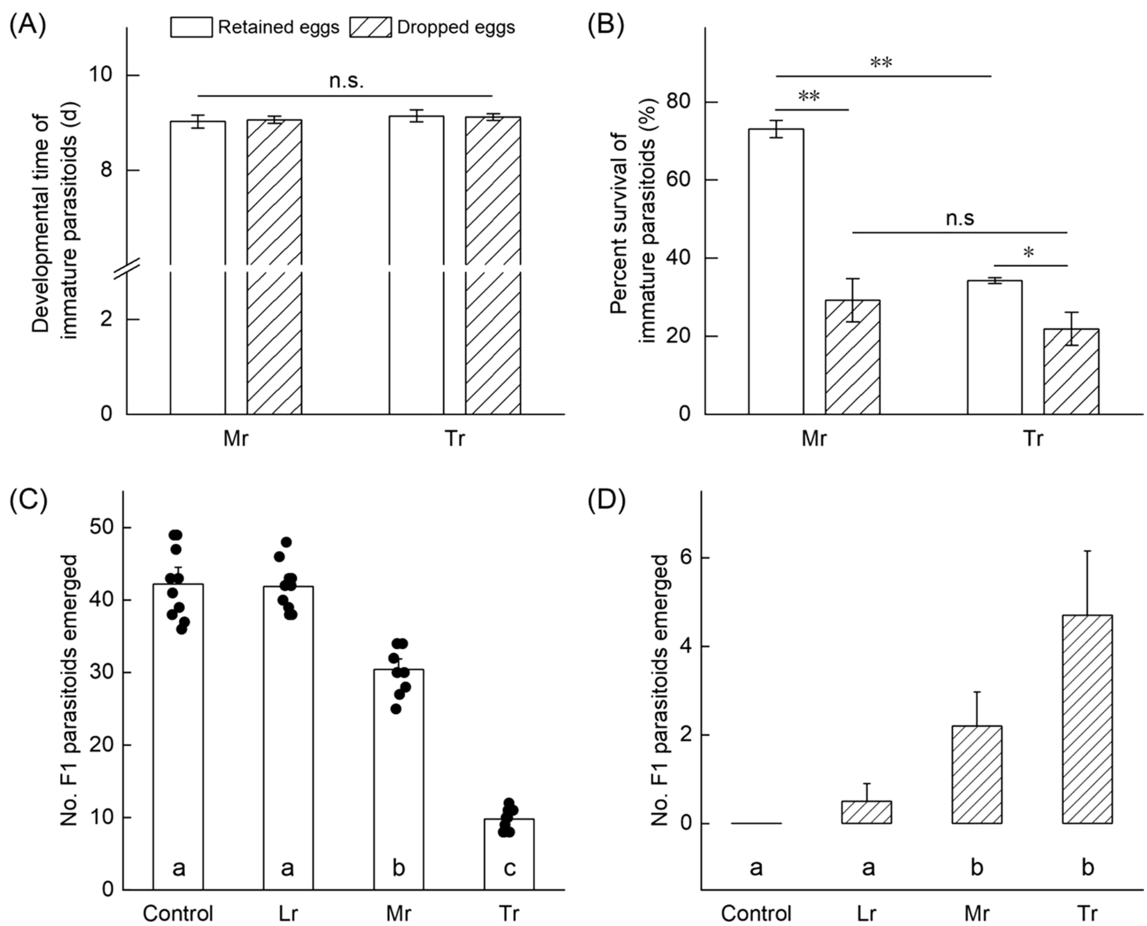

Fig. 5 Immature parasitoid developmental time (**A**) survival of immature parasitoids (**B**), emergence of F1 parasitoids from eggs retained on host plants (**C**), and emergence of F1 parasitoids from eggs dislodged by rain (**D**), where control = no rainfall (0 mm/h), Lr = light rain (5.0 mm/h), Mr = moderate rain (10.2 mm/h), and Tr = torrential rain (42.8 mm/h). (**A** and **B** $P < 0.05$, **$P < 0.01$, two-way ANOVA followed by Tukey method for post hoc test; **C** $P < 0.05$, one-way ANOVA followed by Tukey method for post hoc test; **D** $P < 0.05$, Kruskal–Wallis test followed by Bonferroni adjusted post hoc test)

sp. (Diptera: Culicidae) can survive the impact of raindrops, and, like *Apis mellifera* (Linnaeus) (Hymenoptera: Apidae), can fly in the rain. This rain tolerance may be related to the structural or physical properties of these insects' wings or epidermis, such as strong exoskeletons, hydrophobic hairs, or a lighter mass, facilitating recovery from rain impact and escape from puddles (Dickerson et al. 2012). Tiny wing structures such as denticles in *Acrida cinerea* (Thunberg) (Orthoptera: Acrididae) or bristles in *Vespa dybowskii* (Andre) (Hymenoptera: Vespidae) (Byun et al. 2009) and hydrophobic proteins (*A. mellifera*) may make it easier to separate the wings from raindrops (Liang et al. 2017).

Females that survived exposure to rainfall had almost the same subsequent lifespan as the control (non-rainfall-exposed) population, but parasitized fewer hosts, (i.e., produced fewer eggs, since *T. remus* produces only one offspring per egg when there are sufficient hosts) (Colmenarez et al. 2022). However, exposure to rainfall did not affect the quality of eggs laid by *T. remus* females, since the developmental rate of the immature parasitoid stage and their survival were not affected by rainfall events experienced by parental adults, except for females exposed to torrential rainfall, whose offspring had a significantly longer developmental time. This outcome may be due to a longer quiescence period after torrential rainfall, with lower adult host searching activity, causing a relative delay in the emergence of the next generation of parasitoids (Chen et al. 2019). In general, the strategy of sacrificing fecundity to enhance survival can be be adaptive, and in this study, we showed that exposure to rainfall of immature stages was unfavorable for their survival (Yan et al. 2023). If such behaviors allow females to survive longer, they may be able to better use resources if a more suitable site for egg laying can be located (Awmack and Leather

2002), as for example, was shown by Awmack and Leather (2002). Similarly, a short time (4 h) of thermal acclimatization significantly enhanced the subsequent survival of *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae) adults at 41 °C, but at the cost of reduced fecundity (Huang et al. 2007).

Being washed off the host's plant is another hazard of torrential rainfall for parasitoids. In our study, 12 to 44% of the host eggs were dislodged from the maize leaves as the intensity of rainfall increased. In other studies, also based on artificially simulated rainfall, 82.6% of the eggs and 60.7% of the third instar larvae of *P. xylostella* located on the upper surface of cabbage leaves were washed away by 17.3 mm of rain over a 1 h period (Kobori and Amano 2003). Wan et al. (2023) found that 7.2, 16.3, and 34.4% of *S. frugiperda* eggs (unparasitized) were dislodged by 10.2 mm/h, 26.5 mm/h, and 42.8 mm/h rainfall, respectively, over a 1-h period. Eggs of *P. xylostella* were morlikely to be dislodged from their host plants by rainthan were *S. frugiperda* eggs, Different lifestages were also found to have different risks of being dislodged by rain, perhaps related to differences in their size and physical charactera (Byun et al. 2009), or in surface hydrophobic proteins on their exoskeletons (Liang et al. 2017). *Spodoptera frugiperda* eggs and *P. xylostella* pupa, for example, are encased in a scaly layer and a silk cocoon, respectively, which may affect the degree of adhesion to the attachment surface, potentially mitigating the physical impact of rain (Rahman et al. 2019; Wan et al. 2023). However, the above researchers did not track individuals dislodged from their hosts. In our study, we found that the probability of successful development of parasitoids in dislodged host eggs to parasitoid adults was drastically reduced compared to that of retained eggs, which could be attributed to the fact that the egg masses suffered from two types of injury, namely, raindrop impact and collision with the ground. Also the egg masses may become covered by soil or fall into puddles, leading to death by mechanical injury or asphyxiation (Dickerson et al. 2012; Jones et al. 2018).

In our study, the survival of immature parasitoids in host eggs that were not dislodge by moderate or torrential rain was significantly reduced, but the developmental duration of the immature parasitoid stage was not significantly affected. Wan et al. (2023) found that the percentage of eggs retained on maize leaves after exposure to 10.2 mm/h, 26.5 mm/h, and 42.8 mm/h rainfall events were 87.4, 76.0, and 44.3, respectively. Chen et al. (2019) explored the effects of two frequencies of bouts of rainfall (one bout of 20 min vs. tTree of 5 min) (intensity: 20.9 mm/h) on the survival and development of *P. xylostella* on black mustard. Their results showed that the two rainfall treatments testd significantly reduced the survival and prolonged the developmental time of *P. xylostella* larvae, by 36% and 64%, respectively.

The above results suggest that rainfall can have different adverse effects on insect survival. For example, Chen et al. (2019) observed that the surface temperature of *Mutarda nigra* (L.) (Bernh) (Brassicales: Brassicaceae) leaves decreased by about 5 °C after rainfall, which may be the main reason for the prolongation of larval developmental time and this stage lengthening may have also indirectly affected larval survival. In contrast, in our study there was only one rainfall event, and the test was run under controlled conditions, equipped with air-conditioning, which prevented the parasitoid wasps from experiencing drastic temperature and humidity fluctuations during the experiment. Consequently, we found no change in the defevelopmental duration of *T. remus*' immature stage due to rainfall.

In all, in augmentative biocontrol programs in field crops, effects of rainfall events on natural enemies should be considered. Furthermore, the negative effect of rainfall on *T. remus* may have been underestimated in this experiment because factors such as sudden changes in temperature, humidity, and pathogen outbreaks accompanying rainfall can also seriously threaten natural enemy populations. Finally, in adjusting to rainfall events, the combined effects of rainfall on plant–insect-natural enemy interactions should be further studied in the future.

Conclusion

Whether occurring before or after parasitism, rainfall of moderate (10.2 mm/h) and torrential (42.8 mm/h) intensity, falling over a 30 min period, has a significant adverse effect on the survival of *T. remus*, and this effect is enhanced with increasing rainfall intensity. Also, rainfall of any intensity (5.0, 10.2, or 42.8 mm/h) will result in a notable decline in the number of hosts parasitized by *T. remus* adults for up to 12 h following rainfall. These findings suggest biocontrol practitioners should avoid releasing natural enemies on rainy days or when rain is forecast. Also, compensatory releases should be made quickly if unanticipated rainfall of relatively high intensity (> 10.2 mm/h) occurs during or just after such releases.

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Author contributions

SY and BL performed conceptualization; SY and QZ performed date curation; BL acquired funding; HL, JT, QZ and BJ performed research; SY and BL performed methodology; SY wrote the paper; BL, LZ and XH reviewed the paper. All authors have read and agreed to the published version of the manuscript.

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Data availability
The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Competing interests
The authors declare no competing interests.

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