

Determination of the Flight Capacity of *Tuta absoluta* (Lepidoptera: Gelechiidae)¹

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Abstract Since invading Xinjiang, China in 2017, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), commonly known as the tomato leafminer or the South American tomato pinworm moth, has continuously expanded its scope of devastation. Because flight is a major means by which insects disperse, an insect flight mill was employed to elucidate the physiological boundaries and basic parameters of *T. absoluta* flight biology. The system was used to measure the average flight distance, flight time, and flight speed of adult male and female *T. absoluta* of different ages, including 5-d-old (post emergence) adults in different mating states that had received supplementary nutrition (5% honey water). Tests of 12 h of continuous suspension in a flight mill showed that 4 through 7-d-old adults had strong flying ability, but 5-d-old adults were the strongest flyers. The mean (\pm SEM) flight distance, flight time, and flight speed of 5-d-old females were 1.805 ± 0.040 km, 1.467 ± 0.036 h, and 1.231 ± 0.226 km/h, respectively. The mean (\pm SEM) flight distance, time, and speed of 5-d-old males were 1.627 ± 0.363 km, 1.950 ± 0.056 h, and 0.834 ± 0.202 km/h, indicating significant differences in flight ability between male and female adults. After feeding on 5% honey water, the flight ability of 5-d-old *T. absoluta* improved significantly compared with the control. The distance, time, and flight speed of honey-water fed 5-d-old virgin females increased by 16.73%, 8.32%, and 8.37%, compared with the control (fed honey-free water). The flight distance, time, and speed of 5-d-old males increased by 7.87%, 0.56%, and 7.07% respectively, compared with the control. After mating, the distance, time, and flight speed of 5-d-old female adults increased by 11.91%, 0.48%, and 11.29% compared with virgin female adults. However, after 5-d-old males mated, their corresponding flight ability decreased by 11.13%, 3.34%, and 7.34%, compared with virgin male adults. In summary, sex, supplementary nutrition, and mating status all have a significant impact on the flight ability of *T. absoluta*.

Key Words *Tuta absoluta*, flight capacity, complementary nutrition, flight mill

Tuta absoluta (Meyrick) (Lepidoptera: Gelechiidae) is commonly known as the tomato leafminer or the South American tomato pinworm (Desneux et al. 2010, Karadjova et al. 2013). It primarily attacks *Solanum lycopersicum* L., followed by *Solanum tuberosum* L., *Solanum melongena* L., *Capsicum annuum* L., *Argentina anserine* L., and other solanaceous crops (Abbes et al. 2016, Bawin et al. 2016, CABI

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2022, Campos et al. 2017, Desneux et al. 2010). Adults often fly above host plants, but fly close to ground level during courtship. Actual mating occurs on the ground or on plant leaves. Average mating duration is 4–5 h. Females generally prefer to lay eggs before noon on the young leaves of host plants, with most eggs laid on the upper and lower surfaces of the leaves (Hai and Liu 2022). After hatching, the larvae feed on (leaf) mesophyll and form translucent, variously shaped tunnels or spots within or on the leaves on which they feed. When the larval density is high, they will cause leaf shrinkage and desiccation, leaving only green veins and, thus, seriously affecting the photosynthesis of the host plant. Larvae can also eat flower buds or fruits, causing buds to fall off or fruits to deform and stop growing, resulting in significant reductions in yield (Araujo and Soares 2022, Biondi et al. 2018, Zhang et al. 2018).

Tuta absoluta is a worldwide “quarantine pest” endemic to the Central Highlands of Peru in western South America. It became an important pest of tomatoes in South American countries in the 1950s and had spread to other Latin American countries by 1960 (Bawin et al. 2016, Campos et al. 2017). It was accidentally introduced into Spain in 2006 and quickly spread to other regions of Europe, as well as Africa, Asia, the Middle East, Central Africa, and more, in subsequent years (Shashank et al. 2015). Around the world, scholars have conducted extensive research on the morphology, biology, and control of *T. absoluta*. For example, Musa (2020) studied the flight of *T. absoluta* induced by pheromone, and Ataide (2017) studied the effects of plant volatile compounds on *T. absoluta* flight. There, however, have been no relevant reports on its flight ability in nature.

Flight is a survival mechanism insects use to adapt to or alter their living environments and to maintain populations. It is also an important way in which they disperse and expand their range. Insects able to fly above the boundary layer can use wind power to spread to distant hosts during specific seasons. The flight ability parameters (distance, time, and speed) of insects directly determine the dispersal rate of their populations, and are also key factors in determining their migration range (Hu et al. 2020, Wang et al. 2017). Insect flight ability is influenced by various factors, including age, sex, mating status, nutritional status, temperature, light, etc. (Lopez et al. 2014). For example, the flight ability of *Loxostege sticticalis* (L.) (Lepidoptera: Crambidae) increases with increasing temperature between 14 and 26°C (Tang et al. 2016). Female *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) exhibit the strongest flight ability at 3 d old (post emergence) and the weakest at 1 d old (Wei et al. 2013). Feeding can significantly improve the flight ability of both male and female *Agrius mali* Matsumura (Coleoptera: Buprestidae), while mating can significantly improve the flight ability of females (Ma et al. 2020). Measuring flight ability is the foundation for studying insect flight biology which is necessary to explore the mechanisms of local insect dispersal via flight. Currently, the preferred method is to use an insect flight mill to obtain insect flight ability parameters (Cui et al. 2016, Kees et al. 2017).

Since its invasion in 2017, the range of *T. absoluta* in China has increased continuously. In order to reduce the growing losses by this insect, it is important to understand the degree to which the spread of *T. absoluta* is related to its flight capacity. Furthermore, knowing how the physiological state of *T. absoluta* affects its flight ability could greatly assist efforts to prevent or control the spread of the

insect. Therefore, this study utilized an insect flight mill to measure parameters indicative of the flight ability of male and female *T. absoluta* adults of different ages, nutritional supplementation, and mating state, in order to understand its flight biology and to determine its dispersal mechanisms. This, in turn, provides information useful for predicting its future spread if left unchecked, as well as insight into ways to control or prevent such spread.

Materials and Methods

Insects. Larvae of *T. absoluta* were collected from a tomato greenhouse at the Jumachang Farm (N 38.515099, E 106.051691) in Xixia District, Yinchuan City, Ningxia Hui Autonomous Region. Infested tomato branches and leaves were brought to the laboratory and fed in an environmental chamber maintained at $25 \pm 1^\circ\text{C}$, $60\% \pm 5\%$ relative humidity (RH), and on a photoperiod of 16 h : 8 h (L:D). After emerging from pupation, adult moths were placed in Petri dishes with moist filter paper for feeding. During the feeding process, indoor insect sources were replenished every week. After the laboratory population emerged, males and females were placed in separate breeding boxes of the same size (10 cm long \times 5 cm wide \times 5 cm high), and labeled with the date of emergence and sex. Ten ml of water was added daily to supplement nutrition. Test flight time was from 2100 h to 0900 h the next day.

Flight performance. *Tuta absoluta* adults of different ages were randomly selected from the laboratory population to ensure their health and normal flight, placed in a centrifuge tube, and numbered. Test insects were first lightly anesthetized with 1 μl of ether, and a brush (0.5 cm) was used to gently remove the scales and setae at the junction between the thorax and abdomen. Moths were placed at the distal end of the flight mill (Henan Jiaduoke Industry and Trade Co., Ltd., Hebi City, Henan, China) by lifting the arm and rotating in a tangential direction around the center axis of the flying mill in a horizontal perspective. The test adults, thus, rotated horizontally around the central axis.

Flight ability of virgin male and female moths of different ages was measured by selecting 1 to 10-d-old virgin moths from separate breeding boxes where they were fed 5% honey water. Moths were in continuous suspension in a flight mill for 12 h. Over a 3-d period, 5 adults were tested per day, for a total of 15 trials, from which the average optimal flight age for *T. absoluta* was determined. In this test, no attempt was made to test whether the optimal flight age for males differs from that of females. The overall average was determined using moths of both sexes flown together.

Flight ability based on sex was subsequently determined based on the optimal flight age test results. Fifteen male and 15 female moths that had been fed 5% honey water were suspended continuously on flight mills for 12 h. Their flight parameters were recorded.

Supplementary nutrition impacts on flight ability were determined by feeding 10 females and 10 males with either 5% honey water or water (control). Moth flight parameters were recorded over 12 h of continuous flight in a flight mill.

Impact of mating on flight ability was determined using females and males that had been fed 5% honey water. In one treatment, 1 virgin male and 1 virgin female were placed in the same breeding box and allowed to mate freely. In a second treatment, the male moth was placed in a separate box from the female with no mating occurring. Moths in both treatments were continued to be fed 5% honey

water. Ten mated males, 10 mated females, 10 unmated males, 10 mated males were placed individually in flight mills where they flew for 12 h continuously. After the tests were completed, the females were held and observed for egg laying for 3 d in order to confirm whether or not mating had occurred.

Statistical analyses. All data were processed and analyzed using Excel 2012 (Microsoft, Inc., Bellevue, WA), SPSS 26 (IBM Corp.; Armonk, NY), and Drawing software Origin 2021 (OriginLab Corp., Northampton, MA). The impact of different factors on flight ability was analyzed using a 1-way analysis of variance (ANOVA), and the flight distance, time and speed between male and female insects under different physiological states (supplementing exogenous nutrients and different mating states) were processed by paired sample *t* test method. The flight ability of male and female adults, with different levels of supplementary nutrition, and in different mating states was compared using *t* tests for significant differences. Before data analysis, normality tests were conducted on the original data of average flight time, distance, and speed. When the data did not conform to a normal distribution, a square root transformation was performed before statistical analysis. The significant difference level for all experiments was $P < 0.05$.

Results

The flight ability of males and females of *T. absoluta* was closely related to the age of the insects and showed a trend of first increasing and then decreasing with the increase of age, as shown in Table 1. The results of continuous suspension flight for 12 h showed that there were significant differences in the flight ability of male and female adults at different ages. There were significant differences in flight distance ($F = 48.812$, $df = (9, 20)$, $P < 0.05$), flight time ($F = 38.462$, $df = (9, 20)$, $P < 0.05$), and flight speed ($F = 20.945$, $df = (9, 20)$, $P < 0.05$) among female adults of different ages. There were also significant differences in flight distance ($F = 52.605$, $df = (9, 20)$, $P < 0.05$), flight time ($F = 16.396$, $df = (9, 20)$, $P < 0.05$), and flight speed ($F = 46.754$, $df = (9, 20)$, $P < 0.05$) among male adults of different ages. The flight ability of male and female adults aged 4–7 d is stronger and gradually decreases with the increase of age. The flight ability of adults is the weakest at the age of 10 d. The flight ability of both male and female adults reaches its peak at the age of 5 d. The mean (\pm SEM) flight distance of female adults is 1.627 ± 0.363 km, the mean (\pm SEM) flight time is 1.950 ± 0.056 h, and the mean (\pm SEM) flight speed is 0.834 ± 0.202 km/h. The mean (\pm SEM) flight distance of male adults is 1.805 ± 0.040 km, the mean (\pm SEM) flight time is 1.467 ± 0.036 h, and the mean (\pm SEM) flight speed is 1.231 ± 0.226 km/h. The mean (\pm SEM) flight distance, flight time, and flight speed of male adults of *T. absoluta* are higher than those of female adults, and there are significant differences ($P < 0.05$) in the mean (\pm SEM) flight distance ($t = 3.959$, $df = 4$, $P = 0.017$), flight time ($t = 63.031$, $df = 4$, $P < 0.01$), and flight speed ($t = 40.154$, $df = 4$, $P < 0.01$) between male and female adults.

The flight ability of unmated male and female adults reached its peak at 5 d of age. The flight ability of unmated 5-d-old female and male adults under different nutritional states was measured for 12 h of continuous suspension. The results (Fig. 1) show that the flight distance (Fig. 1A), flight time (Fig. 1B), and flight speed (Fig. 1C) of tomato leaf miner adults fed on 5% honey water were greater than those

Table 1. Average flight distance, flight duration, and flight speed of different day-old adults of *Tuta absoluta*.*

Age of days	Average Flight Distance (km)		Average Flight Duration (h)		Average Flight Speed (km/h)	
	♀	♂	♀	♂	♀	♂
1	1.119 ± 0.004ef	1.148 ± 0.006d	1.672 ± 0.006e	1.203 ± 0.005c	0.672 ± 0.006d	0.954 ± 0.003d
2	1.167 ± 0.116de	1.195 ± 0.022d	1.721 ± 0.241de	1.215 ± 0.011c	0.679 ± 0.009cd	0.984 ± 0.015cd
3	1.228 ± 0.009cd	1.389 ± 0.021c	1.769 ± 0.187cd	1.269 ± 0.012c	0.694 ± 0.003cd	1.095 ± 0.249cd
4	1.305 ± 0.009c	1.597 ± 0.075b	1.843 ± 0.316b	1.352 ± 0.021b	0.708 ± 0.009cd	1.180 ± 0.364cd
5	1.627 ± 0.363a	1.805 ± 0.040a	1.950 ± 0.056a	1.467 ± 0.036a	0.834 ± 0.202a	1.231 ± 0.226a
6	1.430 ± 0.059b	1.635 ± 0.043b	1.824 ± 0.056bc	1.394 ± 0.016ab	0.784 ± 0.002b	1.173 ± 0.348b
7	1.306 ± 0.045c	1.554 ± 0.020b	1.786 ± 0.055bcd	1.437 ± 0.017a	0.731 ± 0.005c	1.082 ± 0.002c
8	1.224 ± 0.010cd	1.373 ± 0.022c	1.754 ± 0.222d	1.410 ± 0.027ab	0.698 ± 0.007cd	0.974 ± 0.111cd
9	1.034 ± 0.824f	1.166 ± 0.027d	1.663 ± 0.256e	1.351 ± 0.036b	0.621 ± 0.407e	0.863 ± 0.010e
10	0.831 ± 0.322f	1.017 ± 0.028e	1.446 ± 0.038f	1.250 ± 0.051c	0.575 ± 0.016e	0.814 ± 0.006e

* Means (±SEM) followed by the same lowercase letters within the same column are not significantly different ($P = 0.05$).

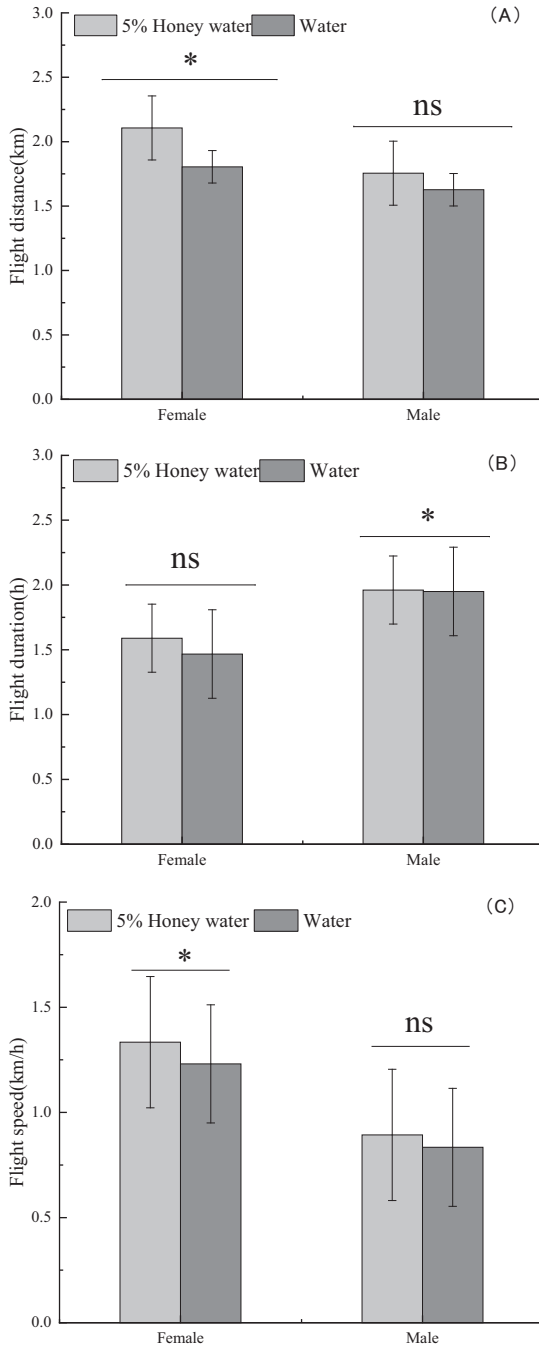


Fig. 1. Comparison of flight distance (A), time (B) and speed (C) of male and female *Tuta absoluta* adults fed 5% honey water and water.

of the control (fed on water). The flight distance ($t = 1.531$, $df = 6$, $P < 0.05$) and flight speed ($t = 1.964$, $df = 6$, $P < 0.05$) of female adults feeding on 5% honey water were significantly different from the control, while the flight time ($t = 0.684$, $df = 6$, $P > 0.05$) was not significantly different from the control. The flight time of 5% honey-fed male adults was significantly higher than that of the control ($t = 0.14$, $df = 6$, $P < 0.05$), while the flight distance ($t = 1.07$, $df = 6$, $P > 0.05$) and flight speed ($t = 1.879$, $df = 6$, $P > 0.05$) were not significantly different from the control. The flight ability of *T. absoluta* adults varies under different nutritional (water or honey water) states, and both males and females improve their flight ability after feeding (Fig. 1). The mean (\pm SEM) flight distance (2.107 ± 0.197 km), time (1.589 ± 0.179 h), and speed (1.334 ± 0.053 km/h) of females after feeding increased by 16.73%, 8.32%, and 8.37% compared with those females feeding only on water with the mean (\pm SEM) flight distance (1.805 ± 0.151 km), flight time (1.467 ± 0.137 h), and flight speed (1.231 ± 0.044 km/h). The flight distance (1.755 ± 0.12 km), flight time (1.961 ± 0.078 h), and flight speed (0.893 ± 0.031 km/h) of male adults after feeding increased by 7.87%, 0.56%, and 7.07% compared with the mean (\pm SEM) flight distance (1.627 ± 0.095 km), flight time (1.950 ± 0.059 h), and flight speed (0.834 ± 0.029 km/h) of male adults feeding only on water.

The flight ability of unmated male and female adults reached its peak at 5 d of age. The flight ability of 5-d-old female and male adults in different mating states was measured for 12 h of continuous flight. The results showed that the flight ability of female adults of *T. absoluta* increased after mating, while the flight ability of male adults decreased after mating (Fig. 2). The flight distance ($t = 1.384$, $df = 6$, $P < 0.05$) and flight speed ($t = 2.690$, $df = 6$, $P < 0.05$) of the female adult after mating were significantly greater than those of the unmated, and the flight time ($t = 0.076$, $df = 6$, $P > 0.05$) was not significantly different from that of the unmated female. After mating, the flight distance ($t = 2.073$, $df = 6$, $P < 0.05$) of male adults was significantly lower than that of unmated males, and there was no significant difference in flight time ($t = 0.584$, $df = 6$, $P > 0.05$) and flight speed ($t = 2.093$, $df = 6$, $P > 0.05$) between mated male adults and unmated males. The flight time of female adults is prolonged after mating, while the flight time of male adults is shortened after mating. After mating, the mean (\pm SEM) flight distance (2.020 ± 0.115 km), flight time (1.474 ± 0.070 h), and flight speed (1.370 ± 0.037 km/h) of female adults were increased by 11.91%, 0.48%, and 11.29% compared with those of unmated female adults the mean (\pm SEM) flight distance (1.805 ± 0.040 km), flight time (1.467 ± 0.036 h), and flight speed (1.231 ± 0.023 km/h). The mean (\pm SEM) flight distance (1.464 ± 0.055 km), flight time (1.887 ± 0.081 h), and flight speed (0.777 ± 0.017 km/h) of mated male adults decreased by 11.13%, 3.34%, and 7.34%, respectively, compared with the mean (\pm SEM) flight distance (1.627 ± 0.036 km), flight time (1.950 ± 0.006 h), and flight speed (0.834 ± 0.020 km/h) of unmated male adults.

Discussion

The results from our flight mill tests showed that flight ability of *T. absoluta* changes with age of the moths. In the early stages after emergence from pupation,

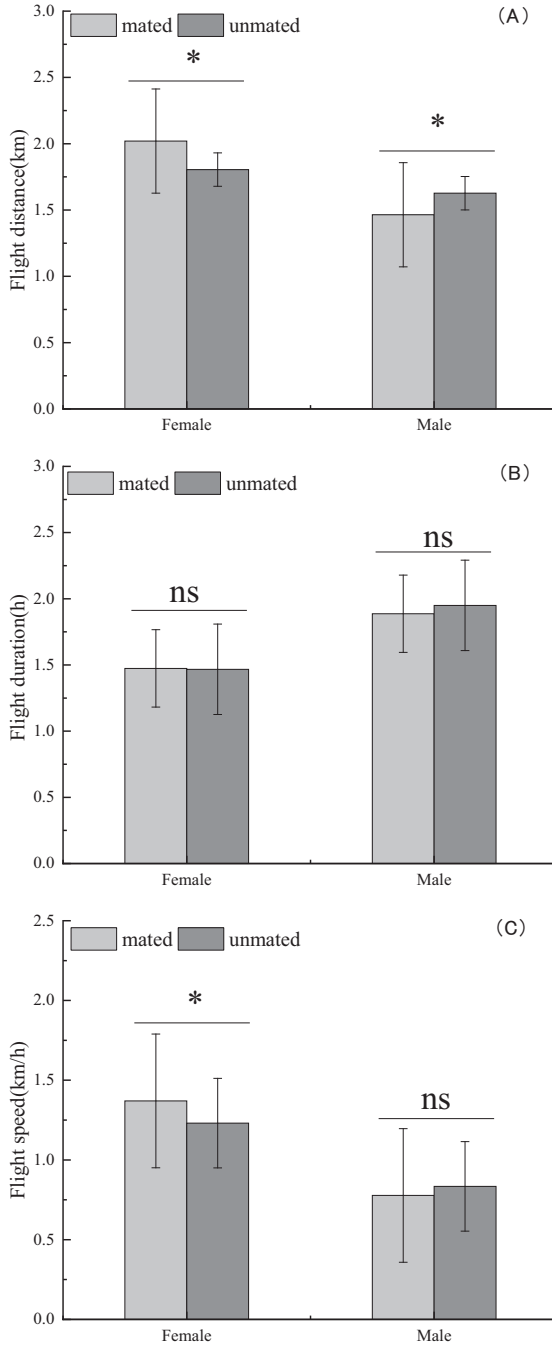


Fig. 2. Comparison of flight distance (A), time (B) and speed (C) of male and female *Tuta absoluta* mated and nonmated adults.

adult flight ability gradually strengthens with increasing age, reaching peak performance at 5 d after emergence. After that, flight ability gradually decreases with increasing age with 10-d-old adults having the weakest flight ability. This pattern of flight ability coinciding with age is similar to that observed with *Athetis lepigone* (Möschler) (Zheng et al. 2014), *Mamestra brassicae* (L.) (Wu et al. 2016), *Exorista civilis* (Rondani) (Yue et al. 2016), *Spodoptera frugiperda* (J.E. Smith) (Ge et al. 2019), and *Lithocolletis ringoniella* (Matsumura) (Hou et al. 2022).

The weak flight ability of *T. absoluta* after emergence from pupation might be due to adult wings are not completely formed and dried, the adult body is not yet fully sclerotized, incomplete development of the flight muscles, low energy reserves or related enzymatic activities, or incomplete nutrient supply, accumulation, and absorption during the larval stage (Sun et al. 2013). As the flight muscles mature and as energy reserves and enzymatic activity gradually increase, so does flight ability. When a certain stage of development is reached, the resource allocation in the body of a female insect may shift to reproduction, leading to the degradation of flight muscles resulting in a decrease in flight ability (Sun et al. 2013).

The flight ability of *T. absoluta* was not as strong as that reported for *S. frugiperda* (Ge et al. 2019, Wang et al. 2021), *L. ringoniella* (Hou et al. 2022), *S. exigua* (Hübner) (Zou et al. 2017), and other insects. It, therefore, can disperse for only relatively short distances, while several of the aforementioned pests migrate over long distances seasonally (i.e., *S. frugiperda*). Quarantine measures designed to limit the spread of *T. absoluta*, therefore, should be in place and strengthened.

We further determined that the flight abilities of male and female *T. absoluta* adults are similar; however, the average flight distance, time, and speed of females are significantly greater than those of males. This finding is similar to those with *Hyphantria cunea* Drury (Lepidoptera: Erebidae) (Li et al. 2023), *Corythucha ciliata* (Say) (Hemiptera: Tingidae) (Lu et al. 2019), and *Agrotis segetum* (Schiffermüller) (Lepidoptera: Noctuidae) (Guo et al. 2016), but are contrary to those of *Agrius mali* Matsumura (Coleoptera: Buprestidae) (Ma et al. 2020), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) (Wei et al. 2013), and *Heilipus lauri* Boheman (Coleoptera: Curculionidae) (Hodde et al. 2022).

The flight parameters of female *T. absoluta* are greater than those of males which might be attributed to females having a stronger demand for flight than males in order to find suitable oviposition sites after mating. In general, larger insects have a stronger flight ability than smaller individuals of the same species and, furthermore, male insects usually exhibit stronger flight ability than females (Wang et al. 2015). We, however, found that female *T. absoluta* have higher flight ability than males. We attribute this to females moving over larger areas to find suitable oviposition sites after mating than males move to locate reproductive females for mating.

Carbohydrates play an important role in insect flight (Yuan et al. 2015). Furthermore, supplementary nutrition has a significant impact on flight ability. Our results showed that the average flight distance and speed of both male and female *T. absoluta*, whose diets had been supplemented with honey water (5%), were significantly improved. Therefore, we infer that timely supplementation of nutrients during the adult stage may be a key factor in enhancing the dispersion and spread of *T. absoluta*. These results and inferences corroborate those of Su et al. (2022) in their research with *Grapholita molesta* (Busck).

During the mating process, male *T. absoluta* transfer a variety of physiological mating factors, for example, peptides, to the female. This transfer of energy and other nutrients increases the male's fitness, but also ostensibly reduces subsequent flight ability. However, we observed that the flight ability of female *T. absoluta* increased after mating, while that of unmated females did not. Increased flight ability following mating is not only conducive to finding suitable host plants for oviposition (Hashiyama et al. 2013), but also for dispersal and expansion of range. Almbro and Kullberg (2012) reported that unmated *Pieris napi* (L.) males fly faster than mated males, and their flight ability is reduced after mating.

In summary, use of the flight mill to study insect flight is convenient and indispensable in providing data and information. However, limitations of the use of flight mills include inconsistent friction resistance caused by the material and thickness of the radial flight arm, different bonding methods for insect testing, and the differing anatomy of insects. Although the flight parameters obtained via flight mills may not be completely accurate in reflecting the flight ability of insects, they provide important points of reference (Cui et al. 2016). While we attempted to study the flight ability of *T. absoluta* in conditions that reflected natural conditions, the insects tested were only recently removed from the wild, and the flight ability of the population may differ somewhat from that of the wild population. However, the indoor flight test cannot fully simulate the stress generated by the natural environment to promote insect flight. The effects of age, sex, carbohydrate intake and mating status on the flight ability of tomato leaf miner were preliminarily determined through flight experiments on indoor population of tomato leaf miner. We also recognize that other factors affecting insect flight ability include temperature, humidity, population density, and light intensity (Emberts 2023, Fahrner et al. 2015, Martini et al. 2018). The effects of such factors on the flight ability of *T. absoluta* still requires further study and exploration. We obviously cannot be assured that the flight parameters were identified with *T. absoluta* reliably defined those under natural conditions and with insects from natural habitats. It, therefore, is imperative to study further factors that may affect the flight ability of *T. absoluta* by combining indoor and outdoor testing methods.

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