

## Article

# Adaptive strategies of Rice Leaf Roller, *Cnaphalocrocis medinalis* in response to different rearing temperatures

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**Simple Summary:** Temperature directly affects the immature development, adult reproduction and subsequent migratory behavior for migratory insects. However, the adaptive strategies how to cope with stressful temperatures throughout their life cycle in some migratory insects are not well understood. In this study, we investigated the effects of rearing temperatures in the immature stage on immature development, adult reproduction and flight performance of *Cnaphalocrocis medinalis*, one major migratory pest feeding on rice. Our data suggest that *C. medinalis* may use different adaptive strategies to buffer the impacts of unsuitable temperatures. *C. medinalis* at high rearing temperatures can accelerate maturation development and invest more energy in migration to improve survival at the costs of delayed reproduction processes and reduced reproduction output. However, *C. medinalis* at low rearing temperatures accelerates reproduction processes and stimulates adult reproduction but delays maturation development.

**Abstract:** Understanding how species that follow different life-history strategies respond to stressful temperature can be essential to efficient treatments against agricultural pests. Here we focus on how the development and reproduction of *C. medinalis* is influenced by exposure to different rearing temperatures in the immature stage. We found that low (18 or 22 °C) or high (30 and 34 °C) rearing temperatures negatively affected the immature development and flight performance compared to the normal temperature 26 °C, with higher larval and pupal mortality, lower pupation and eclosion rates and shorter flight duration and distance. Low rearing temperatures significantly slowed down the immature process, but accelerated adult reproduction. However, high rearing temperatures had the opposite impacts. Interestingly, the flight of adults with un-mature rearing low temperatures (18 and 22 °C) significantly decreased their lifetime fecundity and mating frequency, but increased pre-oviposition period of females compared to the control; On contrast, high rearing temperatures (30 and 34 °C) significantly accelerated onset of oviposition and enhanced synchrony of spawning. These results indicate high rearing temperatures in the immature stage are more likely to trigger the onset of migration, but low rearing temperatures induces adults to have a greater resident propensity with stronger reproductive ability.

**Keywords:** *Cnaphalocrocis medinalis*; rearing temperatures; development; reproduction; flight performance

## 1. Introduction

Temperature is the major determinant factor influencing the organismal performance and the response to biotic and abiotic stressors as well as the biological processes of insects [1–4]. Previous studies have widely reported variations of development rates, survival rates, fecundity, longevity and other life-history characteristics in response to rearing temperatures in Lepidoptera and other insect species [5–7]. Development and reproduction of insects are largely dependent on environmental temperatures, with op-

timal environmental temperatures having a positive effect. On contrast, high or low temperatures negatively impact reproduction and population growth [8–10]. Jiang et al. [11] reported that the development, reproduction and longevity of *Mythimna separata* (Walker) exposed to high temperatures (above 30°C) were restrained, as demonstrated in *Sitophilus granaries* (L.) and other insect species [12–13]. Low temperatures reduced the development and fecundity in *Autographa gamma* (L.) [14] and delayed the pre-calling period in *M. separata* (Walker) [15]. To ensure survival and reproduction, insects adjusted their development and physiology to deal with extreme environmental conditions throughout their life cycle [16]. Ma et al. [17] revealed that trade-off between reproductive traits and response to environmental impacts was an important part of the life history strategy in insects, which impaired the damage of extreme temperatures on the insects.

Seasonal migrations like many bird species occur on a large scale and frequently in many migratory insects [18]. Long-distance migration behavior has been an important adaptive life history strategy for population maintenance and evolution of migratory insects [19–20], which allows migratory species to leave deteriorating habitats and seek for new breeding habitats [21–22]. Energetic investments in migration and flight organs are costly for limited internal resources, which may reduce energy investment in reproduction at the result of producing fewer offspring [23–24]. Resource trade-off between reproduction and flight associated characters during migration is common in most insects, such as *Aphis glycines* (Matsumura), *Spodoptera exempta* (Walker) and crickets [25–27], and this phenomenon was termed as the oogenesis-flight syndrome [28]. Zhang et al. [24] reported that migration-mediated reproductive costs were not absolutely negative, but instead depended on age, duration and frequency of the moth's initial flight. However, the trade-off between migration and reproduction under different rearing temperatures remains unknown in most long-distance migrants.

The rice leaf roller, *Cnaphalocrocis medinalis* (L.) (Lepidoptera: Pyralidae), is one predominant herbivorous pest in the rice ecosystems, which has caused serious economic losses in Asia, Australia and East Africa, especially in China [29–30]. In China, *C. medinalis* has been confirmed that they cannot overwinter in the north area of 30°N [31]. It is most likely that migration in *C. medinalis* is an important adaption to seasonal and regional variations, similar to *M. separata* [32–33]. Most studies have been conducted on long-term monitoring and seasonal migratory mechanism of *C. medinalis* adults [30, 34–35]. However, it remains unknown how *C. medinalis* copes with temperature variations throughout their life cycle and temperature stress to affect the trade-off between migration and reproduction. To gain insight into these questions above, we investigated the larval development, adult reproduction and flight capacity at different rearing temperatures in laboratory conditions. These results revealed *C. medinalis* larvae and adults can deal with ambient temperature stress to ensure survival and reproduction. This study expands our knowledge of the population adaptation strategy of *C. medinalis* with complex ambient environments and contributes to the pest management.

## 2. Materials and Methods

### 2.1 Insect rearing

Rice leaf roller pupae were collected from rice fields in Changde, Hunan Province, China, and then the populations were reared for obtaining eggs under laboratory conditions (26 ± 1°C, 85 ± 5% relative humidity (RH) and a photoperiod of 16L: 8D). Larvae in this experiment were reared with fresh corn seedlings 7–9 cm in height in the glass bottles (9 cm×13 cm, diameter×height) until pupation. After pupation, the pupae were transferred from leaves in glass bottles with moist cotton wool on the bottom to optimize conditions. After emergence, each pair of newly female and male moth was immediately transferred into new cylindrical plastic cages (10 cm×20 cm, diameter× height) and fed with fresh 10% honey solution (v/v) daily until the death of adults [24].

### 2.2 Temperature treatments

To investigate the influence of rearing temperature on development of immature stage (from egg to pupae stage), five temperature treatments were selected in this experiment, including 18, 22, 26, 30 and 34 °C (encountered by *C. medinalis* in the field) under which *C. medinalis* were reared during immature stage. The eggs and subsequent hatched larvae were reared at the five constant rearing temperatures under a photoperiod of 16L: 8D and  $85 \pm 5\%$  humidity until the eclosion of moths. Larvae were reared in culture plates (1 larval/well) and fed with maize seedlings at  $85 \pm 5\%$  relative humidity (RH) with a 16:8 h light: dark.

### 2.3 Larval development of *C. medinalis*

For the each temperature treatment, eggs laid at the same time were gently collected and individually placed in every well of 6-well plates to observe hatching every day. Subsequently, all the hatched larvae were reared on fresh corn leaves until pupation, and the instar stage and number of surviving larvae were examined and recorded daily. Egg-larval period included the duration from egg hatching to pupation, and pupal period was the duration between pupation to adult emergence. Subsequently, all the hatched larvae were reared on fresh corn leaves until pupation, and the instar stage and number of surviving larvae were examined and recorded daily. The individuals in each temperature treatment were divided into 3 replicates to count the larval and pupal mortality rate. Similarly, pupation and eclosion rates were calculated based on the number of pupae and emerging adults. The period of synchronized eclosion was defined as the number of days between a pupa's period of eclosion and the minimal period of eclosion among all pupae in the same treatment. It was used to measure the synchronization of adult emergence. The lower value of the period of eclosion represented the synchronized eclosion. The sex ratio was used to calculate the proportion of female and male adults [36].

### 2.4 Reproductive parameter determination

This experiment was designed to detect the influence of larval rearing temperatures on adult reproduction. After emergence, females and males from five temperature treatments were immediately paired (one male and one female) at each treatment and fed in cylindrical plastic cages (10 cm×20 cm, diameter×height) at  $26 \pm 1^\circ\text{C}$ , 85%-95% RH with a photoperiod of 14L:10D. The oviposition of the adults was observed and recorded daily until death. The reproductive parameters were measured based on previous studies [37–38], which were used to evaluate the variations in response to different temperatures. The pre-oviposition period (POP) was an important parameter to describe the duration from newly emergence to the first oviposition of adults. The period of first oviposition (PFO) was used to compute and evaluate the synchronization of first oviposition, which defined as the period from a female's POP to the minimal POP in a treatment. The lower PFO value showed the more synchronized initial oviposition [39]. After female death, the number of spermatophores was observed, and the mating frequency and mating rate were calculated [24]. Data were excluded from the analyses if either male or female escaped during the experiment. The experiments were terminated when all of the males and females died.

### 2.5 Flight treatment and capacity assessments

The measurement of flight performance was conducted with a 48-channel flight mill system, which automatically recorded the flight parameters (flight duration, flight distance and average flight velocity) [24, 40].

All the newly emerged moths including one-day-old females and males were anesthetized with ether, and the scales on the junction between the metathorax and abdomen were brushed away. A short hollow-plastic tether was glued to the dorsal surface of the metathorax using 502 super adhesives (Beijing Chemical Co.) and the adults were provided with 10% honey solution (v/v) before tethered flight. All tethered moths were tested for 6-h flight (23:00–05:00) on flight mills under dark condition at  $26 \pm 1^\circ\text{C}$  and

80%-85% RH [24, 35, 36]. The number of replicates of five immature temperature treatments (18, 22, 26, 30 and 34°C) were 14, 28, 19, 14 and 26 females, and 14, 30, 28, 15, 30 males, respectively. After tethered flight test, females and males were immediately paired and fed in cylindrical plastic cages under laboratory conditions. The reproductive parameters mentioned above were observed and recorded daily until death. The moths which were not tethered flight were used as the control.

## 2.6 Data analysis

All larval development parameters, flight capacity and reproductive parameters of adults were analyzed using one-way analysis of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) test ( $P < 0.05$ ) or independent samples t-tests ( $P < 0.05$ ). Flight capacity was also analyzed by a two-way ANOVA with sex (two levels) and rear temperature (five levels). To compare the impact of flight (flying vs. non-flying) and rear temperatures (18, 22, 26, 30 and 34 °C) on adult reproduction, two-way analysis of variance (ANOVA) was also used. All statistical analyses were performed with SPSS software (version 18.0; SPSS, Chicago, IL, USA).

## 3. Results

### 3.1 Development of *C. medinalis* exposed to different un-mature rearing temperatures

Rearing temperatures had a significant influence on *C. medinalis* from egg to larval period ( $F_{4, 1132} = 3246.68$ ,  $P < 0.01$ ) and pupal period ( $F_{4, 1132} = 771.84$ ,  $P < 0.01$ ). Low temperatures (18 and 22 °C) significantly extended the larval period and pupal period compared to the treatments of 26, 30 and 34 °C at the result of significantly delaying larval and pupal development under these temperatures. However, the mostly significant effects on larval period and pupal periods were found in the *C. medinalis* reared at 30 °C compared with other treatments (Table 1). Below or above 26 °C increased the mortality rate of larvae and pupae, and reduced the pupation rate, eclosion rate and sex ratio, although there were no significant differences (Table 1) ( $P > 0.05$ ). However, *C. medinalis* pupae exposed to low temperatures (18 and 22 °C) had a significantly higher period of synchronized eclosion than those at 26, 30 and 34 °C ( $F_{4, 1132} = 64.21$ ,  $P < 0.01$ , Table 1).

### 3.2 Flight capacity of *C. medinalis* emerged from different un-mature rearing temperatures

Rearing temperatures had significant effects on the flight duration and flight distance. However, the sex and interaction between rearing temperatures and sex had no effect on the flight duration and flight distance (Table 2, 3). There were no significant differences in average velocity of females and males (Table 2, 3).

Females at 26 °C had the longest flight duration and flight distance, which were significantly higher than those at 30 °C (flight duration:  $F_{4, 110} = 2.83$ ,  $P = 0.03$ ; flight distance:  $F_{4, 110} = 3.14$ ,  $P = 0.02$ , Table 3). Similarly, high rearing temperatures (30 and 34 °C) significantly decreased flight duration and flight distance of males compared to the moths exposed to 26 °C (flight duration:  $F_{4, 105} = 3.98$ ,  $P = 0.03$ ; flight distance:  $F_{4, 105} = 3.17$ ,  $P = 0.02$ , Table 3).

Comparisons of flight capacity between females and males showed that females exposed to 18 °C had a lower flight duration, flight distance and average velocity than males; in contrast, their flight duration, flight distance and average velocity exceeded males in the above 18 °C treatments, especially the 34 °C, significant decrease was observed in flight duration ( $t_{53} = 2.51$ ,  $P = 0.02$ ), indicating that females might have greater flight potential than males at above 18 °C (Table 3).

### 3.3 Influence of un-mature rearing temperature and flight on reproduction

Rearing temperature and the interaction between flight and rearing temperature significantly affected the POP (Rearing temperature:  $F_{4, 239} = 3.21$ ,  $P = 0.01$ ; Flight \* rearing temperature:  $F_{4, 239} = 5.88$ ,  $P < 0.01$ , Table 4).

The PFO was significantly influenced by the flight and the interaction between flight and rearing temperature (Flight:  $F_{1, 239} = 7.44$ ,  $P < 0.01$ ; Flight \* rearing temperature:  $F_{4, 239} = 5.50$ ,  $P < 0.01$ , Table 4). Flight, rearing temperature and their interaction had significant effects on the lifetime fecundity, mating frequency and female longevity (Table 4). The oviposition period was significantly affected by flight and rearing temperature, but not by their interaction (Flight:  $F_{1, 239} = 5.23$ ,  $P = 0.02$ ; Rearing temperature:  $F_{4, 239} = 5.88$ ,  $P < 0.01$ , Table 4). Only flight had significant effects on the mating rate (Flight:  $F_{1, 239} = 4.48$ ,  $P = 0.04$ , Table 4).

Rearing temperature had a significant effect on the POP of females between the two groups (Flying group:  $F_{4, 99} = 2.49$ ,  $P = 0.05$ ; Nonflying group:  $F_{4, 140} = 6.13$ ,  $P < 0.01$ , Fig 1). Nonflying females at 18 and 22 °C had significantly shorter POPs than the moths at 26 °C. However, in the flying groups, females at 18 °C had the longest POP in all temperature treatments, which was significantly longer than the moths at 30 °C (Fig 1). In the non-flying groups, high rearing temperatures (30 and 34 °C) increased the PFOs of females compared to the treatments of 18, 22 and 26 °C, but there were no significant differences ( $F_{4, 140} = 2.42$ ,  $P > 0.05$ , Fig 2). However, in the flying group, high rearing temperatures (30 and 34 °C) significantly reduced the PFO of flying females compared to the treatment of 22 °C ( $F_{4, 99} = 4.40$ ,  $P < 0.01$ ), causing a better synchronization of first oviposition under these high treatments (Fig 2). There were significant differences in lifetime fecundity of females between the two groups treated by different rearing temperatures (Flying group:  $F_{4, 99} = 3.48$ ,  $P = 0.01$ ; Nonflying group:  $F_{4, 140} = 9.23$ ,  $P < 0.01$ , Table 5). Females at 18 and 22 °C laid more eggs than the moths at 26, 30 and 34 °C in the nonflying group. Similarly, flight-induced lifetime fecundity of females at 18 °C was significantly higher than that in the 34 °C treatment (Table 5).

Rearing temperature significantly affected the mating frequency of females in the nonflying group ( $F_{4, 140} = 2.21$ ,  $P < 0.01$ ). Females at 18 °C had the greatest mating frequency, which was higher than those in the 26, 30 and 34 °C treatments of the nonflying group. But there was no significant difference in mating frequency of females in the flying group ( $F_{4, 99} = 0.53$ ,  $P > 0.05$ , Table 5). Significant differences were found for the female longevity between the two groups treated by different rearing temperatures (Flying group:  $F_{4, 99} = 7.40$ ,  $P = 0.01$ ; Nonflying group:  $F_{4, 140} = 8.48$ ,  $P < 0.01$ , Table 5). High rearing temperatures (30 and 34 °C) significantly decreased the female longevity compared to the treatments of 18 and 26 °C in the nonflying group. The female longevity at 34 °C was also significantly shorter than the moths at 18 °C in the flying group (Table 5). Likewise, the oviposition period ( $F_{4, 140} = 8.48$ ,  $P < 0.01$ ) and mating rate ( $F_{4, 140} = 2.76$ ,  $P = 0.03$ ) of moths at 30 and 34 °C were significantly lower than those in the 18 and 22 °C treatments of the nonflying group (Table 5). In the flying group, the greatest oviposition period occurred in females exposed to 18 °C, which was significantly higher than that in the 22, 30 and 34 °C treatments ( $F_{4, 99} = 6.79$ ,  $P < 0.01$ , Table 5). However, rearing temperature had no significant differences in mating rate of flying moths ( $F_{4, 99} = 0.53$ ,  $P > 0.05$ , Table 5).

Flight significantly reduced the POPs of females treated with 26, 30 and 34 °C compared to the controls (the nonflying moths) at each rearing temperature (26 °C:  $t_{56} = -2.06$ ,  $P = 0.04$ ; 30 °C:  $t_{34} = -3.34$ ,  $P < 0.01$ ; 34 °C:  $t_{45} = -3.49$ ,  $P < 0.01$ ), resulting in beginning to oviposit significantly earlier under these temperatures. However, flying females at 18 °C showed a significant delay in spawning ( $t_{44} = 2.98$ ,  $P < 0.01$ , Fig 1). The PFOs of moths at 30 and 34 °C were significantly decreased by the flight compared to the controls at the same temperature (30 °C:  $t_{34} = -4.64$ ,  $P < 0.01$ ; 34 °C:  $t_{45} = -3.49$ ,  $P = 0.01$ ), indicating the synchronized oviposition of flying females exposed to high temperatures was better than the nonflying moths. Furthermore, flying females at 18 and 22 °C had a higher PFO than the nonflying females, but the difference was not significant (Fig 2). Flight also significantly decreased the lifetime fecundity (18 °C:  $t_{44} = -3.73$ ,  $P < 0.01$ ; 22 °C:  $t_{65} = -4.94$ ,  $P < 0.01$ ) and mating frequency (18 °C:  $t_{44} = -3.25$ ,  $P < 0.01$ ; 22 °C:  $t_{65} = -2.38$ ,  $P = 0.02$ , Table 5) of females exposed to 18 and 22 °C than the nonflying moths. Similarly, flying females at 22 and 26 °C had significantly shorter longevities than the nonflying moths (22 °C:  $t_{65} = -3.41$ ,



$P < 0.01$ ; 26 °C:  $t_{56} = -2.99$ ,  $P < 0.01$ , Table 5). Compared to the nonflying moths, the oviposition period of females at 22 °C was significantly shortened by the flight ( $t_{56} = -3.85$ ,  $P < 0.01$ , Table 5). Similarly, flight significantly decreased the mating rate of females at 18 °C compared to the nonflying moths ( $t_{44} = -2.464$ ,  $P = 0.018$ , Table 5).

3.4. Tables and Figures

**Table 1** Larval development of *C. medinalis* under different rearing temperatures.

Development parameter	Rearing temperatures				
	18 °C	22 °C	26 °C	30 °C	34 °C
Egg-larval period (d)	53.80 ± 0.39 a	30.59 ± 0.23 b	23.76 ± 0.08 c	21.76 ± 0.17 d	23.25 ± 0.14 c
Pupal period (d)	17.83 ± 0.31 a	8.87 ± 0.19 b	5.78 ± 0.09 c	4.41 ± 0.11 d	4.99 ± 0.10 d
Larval mortality rate (%)	74.00 ± 10.51 a	49.35 ± 12.52 a	46.00 ± 25.14 a	59.72 ± 8.30 a	53.05 ± 18.49 a
Pupal mortality rate (%)	36.45 ± 23.86 a	25.62 ± 8.71 a	18.85 ± 3.45 a	27.06 ± 11.67 a	27.70 ± 5.04 a
Pupation rate (%)	35.14 ± 25.47 a	50.65 ± 12.52 a	54.00 ± 25.14 a	40.28 ± 8.30 a	46.95 ± 18.49 a
Eclosion rate (%)	71.34 ± 8.15 a	59.94 ± 23.97 a	76.64 ± 3.98 a	70.82 ± 13.31 a	68.61 ± 6.28 a
Period of synchronized eclosion (d)	9.40 ± 0.48 a	5.66 ± 0.24 b	4.08 ± 0.13 c	4.29 ± 0.20 c	4.61 ± 0.17 c
Sex ratio (♀: ♂)	1.06 ± 0.40 a	1.28 ± 0.31 a	1.36 ± 0.35 a	1.11 ± 0.71 a	1.24 ± 0.78 a

Means with the different letters in the same row represent significant differences at the 5% level by Tukey’s HSD test. Sample sizes of 18, 22, 26, 30 and 34 °C treatments are 153, 356, 443, 217 and 318, respectively.

**Table 2** Results of two-way ANOVA analysis of rear temperature and sex on flight capacity of *C. medinalis*.

Parameters	Source	Df	MS	F	P
Flight duration (h)	Rear temperature	4	17.56	5.12	< 0.001
	Sex	1	2.88	0.84	0.360
	Rear temperature × Sex	4	4.97	1.46	0.217
	Error	211	3.41		
Flight distance (km)	Rear temperature	4	137.61	5.38	< 0.001
	Sex	1	5.25	0.21	0.651
	Rear temperature × Sex	4	17.95	0.70	0.592

	Error	211	25.58		
Average velocity (km/h)	Rear temperature	4	1.63	3.02	0.119
	Sex	1	0.07	0.13	0.721
	Rear temperature $\times$ Sex	4	0.12	0.22	0.928
	Error	211	0.54		

**Table 3** Flight capacity of *C. medinalis* males and females exposed to different rearing temperatures in the immature stage.

Parameters	Sex	Rearing temperatures				
		18 °C	22 °C	26 °C	30 °C	34 °C
Flight duration (h)	Female	2.34 $\pm$ 0.47 ab	3.37 $\pm$ 0.36 ab	3.87 $\pm$ 0.37 a	2.15 $\pm$ 0.42 b	3.25 $\pm$ 0.36 ab*
	Male	3.09 $\pm$ 0.55 ab	3.04 $\pm$ 0.34 ab	3.74 $\pm$ 0.34 a	1.86 $\pm$ 0.43 b	2.02 $\pm$ 0.34 b
Flight distance (km)	Female	4.42 $\pm$ 1.14 ab	7.13 $\pm$ 1.09 ab	8.12 $\pm$ 1.13 a	2.78 $\pm$ 0.55 b	6.30 $\pm$ 0.98 ab
	Male	6.07 $\pm$ 1.29 ab	6.34 $\pm$ 0.96 ab	7.92 $\pm$ 0.97 a	2.62 $\pm$ 0.74 b	4.15 $\pm$ 0.91b
Average velocity (km/h)	Female	1.54 $\pm$ 0.21 a	2.24 $\pm$ 0.17 a	2.24 $\pm$ 0.14 a	2.63 $\pm$ 0.13 a	2.76 $\pm$ 0.18 a
	Male	1.75 $\pm$ 0.21 a	1.82 $\pm$ 0.15 a	1.92 $\pm$ 0.13 a	1.22 $\pm$ 0.13 a	1.67 $\pm$ 0.14 a

Different lowercase letters in the same row indicate significant differences by Tukey's HSD test at 5% level. "\*", "\*\*\*" represent significant or highly significant differences in the same column by t-test ( $p < 0.05$  or  $p < 0.01$ ). Sample sizes, from low to high temperature treatment, are 14, 28, 29, 14 and 26 females, and 14, 30, 28, 15 and 29 males, respectively.

**Table 4** Results of two-way ANOVA of rear temperature and flight treatments (flying vs. non-flying) on oviposition parameters of *C. medinalis*.

Parameters	Source	Df	MS	F	P
Preoviposition period (d)	Flight	1	0.18	0.02	0.881
	Rear temperature	4	25.95	3.21	0.014
	Flight $\times$ rear temperature	4	47.55	5.88	< 0.001
	Error	239	8.09		
Period of first oviposition (d)	Flight	1	60.21	7.44	0.007

	Rear temperature	4	1.80	0.22	0.926
	Flight × rear temperature	4	44.54	5.50	< 0.001
	Error	239	8.09		
Lifetime fecundity	Flight	1	239587.29	25.23	< 0.001
	Rear temperature	4	78574.77	8.28	< 0.001
	Flight × rear temperature	4	38170.91	4.02	0.004
	Error	239	9495.81		
Mating frequency	Flight	1	3.18	9.39	0.002
	Rear temperature	4	1.05	3.10	0.016
	Flight × rear temperature	4	0.99	2.93	0.022
	Error	239	0.34		
Female longevity (d)	Flight	1	121.79	5.82	0.017
	Rear temperature	4	239.13	11.43	< 0.001
	Flight × rear temperature	4	70.42	3.37	0.011
	Error	239	20.93		
Oviposition period (d)	Flight	1	81.24	5.23	0.023
	Rear temperature	4	137.87	8.88	< 0.001
	Flight × rear temperature	4	36.10	2.33	0.057
	Error	239	15.52		
Mating rate	Flight	1	1.08	4.48	0.035
	Rear temperature	4	0.41	1.70	0.152
	Flight × rear temperature	4	0.23	0.950	0.437
	Error	239	0.24		

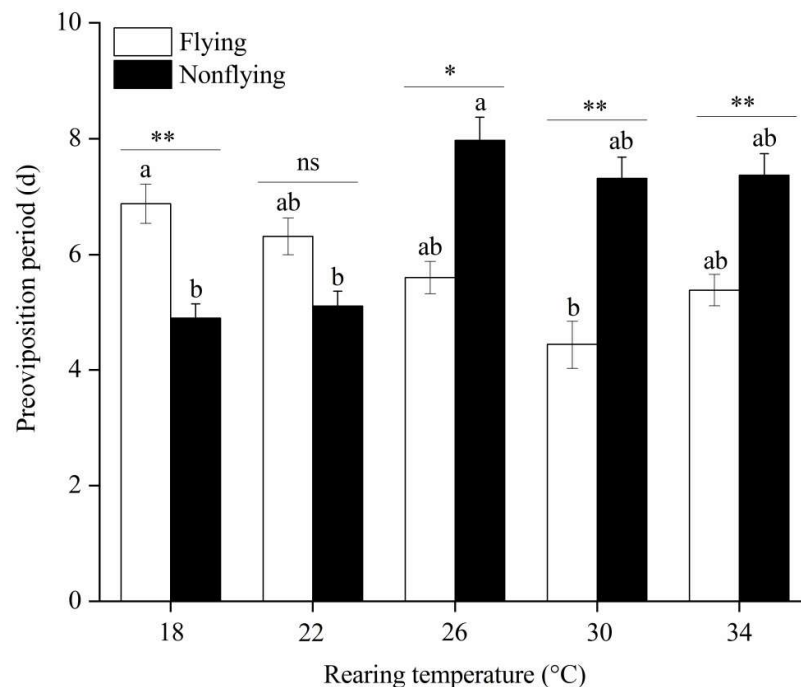
**Table 5** Reproductive performance of *C. medinalis* females between the flying and non-flying groups treated by different rearing temperatures in the immature stage.

Parameters	Treatments	Rearing temperatures				
		18 °C	22 °C	26 °C	30 °C	34 °C
Lifetime fecundity	Flying	94.75 ± 16.34 a**	46.16 ± 10.48 ab**	78.30±17.70 ab	48.00 ± 23.00 ab	30.35 ± 8.61 b

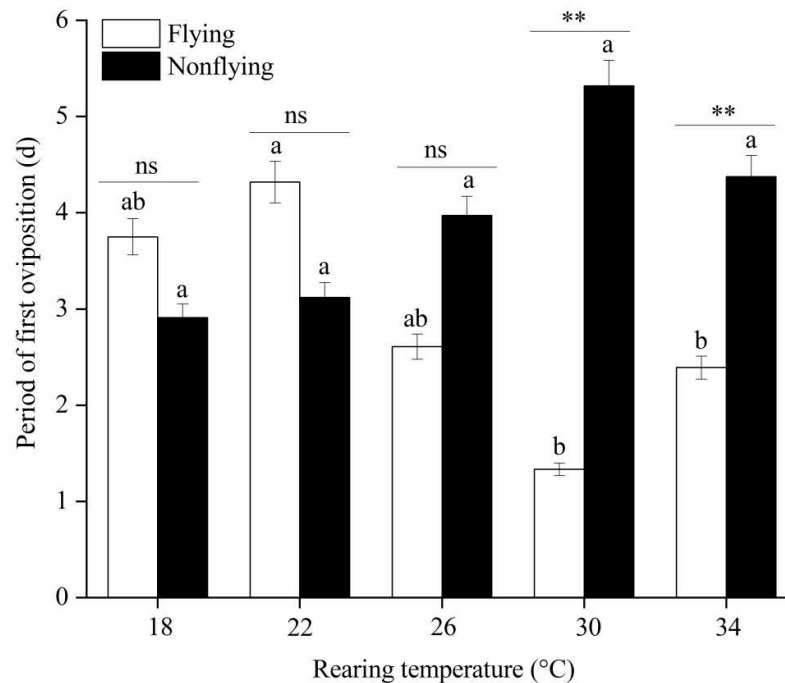


	Nonflying	214.23 ± 28.31 a	181.40 ± 20.13 a	103.20 ± 17.38 b	57.77 ± 18.33 b	74.62 ± 20.83 b
Mating frequency	Flying	0.33 ± 0.10 a**	0.44 ± 0.10 a*	0.48 ± 0.11 a	0.33 ± 0.17 a	0.30 ± 0.10 a
	Nonflying	1.05 ± 0.20 a	0.81 ± 0.10 ab	0.51 ± 0.08 bc	0.32 ± 0.10 c	0.42 ± 0.10 bc
Female longevity (d)	Flying	15.21 ± 1.07 a	9.44 ± 0.89 b**	11.96 ± 1.05 ab**	13.33 ± 1.59 ab	9.13 ± 0.55 b
	Nonflying	16.27 ± 0.93 a	13.74 ± 0.82 ab	15.54 ± 0.68 a	10.45 ± 0.89 b	10.58 ± 0.97 b
Oviposition period (d)	Flying	7.92 ± 0.75 a	3.72 ± 0.63 b**	5.56 ± 0.95 ab	3.67 ± 1.33 b	3.26 ± 0.44 b
	Nonflying	8.05 ± 0.98 a	7.76 ± 0.72 a	6.74 ± 0.79 ab	3.68 ± 0.64 c	4.04 ± 0.63 bc
Mating rate (%)	Flying	33.33 ± 9.83 a*	44.00 ± 10.13 a	47.83 ± 10.65 a	33.33 ± 16.67 a	30.43 ± 9.81 a
	Nonflying	68.18 ± 10.16 a	66.67 ± 7.36 a	51.43 ± 8.57 ab	31.82 ± 10.16 b	41.67 ± 10.28 ab

Different lowercase letters in the same row indicate significant differences by Tukey's HSD test at 5% level. "\*\*", "\*\*\*" represent significant or highly significant differences in the same column by t-test ( $p < 0.05$  or  $p < 0.01$ ). Sample sizes for each flying treatment are 22, 42, 35, 22 and 24 females, and each control treatment are 24, 25, 23, 15 and 23 females, from left to right, respectively.



**Figure 1.** Preoviposition period (POP) of *C. medinalis* in the flying vs. non-flying groups under different rearing temperatures. Data are presented as mean ± SE. Different lowercase letters indicate significant differences by Tukey's HSD test at 5% level. "\*\*", "\*\*\*" represent significant or highly significant differences in the same bars by t-test ( $p < 0.05$  or  $p < 0.01$ ). Sample sizes for each flying treatment are 22, 42, 35, 22 and 24 females, and each control treatment are 24, 25, 23, 15 and 23 females, from low to high temperature, respectively.



**Figure 2.** Period of first oviposition (PFO) of *C. medinalis* in the flying vs. non-flying groups under different rearing temperatures. Different lowercase letters above group bars indicate significant differences by Tukey's HSD tests ( $p < 0.05$ ). \*, \*\* above bars represent significant or highly significant differences between the flying and non-flying treatments at the same temperature (t-test,  $p < 0.05$  or  $p < 0.01$ ). Sample sizes, from low to high temperature, in flying treatments are 22, 42, 35, 22 and 24 females, and in control treatments are 24, 25, 23, 15 and 23 females, respectively.

#### 4. Discussion

Temperature is considered one major environmental factor as it could profoundly influence the population development and reproduction as well as subsequent migratory capacity and behavior of migratory insects [41–43]. In this study, we found that below or above the optimal rearing temperatures in the immature stage (including egg, larval, or pupal stages) negatively affected the larval development and subsequent adult reproduction and flight capacity of *C. medinalis*, which were consistent with previous findings [10, 44]. Low rearing temperatures (18 and 22 °C) significantly delayed the larval development, but accelerated adult reproduction compared to the 26 °C treatment. However, high rearing temperatures (30 and 34 °C) accelerated the development of larva and pupa, but caused the delay of adult oviposition and the decrease of egg production. Furthermore, flight also significantly affected the reproduction of adult from different rearing temperature treatments. Flight favored the migration of *C. medinalis* adults after experiencing high rearing temperatures (30 and 34 °C), via shortening the preoviposition period and increasing the synchronized oviposition. On contrast, flight significantly promoted the lifetime fecundity and mating frequency of moths treated by low rearing temperatures (18 and 22 °C), thereby reducing the motivation of migration. These results may reflect adaptive ecological strategies to different environmental temperatures for *C. medinalis*.

Development of *C. medinalis* differed significantly under different un-mature rearing temperatures. Both high and low temperatures (above 26 °C) caused higher larval and pupal mortality, and lower pupation and eclosion rate. On contrast, *C. medinalis* larvae

and pupae developed well at normal temperature 26 °C, with the lowest mortality and the highest pupation rate and eclosion rate. Thus, these results were consistent with previous reports that extreme low and high temperatures negatively influenced the larval growth and development [45–46], such as *Spodoptera exigua* (Hübner) [47], *M. separata* (Walker) [13] and other Lepidopteran insect species. As expected, low temperature resulted in slower growth rate and longer development time in insects [48], while high temperature accelerated the development of the egg, larval and pupal period [40]. Our results also found that low rearing temperatures (18 and 22 °C) significantly slowed down the larval development and caused poor synchronized eclosion of *C. medinalis*, with significant increases in larval and pupal period as well as the lengthening of the period of synchronized eclosion compared to 26 °C. However, high rearing temperatures (30 and 34 °C) reduced the larval and pupal period, but accelerated maturation processes.

Reproductive traits are sensitive to thermal variations, but the effect of stressful temperatures in early life stages on adult performance is still a matter of debate in insects [17]. Potter et al. [49] stated that early life stress had no effect on adult performance based on the adaptive decoupling hypothesis and life cycle modularity hypothesis. However, recent studies have found that extreme high temperatures occurring in immature stage (including egg, larval, or pupal stages) can decrease the fecundity of adults through carry-over effects [50–51] or even reduce the offspring survival via transgenerational effects [52]. Our results showed that high rearing temperatures (30 and 34 °C) in immature stage negatively affected the reproduction and longevity of adults. However, low rearing temperatures in early life stages positively stimulated adult reproduction, which resulted in decreased POP and increased egg production of females. These findings suggested that rearing temperature in the immature stage can influence reproductive performance of *C. medinalis* adults. In many migratory insect species, relatively long POP was an important behavioral characteristic of migrants [19, 23, 39], which might reduce the number of days available for reproduction but result in increased flight potential and time window to engage in migration [43], such as *Loxostege sticticalis* (L.) [53], *M. separata* (Walker) [54] and *C. medinalis* (Guenée) [55]. We therefore speculated that rearing temperatures in the immature stage might determine the migration and differentiation of *C. medinalis* adults. Our results were consistent with the previous findings that rearing temperature in the immature stage could induce development into either resident or migrant adults for *M. separata* [33, 37]. Females at low un-mature rearing temperature had a greater resident propensity with strong reproductive ability [56]. On contrast, high un-mature rearing temperature increased their migratory propensity and motivation [11]. Field studies also indicated that the primary driver of *C. medinalis* northward migration over the summer months was typically assumed to escape from high temperature [31].

Temperature can directly influence flight like other insect behaviors by physiological regulations [57–59]. Below or above the optimal threshold temperature negatively affects the flight performance of migratory insects [60], such as *M. separata* (Walker) [11], *Mythimna loreyi* (Walker) [40], and *Bactrocera dorsalis* (Hendel) [59]. Similar results were obtained in our study with the treatments below or above 26 °C in the immature stage reducing the flight duration and flight distance of *C. medinalis* adults. The reason for the negative effect may be closely related with the activity of metabolic rate and flight muscle power output regulated by temperature [61]. Below the optimal temperature, an insect reduces the locomotor activities of flight muscles which should be provided energy during flight as a consequence of lower metabolic rate [62]. High temperatures cause the inactivation of its nervous system due to increasing heat production by flight muscles above the upper critical thermal limit [63].

Interestingly, female moths have stronger flight propensity than males in some species [64], which undertake the task of finding food and oviposition sites [65]. Guo et al. [36] reported that female *C. medinalis* had a greater migratory propensity and flight capability than males at constant 26 °C in a laboratory population. Similar patterns were observed in *M. separata* [66] and *Culex pipiens pallens* [67]. However, differential flight

performances between the sexes in response to rearing temperatures in the immature stage are less common in migratory insects. In this study, we further found that flight performances of *C. medinalis* females and males largely depended on rearing temperatures. Females exhibited better flight performance than males at above 18 °C, with greater flight duration, distance and velocity. On contrast, 18 °C caused poorer flight performance of females than males.

Generally, migration is an energy-intensive activity, along with worse environments, new enemies and increased risk of mortality [19, 22]. Migration-mediated reproductive costs are not absolutely negative, and differ from species to species and the flight stage in some migratory insects [37, 68]. Previous studies have demonstrated that insects can choose an appropriate take-off time or migration stage to weaken the oogenesis-flight syndrome and therefore pay no reproductive costs for their migration [25, 37]. Zhang et al. [24] reported that flight on the first day after emergence significantly promoted the reproduction of *C. medinalis* under laboratory conditions. Our study further revealed that the effects of flight on reproduction of *C. medinalis* on the first day after emergence were also mediated by rearing temperatures in the immature stage. Compared to control females, flying females after experiencing low rearing temperature treatments (18 and 22 °C) started laying eggs at a later age and had lower total fecundity and mating frequency. These results suggested that low rearing temperatures negatively affected the migration at the expense of huge reproductive costs, probably because larvae which experienced low temperature were conducive to develop into residents. Supporting evidence for this comes from previous studies of the reproductive benefits of low temperature in *M. separata* [11, 33, 56]. However, high rearing temperatures of 30 and 34 °C significantly decreased the POP and increased the synchrony of egg-laying of flying females with a significant decrease in PFO, causing an increase of subsequent larval densities and even population outbreaks. A similar effect has been observed in *Loxostege sticticalis* [39]. Combined with decreased reproductive performance and enhanced migratory propensity of *C. medinalis* treated with high rearing temperatures, we therefore supposed that high rearing temperatures (30 and 34 °C) were most likely to trigger the onset of migration of *C. medinalis* adults for survival, which was consistent with the main motivation of insect migration triggered as a response to external environmental factors [22].

## 5. Conclusions

Taken together, our data indicate that *C. medinalis* can choose different adaptive strategies to help buffer the impacts of unsuitable temperatures. When rearing temperature in the immature stage surpasses the optimum for reproduction, *C. medinalis* accelerates maturation development and tends to invest more energy in migration to improve survival, generating the costs of delayed reproduction processes and reduced reproduction output. However, rearing temperature below the optimum for reproduction, *C. medinalis* delays maturation development but can also accelerate reproduction processes and stimulate adult reproduction. These findings enhance our understanding of diverse adaptive strategies in response to different temperatures in insects and provide valuable information for *C. medinalis* pest management.

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