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Pollen and nectar have different effects on the development and reproduction of noctuid moths

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Although many noctuid insects are agricultural pests that threaten food production, they are also the major nocturnal pollinators of flowering plants. Larval foods of noctuid pest insects have been well studied for developing control strategies, but knowledge on host plants for the adults is rather scarce. Here, the impact of plant-derived foods on adult survival, fecundity and reproductive physiology of four global species of noctuid pests (*Mythimna separata* Walker, *Mythimna loreyi* Duponchel, *Athetis lepigone* Möschler, and *Hadula trifolii* Hufnagel) was assessed in laboratory experiments. Our results indicated that nectar slowed testis decay and prolonged the oviposition period and lifespan, increasing fecundity. Acacia nectar increased the longevity of male and female adults by 3.2~10.9 and 2.4~5.0 days, respectively, and fecundity of females by 1.22~3.34 times compared to water-fed individuals. The fitness among the different species of noctuid moths differed on specific pollen diets. On pine pollen, the fecundity of female moths of *M. separata*, *A. lepigone* and *H. trifolii* was 10.06, 33.52, and 28.61%, respectively, lower than those of the water-fed females, but the fecundity of female moths of *M. loreyi* on pine pollen was 2.11 times greater than for the water-fed individuals. This work provides valuable information on the nutritional ecology for noctuid moths, which can aid the development and design of nutritional attractants within noctuid pests-infected cropping systems and provide a basis for effective and targeted management of global noctuid pests.

KEYWORDS

fecundity, ovarian anatomy, testis anatomy, nutritional physiology, supplementary nutrition

Introduction

Among the lepidopteran families, Noctuidae is one of the most diverse and abundant lineage in the number of species. Its members have major roles in the function and stability of terrestrial and aquatic ecosystems (Kristensen et al., 2007; Foottit and Adler, 2009). The larval and adult stages of noctuid species are closely associated with cultivated and wild plants. The larvae feed on the roots, stems or leaves of vascular plants using biting-chewing mouthparts and are agricultural and forestry pests (Cass, 1959; Sharma and Davies, 1983; Jiang et al., 2011; Zhang and Yu, 2021; Duan et al., 2022). The adults usually are anthophilous; they visit flowers and suck nectar and/or pollen using a proboscis and are important nocturnal pollinators of many flowering plants (Krenn, 2010; Devoto et al., 2011; Kato and Kawakita, 2017; Ribas-Marquès et al., 2022). In addition, noctuid insects are important food sources for other aquatic and terrestrial organisms including fishes, frogs, spiders, birds, bats, predatory and parasitic insects (García-Navas and Sanz, 2011; Fox, 2013; Chapman et al., 2015). However, there is no accurate published information on the contribution of noctuid insects to ecological function and stability. Similarly, knowledge on host plants used by adults of Noctuidae is rather scarce.

Many noctuid insects make seasonal migrations across the Earth and lead to outbreaks of agricultural and forestry pests, biological invasion, and pollination over large regions (Chapman et al., 2015; Hu et al., 2016; Song et al., 2021b). Migratory noctuid moths usually feed on nectar and/or pollen to meet energy for development of the internal reproductive system, and reproductive and flight activities (Krenn, 2010; Balzan and Wäckers, 2013; Liu et al., 2017a,b; He et al., 2022). The studies revealed the importance of carbohydrate-rich nectar or pollen as food sources to bolster fitness and raise adult lifespan, reproduction and flight performance (Wu and Guo, 1997; Lee and Heimpel, 2008; Lundgren, 2009; Jiang et al., 2015; Solayman et al., 2016; Liu et al., 2017a; He et al., 2021a). Understanding the interaction between adult food sources and noctuid moths is thus necessary for exploring their behavioral ecology, population dynamics and ecological function, as well as population monitoring and regional management of pests.

Mythimna separata Walker, *Mythimna loreyi* Duponchel, *Athetis lepigone* Möschler and *Hadula trifolii* Hufnagel are well-known migratory noctuid pests in agricultural ecosystems and globally distributed in tropical, subtropical, and temperate regions (**Table 1** and **Figure 1**). They have frequently occurred in crop fields in China and other Asian countries in recent years, posing a threat to food production security. Earlier studies have shown that migratory noctuid insects visit flowers of a wide range of herbaceous and woody plants including maize, rapeseed, sunflowers, and various members of Pinaceae and Rosaceae during migration process and exhibit different host preferences (Liu et al., 2016, 2017a; Chang et al., 2018; Guo et al., 2018; He et al., 2022). Floral nectar is primarily composed of sugar, water, amino acids, inorganic ion, alkaloids and phenolics and a high-value diet for numerous noctuid insects including *A. lepigone*, *Helicoverpa armigera* Hübner, *M. separata*, *Spodoptera exigua* Hübner, *S. frugiperda* Smith and *S. litura* Fabricius (Wu and Guo, 1997; Jiang et al., 2015; Solayman et al., 2016; Liu et al., 2017b; He et al., 2021a). Pollen contains carbohydrates, proteins, lipids, amino acids and vitamins and also provides energy and nutrition for many insects (Wäckers et al., 2007; Ares et al., 2018). A previous study reported that sesame flowers had no effect on adult longevities and fecundities of *H. armigera*, *S. exigua*, *S. litura*, *M. separate*, and *Ostrinia furnacalis* Guenée but *Plutella xyllostella* (L.) females laid more eggs when fed on sesame flowers compared to the water (Liu et al., 2017b). Earlier work on *S. frugiperda* has shown how pollen-containing diets impact adult fecundity and longevity (He et al., 2021a). However, how various plant-derived foods affect reproductive development, fertility and survival of *M. separata*, *M. loreyi*, *A. lepigone* and *H. trifolii* still remains unclear.

In the present study, we thus assessed the life history traits and reproductive physiology of *M. separata*, *M. loreyi*, *A. lepigone* and *H. trifolii* adults when fed different types, concentrations and mixtures of nectar and pollen to better understand flower visitation and/or population dynamics of noctuid pest insects. We predicted longer longevity and higher fecundity for these moths when they fed on nectar and that nectar and pollen would have different effects on the development and reproduction of the four noctuid moths. We also speculated that adults of each noctuid species would differ in their host preferences and that camellia, maize, rose and motherwort might provide highly suitable floral resources for adults of *M. separata*, *M. loreyi*, *A. lepigone* and *H. trifoli*, respectively.

Materials and methods

Larval feeding and adult fecundity trials

Trials were done from May to October 2018 and 2019 at the Xinxiang Experimental Station of the Chinese Academy of Agricultural Sciences (CAAS; 35°18′13.71″ N, 113°55′15.05″E) in Henan Province (China). In May 2018, adults of *M. separata*, *M. loreyi*, *A. lepigone*, and *H. trifolii* were collected using vertically aimed searchlight traps (model JLZ1000BT; Shanghai Yaming Lighting Co., Ltd., Shanghai, China), which were opened at sunset and closed at sunrise. Moths were gathered with a nylon net bag (60 mesh) beneath the trap and reared for three consecutive generations in the laboratory at 24 ± 1°C, 70 ± 5% RH, and 16 h L:8 h D. Larvae of *M. separata* and *M. loreyi* were fed *Zea mays* L. leaves and wheat bran-based artificial diet. *A. lepigone* larvae were fed soybean and wheat bran-based artificial diet. F_1 generation larvae of *H. trifolii* were fed *Chenopodium album* L. leaves, and F_2 and F_3 generation larvae were fed *C. album* leaves and wheat bran-based artificial diet. The larvae of the four species tested were reared in 22 × 15 × 8 cm plastic boxes, and F_3 generation adults were assessed for reproductive output. As soon as larvae were fully developed, they were moved to plastic boxes with vermiculite for pupation. On the 4th-5th day following pupation, the

TABLE 1 Descriptions and references for noctuid moths used in the study.

Taxon, common names	Description	References
Mythimna separata Walker, oriental armyworm (synonym: *Pseudaletia separata*, *Leucania separata*, southern armyworm, Chinese armyworm, sorghum armyworm, paddy armyworm, ear-cutting caterpillar, army caterpillar, paddy cutworm)	Cosmopolitan migratory pest causing serious outbreaks in Australia and Asia. Larvae mainly feed on gramineous species and damage major gramineous food crops (such as wheat, rice and maize, etc.). *M. separata* occurred throughout China except in Xinjiang.	Li et al., 1964; Sharma and Davies, 1983; Li, 2010; Jiang et al., 2011
Mythimna loreyi Duponchel, lorey leafworm (synonym: *Leucania loreyi*, *Acantholeucania loreyi*, maize caterpillar, army worm)	Cosmopolitan migratory pest causing frequent outbreaks in Africa, Australia, and many Asian countries. Its larvae mainly feed on gramineous crops and causes significant economic damage to maize. In recent years, *M. loreyi* frequently broke out in southern China and gradually expanded to northern China.	Ho et al., 2002; Sertkaya and Bayram, 2005; Jalaeian et al., 2017; Nam et al., 2020; Song et al., 2021a; Duan et al., 2022
Athetis lepigone Möschler (synonym: *Proxenus lepigone*)	Cosmopolitan migratory causing frequent outbreaks across Europe and Asia. In China, *A. lepigone* is a fairly new invasive in the summer maize region and expanded quickly to Liaoning, Shanxi, Henan, Shangdong, Jiangsu, and Anhui provinces in 2011 since it broke out in Hebei Province in 2005.	Nowacki et al., 2001; Nikolaevitch and Vjatcheslavovna, 2002; Lindeborg, 2008; Jiang et al., 2008; Poltavsky et al., 2009; Wang et al., 2012, 2013; Fu et al., 2014
Hadula trifolii Hufnagel, clover cutworm (synonym: *Apamea inquieta*, *Discestra trifolii*, *Hadena albifusa*, *Scotogramma trifolii*, nutmeg)	Cosmopolitan migratory pest causing serious outbreaks in Asia, Europe, North Africa and North America. Its larvae feed on more than 20 crop species, including maize, wheat, melon, and legumes. In China, *H. trifolii* mainly occurs in northern regions.	Cass, 1959; Zhao et al., 1992; Ren et al., 2006; Zhang et al., 2010; He et al., 2018; Zhang and Yu, 2021

male and female pupae were separated as described previously (Zhao et al., 2011).

Newly emerged adults (♀:♂ = 1:1) were paired and moved to 460-ml plastic cups with a 10-cm-long white nylon binding rope and a 10 × 10 cm sterile gauze stopper. The pairs received one of 11 diets in distilled water: distilled water (water), 5% (v/v) acacia nectar (acacia nectar), 1% (m/v) camellia pollen (camellia pollen), 1% (m/v) maize pollen (maize pollen), 1% (m/v) lotus pollen (lotus pollen), 1% (m/v) motherwort pollen (motherwort pollen), 1% (m/v) pine pollen (pine pollen), 1% (m/v) rapeseed pollen (rapeseed pollen), 1% (m/v) rose pollen (rose pollen), 1% (m/v) schisandra pollen (schisandra pollen) and 1% (m/v) sunflower pollen (sunflower pollen). Water and acacia nectar served as control treatments. Acacia nectar was purchased from Beijing Baihua bee Co., Ltd., Beijing, China. All pollen was purchased from Xinzhou Wutaishan Bee Industry Co., Ltd., Shanxi Province, China, except pine pollen which was purchased from Changbai Mountain Yipin Store, Jilin Province, China. One absorbent cotton ball (1 cm in diameter) that had absorbed 5 mL of the test diet solution was put into each cup and replaced every 2 days. Moths were kept at 24 ± 1°C, 75 ± 5% RH and 16 h L:8 h D. On a daily basis, any eggs on the plastic cup, nylon binding rope or sterile gauze stopper were counted, removed from the cup, and placed in a separate 12 × 17 cm zip-lock bag to determine hatchability and document the pre-oviposition time and survival rate of adults that developed from the eggs. Dead female *H. trifolii* moths were dissected using a stereomicroscope (TS-63X; Shanghai Shangguang New Optical Technology Co., Ltd., Shanghai, China) to count the number of spermatophores in the spermathecae and thus ascertain mating frequency.

Examination of reproductive system

Testicular or ovarian anatomy was examined to evaluate the effect of different food items on the reproductive system, for unmated male or female *M. separata* and *M. loreyi* adults. The effect of diets on ovarian development was determined for female adults of varying age (i.e., *M. separata*: 1- to 12-days old; *M. loreyi*: 1- to 11-days old). We measured the major axis length of male testes for adults of varying ages (i.e., *M. separata*: 1- to 12-days old; *M. loreyi*: 1- to 11-days old) (Chen et al., 2017; He et al., 2019, 2021a) to assess the effect of the various diets. Larvae were fed *Z. mays* leaves and wheat bran-based artificial diet, and 1st to 6th instar larvae were reared in 22 × 15 × 8 cm plastic boxes. Once larvae were fully developed, they were transferred to plastic trays with vermiculite for pupation. On the 6th day after pupation, female and male pupae were separated.

After pupal emergence, *M. separata* and *M. loreyi* moths were reared on one of nine food items: distilled water, 5% (v/v) acacia nectar (acacia nectar), 5‰ (m/v) rapeseed pollen, 5‰ (m/v) maize pollen, 5‰ (m/v) sunflower pollen, 5‰ (m/v) rose pollen, 5‰ (m/v) pine pollen, 2.5% (v/v) acacia nectar + 2.5‰ (m/v) rapeseed pollen (acacia nectar + rapeseed

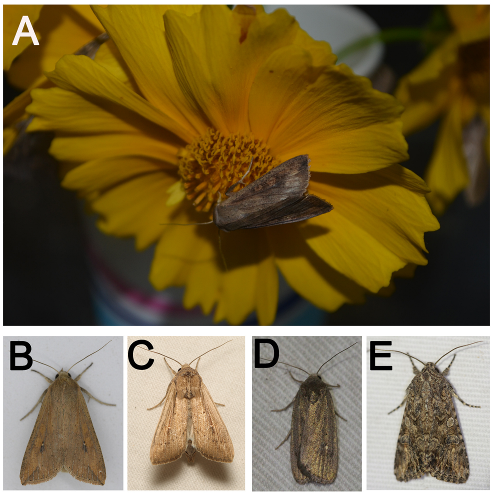

FIGURE 1
Representative images of noctuid moths used in the study **(A)**: *Mythimna separata* male adult, visiting flower and sucking nectar. **(B)**: *M. separata* female adult; **(C)**: *Mythimna loreyi* male adult; **(D)**: *Athetis lepigone* adult; **(E)**: *Hadula trifolii* adult). All images were taken by Limei He and Shengyuan Zhao with Nikon D5100 (A) and Canon EOS 60D **(B-E)**.

pollen) and 2.5% (v/v) acacia nectar + 2.5‰ (m/v) pine pollen (acacia nectar + pine pollen) in 50 × 50 × 50 cm cages (200 mesh nylon, 100 moths per cage) and kept at 25 ± 1°C and 70 ± 5% RH. Water, acacia nectar and combinations of pollen and nectar served as control treatments. Before excision of reproductive organs using a stereomicroscope (TS-63X), female moths were held at −20°C for 4 h, and male moths were immersed in 75% ethanol for 30 s (He et al., 2019, 2021a). The ovarian development index (levels 1–5) was classified based on standard practice (Dai et al., 1962). The major axis length of the testis was determined with OLD-SGD show software (Shanghai Shangguang New Optical Technology Co., Ltd., Shanghai, China). Ten male or female *M. separata* and *M. loreyi* moths of a given age were similarly treated for each diet with three replicates.

Statistical analyses

The effects of the 11 diets on reproductive variables were analyzed using a one-way analysis of variance (ANOVA) followed by Duncan's new multiple range test (MRT). Effects of nectar and pollen diets on the longevity ratio (= Mean longevity on nectar or pollen diet/Mean longevity on water) and ratio of oviposition period (= Mean oviposition period on nectar or pollen diet / Mean oviposition period on water) and fecundity ratio (= Mean number of eggs deposited per female on nectar or pollen diet/Mean number of eggs deposited per female on water) for the four noctuid moths were also analyzed using a one-way ANOVA followed by Duncan's MRT. Pearson linear correlation was used to test for a correlation between longevity and fecundity of female adults. Log rank was used to test for differences in survival curves of male and female adults for the four noctuid moths on the 11 diets. Effects of dietary treatment, sex, access to acacia nectar, and access to pollen on survivorship of *M. separata*, *M. loreyi*, *A. lepigone* and *H. trifolii* were evaluated using Cox proportional hazards model (Wyckhuys et al., 2008). Differences in male testis size, female ovarian development index of *M. separata* and *M. loreyi* reared with different foods or between sexes were analyzed using a two-way ANOVA. Curve Estimation (linear, logarithmic, inverse, quadratic, cubic, power, compound, S-curve, logistic, growth, and exponential) models were used to estimate curves for male testis size and female ovarian development index of *M. separata* and *M. loreyi* adults at different ages. Then, based on statistics such as F value, P value and coefficient of determination R^2 of the significance test of the regression equation, the cubic model was selected as the optimal model for fitting (Cai, 2014). The equation for the cubic model was $y = ax^3 + bx^2 + cx + d$, where a, b, c and d were model parameters, and y was male testis size or female ovarian development index for *M. separata* or *M. loreyi* at x days old. SPSS version 20 (IBM, Armonk, NY, USA) was used for all analyses, except for the log rank test, which was done in GraphPad Prism 8 (GraphPad Software Inc., San Diego, CA, USA).

Results

Survival and longevity

Mythimna separata

The survival rate curves of adults after feeding on different foods differed greatly between the two sexes of *M. separata* (female: $\chi^2 = 89.290$, df = 10, $p < 0.001$; male: $\chi^2 = 170.300$, df = 10, $p < 0.001$; **Figures 2A,B**). Dietary treatment had a significant effect on *M. separata* longevity ($\chi^2 = 4.682$, df = 1, $p = 0.030$), as did sex ($\chi^2 = 4.347$, df = 1, $p = 0.037$), access to acacia nectar ($\chi^2 = 40.845$, df = 1, $p < 0.001$), and access to pollen ($\chi^2 = 5.354$, df = 1, $P = 0.021$). Interactions were significant between sex and access to acacia nectar ($\chi^2 = 12.538$, df = 1, $p < 0.001$) and between sex and diet ($\chi^2 = 5.971$, df = 1, $p = 0.015$). Male moths attained the longest lifespan on acacia nectar, followed by maize pollen, and camellia pollen ($F_{10,\,554} = 2.528$, $p = 0.006$). For female *M. separata*, the longest lifespan was achieved on acacia nectar, followed by maize pollen ($F_{10,\,813} = 9.196$, $p < 0.001$). However, the third best diet for female *M. separata* appeared to be schisandra pollen. Longevity for both male and female *M. separata* was shortest on water. When reared on acacia nectar and maize pollen, males lived longer than females, but females lived longer than males on all other diets (**Table 2**).

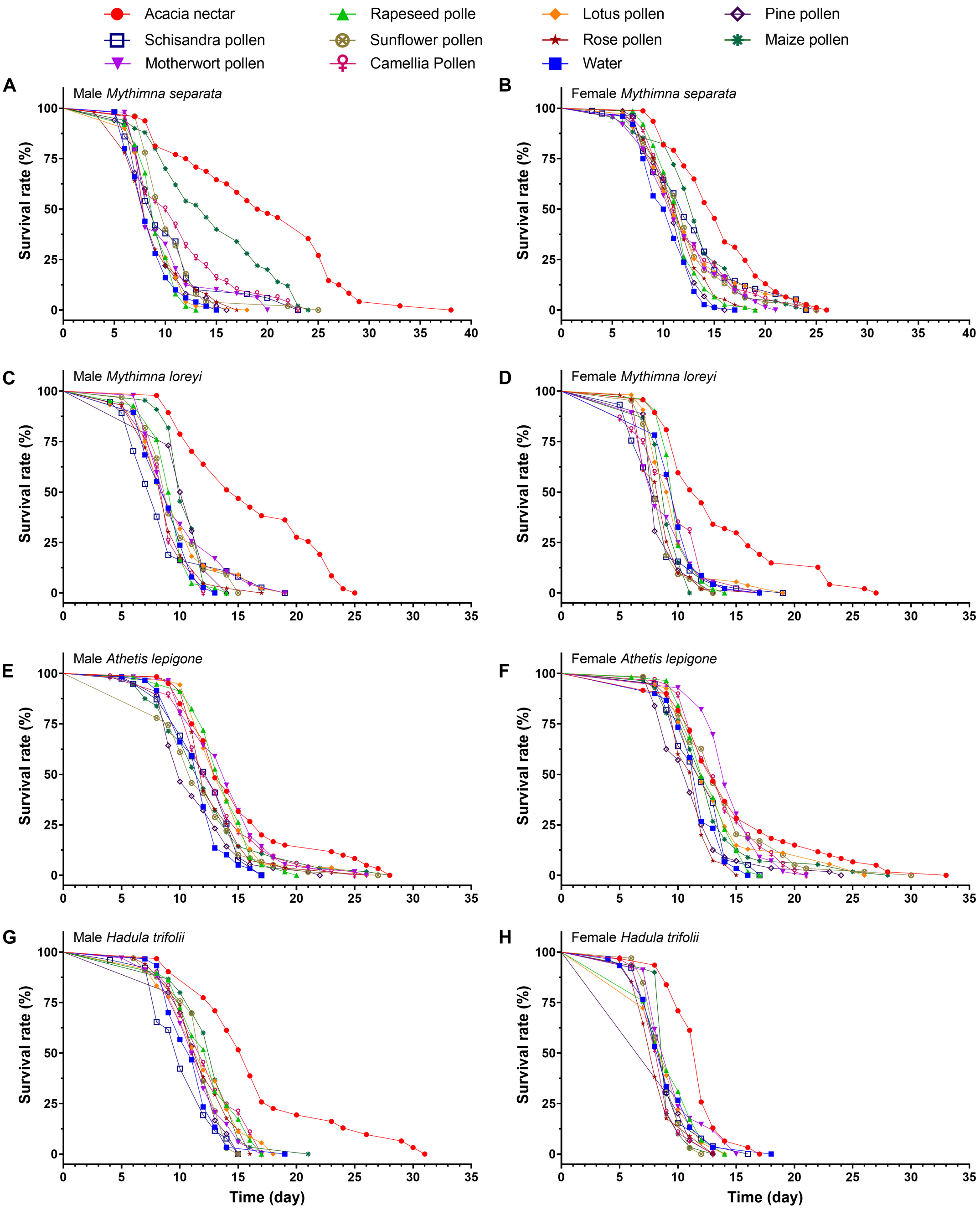

FIGURE 2
Age-specific survival rate of male and female adults of *Mythimna separata* **(A,B)**, *Mythimna loreyi* **(C,D)**, *Athetis lepigone* **(E,F)**, and *Hadula trifolii* **(G,H)** on different diets.

Mythimna loreyi

The survival rate curves of adults after feeding on different foods differed greatly between the two sexes of *M. loreyi* (female: $\chi^2 = 92.090$, df = 10, $p < 0.001$; male: $\chi^2 = 120.300$, df = 10, $p < 0.001$; **Figures 2C,D**). Access to acacia nectar had a significant effect on *M. loreyi* longevity ($\chi^2 = 102.137$, df = 1, $p < 0.001$), as did the interaction between sex and diet ($\chi^2 = 9.427$, df = 1, $p = 0.002$). Male moths attained the longest lifespan on acacia nectar, followed by maize pollen, and pine pollen ($F_{10,\ 459} = 23.497$, $p < 0.001$). For female *M. loreyi*, the longest lifespan was recorded for acacia nectar, followed by rapeseed pollen, and water ($F_{10,\ 549} = 14.496$, $p < 0.001$). Both male and female *M. loreyi* obtained the shortest longevity on schisandra pollen. When reared on acacia nectar, motherwort

TABLE 2 Means (± SE) for longevity and fecundity variables for adults of *Mythimna separata* on different diets.

Diet	Pre-oviposition (d)		Oviposition period (d)		No. eggs depositedper female		Female longevity (d)		Male longevity (d)	
	Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE	*N*
Acacia nectar	7.7 ± 0.3 c	74	6.7 ± 0.4 a	74	648.4 ± 51.5 a	74	15.4 ± 0.5 a	77	19.4 ± 1.1 a	48
Water	8.1 ± 0.3 bc	40	2.8 ± 0.3 d	40	230.6 ± 33.8 b	40	10.4 ± 0.3 e	76	8.5 ± 0.3 e	50
Rapeseed pollen	7.8 ± 0.2 c	57	3.6 ± 0.3 cd	57	234.5 ± 30.3 b	57	11.6 ± 0.3 cde	76	9.2 ± 0.2 de	50
Motherwort pollen	8.1 ± 0.3 bc	51	4.2 ± 0.4 bc	51	297.1 ± 37.1 b	51	11.7 ± 0.4 cde	74	9.9 ± 0.5 cde	49
Lotus pollen	9.0 ± 0.5 ab	49	4.1 ± 0.4 bcd	49	283.1 ± 37.6 b	49	12.3 ± 0.5 bcd	75	8.9 ± 0.4 de	50
Rose pollen	8.6 ± 0.4 abc	45	3.1 ± 0.3 cd	45	228.5 ± 34.3 b	45	11.5 ± 0.3 cde	77	8.9 ± 0.4 de	50
Sunflower pollen	8.6 ± 0.4 abc	51	3.8 ± 0.4 bcd	51	218.9 ± 25.1 b	51	12.3 ± 0.5 bcd	76	10.7 ± 0.5 cd	50
Camellia pollen	8.1 ± 0.4 bc	51	4.8 ± 0.4 b	51	315.4 ± 29.8 b	51	12.5 ± 0.5 bc	75	11.4 ± 0.6 c	50
Schisandra pollen	9.4 ± 0.4 a	53	4.0 ± 0.4 bcd	53	206.5 ± 31.4 b	53	12.8 ± 0.5 bc	76	10.3 ± 0.6 cde	50
Pine pollen	8.1 ± 0.3 bc	41	3.0 ± 0.2 cd	41	207.4 ± 31.4 b	41	11.0 ± 0.3 de	74	9.2 ± 0.4 de	50
Maize pollen	8.8 ± 0.4 abc	53	4.9 ± 0.4 b	53	276.9 ± 32.6 b	53	13.2 ± 0.5 b	68	14.5 ± 0.8 b	50

Values in the same column followed by different letters differed significantly (one-way ANOVA, Duncan's MRT; $p < 0.05$).

pollen, maize pollen, sunflower pollen, pine pollen and rose pollen, males lived longer than females, but females lived longer on the other diets (Table 3).

Athetis lepigone

The survival rate curves of adults after feeding on different foods differed greatly between the two sexes of *A. lepigone* (female: $\chi^2 = 84.510$, df = 10, $p < 0.001$; male: $\chi^2 = 56.570$, df = 10, $p < 0.001$; Figures 2E,F). Dietary treatment had a significant effect on *A. lepigone* longevity ($\chi^2 = 4.594$, df = 1, $p = 0.032$), as did access to acacia nectar ($\chi^2 = 18.166$, df = 1, $p < 0.001$) and to pollen ($\chi^2 = 13.068$, df = 1, $p < 0.001$). However, no significant effect was recorded for sex ($\chi^2 = 0.085$, df = 1, $p = 0.770$). Male moths lived the longest on acacia nectar, followed by motherwort pollen, and lotus pollen ($F_{10, 497} = 4.997$, $p < 0.001$). Females lived the longest on motherwort pollen and acacia nectar, followed by sunflower pollen ($F_{10, 597} = 5.478$, $p < 0.001$). On acacia nectar, rapeseed pollen, lotus pollen, rose pollen, schisandra pollen and pine pollen, males lived longer than females, but females lived longer on the other diets except for water (Table 4).

Hadula trifolii

The survival rate curves of adults after feeding on different foods differed greatly between the two sexes of *H. trifolii* (female: $\chi^2 = 38.670$, df = 10, $p < 0.001$; male: $\chi^2 = 60.810$, df = 10, $p < 0.001$; Figures 2G,H). Access to acacia nectar had a significant effect on *H. trifolii* longevity ($\chi^2 = 6.639$, df = 1, $p = 0.010$), as did sex ($\chi^2 = 4.128$, df = 1, $p = 0.042$). Males lived longest on acacia nectar, followed by maize pollen, rapeseed pollen and camellia pollen, and the shortest on schisandra pollen ($F_{10, 331} = 8.843$, $p < 0.001$). Females lived longest on acacia nectar also, followed by motherwort pollen, pine pollen and rapeseed pollen but the shortest on rose pollen ($F_{10, 331} = 5.565$, $p < 0.001$). Males lived longer than females on all diets (Table 5).

Summary

Briefly, nectar and pollen diets had a significant effect on the longevity ratio of males ($F_{9, 30} = 4.648$, $p = 0.001$; Figure 3A) and females ($F_{9, 30} = 2.454$, $p = 0.031$; Figure 3B). Male and female longevity ratios for acacia nectar were significantly higher than for pollen diets (Figure 3).

Fecundity

Mythimna separata

Dietary treatments greatly affected the reproductive characteristics of *M. separata* adults (Figure 4A), with significant effects on pre-oviposition period ($F_{10, 554} = 2.528$, $p = 0.006$), oviposition period ($F_{10, 554} = 9.917$, $p < 0.001$) and number of eggs deposited per female ($F_{10, 554} = 15.675$, $p < 0.001$) among the 11 food items (Table 2). The pre-oviposition period on acacia nectar and rapeseed pollen were considerably shorter than on other diets, while schisandra pollen yielded the longest pre-oviposition period. Females attained the longest oviposition period on acacia nectar, followed by maize pollen and camellia pollen. While the shortest oviposition period was attained for water-fed adults. Highest female fecundity was recorded on acacia nectar, and fewer eggs were deposited per female on schisandra pollen and pine pollen than on other diets. Compared with the water diet, acacia nectar, rapeseed pollen, motherwort pollen, lotus pollen, camellia pollen and maize pollen prolonged the oviposition period and increased the number of eggs deposited per female of *M. separata* adults. On the contrary, the pine pollen, schisandra pollen, rose pollen, sunflower pollen and rose pollen diets reduced female fecundity (i.e., oviposition period and eggs

TABLE 3 Means (± SE) for longevity and fecundity variables for adults of *Mythimna loreyi* on different diets.

Diet	Pre-oviposition (d)		Oviposition period (d)		No. eggs depositedper female		Female longevity (d)		Male longevity (d)	
	Mean ± SE	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE	N
Acacia nectar	5.9 ± 0.4 ab	47	6.6 ± 0.5 a	47	773.6 ± 65.3 a	47	13.5 ± 0.8 a	47	16.0 ± 0.8 a	47
Water	5.9 ± 0.2 ab	46	2.8 ± 0.2 d	46	231.7 ± 24.2 d	46	10.0 ± 0.3 b	46	8.9 ± 0.3 de	38
Rapeseed pollen	5.5 ± 0.2 bc	51	3.6 ± 0.2 bcd	51	406.5 ± 45.1 bc	51	10.0 ± 0.2 b	51	9.3 ± 0.3 cde	42
Motherwort pollen	4.9 ± 0.3 cd	56	3.2 ± 0.2 cd	56	394.4 ± 37.2 bc	56	8.9 ± 2.4 bcde	56	10.1 ± 0.5 bcd	47
Lotus pollen	5.3 ± 0.2 bcd	54	3.7 ± 0.3 bcd	54	334.7 ± 30.1 cd	54	9.8 ± 0.4 bc	54	9.6 ± 0.5 bcde	44
Rose pollen	4.9 ± 0.2 cd	51	2.8 ± 0.2 d	51	259.8 ± 37.8 d	51	8.6 ± 0.3 de	51	8.9 ± 0.4 de	43
Sunflower pollen	4.7 ± 0.2 cd	43	3.3 ± 0.3 cd	43	288.8 ± 45.6 cd	43	8.6 ± 0.2 de	43	9.6 ± 0.5 bcde	33
Camellia pollen	6.3 ± 0.3 a	52	3.2 ± 0.3 cd	52	232.5 ± 25.3 d	52	9.6 ± 0.4 bcd	52	8.8 ± 0.3 de	43
Schisandra pollen	4.6 ± 0.3 d	45	3.0 ± 0.3 d	45	313.8 ± 40.8 cd	45	8.5 ± 0.4 e	45	8.6 ± 0.6 e	37
Pine pollen	4.6 ± 0.2 d	53	4.0 ± 0.3 bc	53	488.7 ± 32.1 b	53	9.1 ± 0.2 bcde	53	10.5 ± 0.2 bc	44
Maize pollen	3.8 ± 0.1 e	62	4.3 ± 0.2 b	62	812.9 ± 33.4 a	62	8.8 ± 0.2 cde	62	10.8 ± 0.2 b	52

Values in the same column followed by different letters differed significantly (one-way ANOVA, Duncan's MRT; $p < 0.05$).

TABLE 4 Means (± SE) for longevity and fecundity variables for adults of *Athetis lepigone* on different diets.

Diet	N	Pre-oviposition (d)	Oviposition period (d)	No. eggs deposited per female	Female longevity (d)	Male longevity (d)
Acacia nectar	60	3.8 ± 0.2 bc	7.2 ± 0.5 ab	216.2 ± 17.4 ab	14.5 ± 0.8 a	14.8 ± 0.7 a
Water	59	4.1 ± 0.2 abc	5.5 ± 0.3 d	177.2 ± 15.5 bc	11.6 ± 0.3 de	11.6 ± 0.3 ef
Rapeseed pollen	58	3.6 ± 0.2 c	7.2 ± 0.4 ab	215.9 ± 16.5 ab	12.7 ± 0.3 bcde	13.7 ± 0.4 abc
Motherwort pollen	56	4.1 ± 0.2 abc	7.6 ± 0.3 a	219.5 ± 17.8 ab	14.5 ± 0.3 a	14.2 ± 0.5 ab
Lotus pollen	54	3.6 ± 0.2 c	6.6 ± 0.4 abcd	192.9 ± 17.6 ab	13.4 ± 0.6 abc	14.1 ± 0.4 ab
Rose pollen	55	3.7 ± 0.2 c	6.2 ± 0.3 bcd	239.2 ± 16.1 a	11.3 ± 0.2 d	13.2 ± 0.4 bcd
Sunflower pollen	59	3.9 ± 0.2 bc	6.8 ± 0.4 abc	208.4 ± 16.1 ab	13.9 ± 0.5 ab	11.9 ± 0.5 def
Camellia pollen	56	4.4 ± 0.2 ab	6.1 ± 0.4 bcd	169.0 ± 17.8 bc	13.7 ± 0.4 ab	13.2 ± 0.5 bcde
Schisandra pollen	39	4.1 ± 0.2 abc	5.6 ± 0.4 cd	169.9 ± 19.5 bc	12.0 ± 0.4 cde	12.2 ± 0.5 cdef
Pine pollen	56	4.7 ± 0.3 a	4.2 ± 0.4 e	117.8 ± 13.9 d	11.3 ± 0.4 d	11.4 ± 0.4 f
Maize pollen	56	4.4 ± 0.3 ab	5.5 ± 0.4 d	137.4 ± 16.5 cd	12.8 ± 0.6 bcd	12.4 ± 0.6 cdef

Values in the same column followed by different letters differed significantly (one-way ANOVA, Duncan's MRT; $p < 0.05$).

TABLE 5 Means (± SE) for longevity and fecundity variables for adults of *Hadula trifolii* on different diets.

Diet	N	Pre-oviposition (d)	Oviposition period (d)	Number of mating events	Eggs deposited per female	Female longevity (d)	Male longevity (d)
Acacia nectar	31	3.8 ± 0.2 a	5.8 ± 0.4 a	2.3 ± 0.4 a	716.4 ± 66.4 a	11.6 ± 0.4 a	16.8 ± 1.0 a
Water	30	4.4 ± 0.4 a	4.4 ± 0.4 ab	1.4 ± 0.2 b	358.6 ± 37.6 b	9.2 ± 0.5 b	11.2 ± 0.4 b
Rapeseed pollen	29	4.2 ± 0.4 a	4.1 ± 0.4 ab	1.8 ± 0.2 ab	393.6 ± 53.8 b	9.3 ± 0.4 b	12.4 ± 0.5 b
Motherwort pollen	34	4.4 ± 0.4 a	3.8 ± 0.5 b	1.6 ± 0.2 ab	426.4 ± 46.6 b	9.8 ± 0.4 b	11.6 ± 0.4 b
Lotus pollen	36	4.0 ± 0.2 a	3.8 ± 0.6 b	1.6 ± 0.2 ab	393.2 ± 30.3 b	9.1 ± 0.3 b	12.0 ± 0.5 b
Rose pollen	34	3.9 ± 0.3 a	3.8 ± 0.4 b	1.5 ± 0.1 ab	340.4 ± 31.0 b	8.4 ± 0.4 b	11.8 ± 0.4 b
Sunflower pollen	33	4.5 ± 0.2 a	3.8 ± 0.2 b	1.5 ± 0.2 ab	387.7 ± 36.4 b	8.9 ± 0.2 b	11.7 ± 0.4 b
Camellia pollen	29	3.7 ± 0.2 a	3.8 ± 0.8 b	1.3 ± 0.1 b	364.0 ± 40.6 b	8.8 ± 0.3 b	12.4 ± 0.5 b
Schisandra pollen	26	4.8 ± 0.6 a	3.8 ± 0.7 b	1.2 ± 0.2 b	244.4 ± 40.4 b	9.2 ± 0.4 b	10.3 ± 0.5 b
Pine pollen	30	3.6 ± 0.2 a	3.8 ± 0.3 b	1.5 ± 0.2 ab	256.0 ± 26.4 b	9.6 ± 0.2 b	11.6 ± 0.4 b
Maize pollen	30	3.6 ± 0.2 a	3.4 ± 0.3 b	1.2 ± 0.1 b	337.2 ± 30.5 b	9.1 ± 0.2 b	12.8 ± 0.4 b

Values in the same column followed by different letters differed significantly (one-way ANOVA, Duncan's MRT; $p < 0.05$).

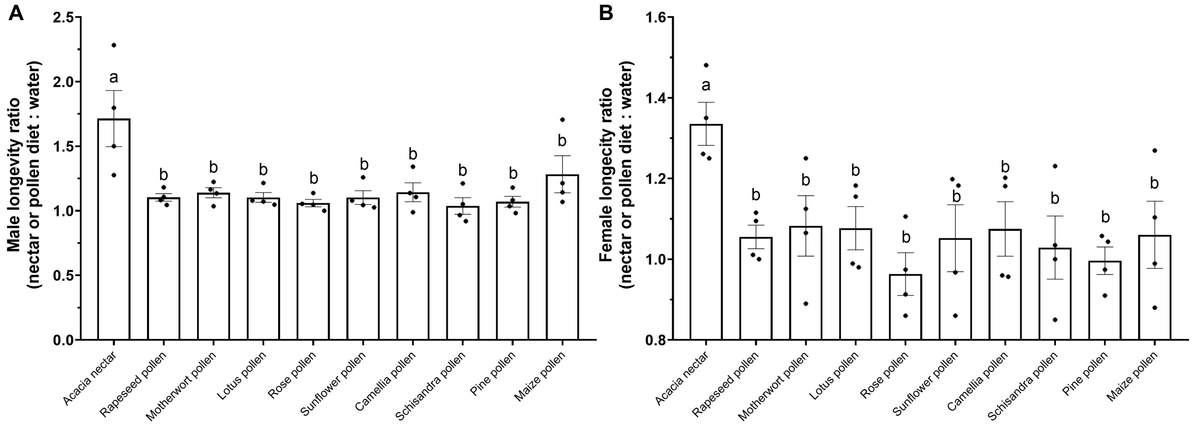

FIGURE 3
Mean (± SE) male **(A)** and female **(B)** longevity ratio of noctuid moths on different nectar or pollen diets. Asterisks for each diet indicate actual ratios for each species of noctuid moths. Different lowercase letters on the top of bar indicates a significant difference in ratios (one-way ANOVA, Duncan's MRT; $p < 0.05$).

deposited per female). Overall, fecundity was positively correlated with the survival of female moths; the longer the longevity, the more eggs were deposited (Pearson's $r = 0.820$, $P < 0.01$).

Mythimna loreyi

Food items affected pre-oviposition ($F_{10,\ 549} = 9.073$, $p < 0.001$), oviposition period ($F_{10,\ 549} = 12.929$, $p < 0.001$) and number of eggs deposited per female ($F_{10,\ 549} = 28.974$, $p < 0.001$; **Figure 4B** and **Table 3**). The pre-oviposition period on acacia nectar and water were longer than on other diets. Females attained the shortest pre-oviposition period on maize pollen, followed by pine pollen and schisandra pollen. The longest oviposition period was attained for acacia nectar-fed adults, the shortest on water. Significantly more eggs were deposited per female on acacia nectar and maize pollen than on other diets. Nectar and pollen diets all enhanced female fecundity. No significant correlation was recorded between the longevity and fecundity of females (Pearson's $r = 0.468$, $p > 0.05$).

Athetis lepigone

Diets had a significant effect on pre-oviposition ($F_{10,\ 597} = 3.090$, $p < 0.001$), oviposition period ($F_{10,\ 597} = 6.667$, $p < 0.001$) and eggs deposited per female ($F_{10,\ 597} = 6.600$, $p < 0.001$; **Figure 4C**) of female (**Table 4**). Compared with water, acacia nectar, rapeseed pollen, motherwort pollen, rose pollen, lotus pollen and sunflower pollen enhanced the fecundity of females, but maize pollen, pine pollen, schisandra pollen and camellia pollen shortened the oviposition period and reduced the number of eggs deposited per female. On motherwort pollen, rapeseed pollen and acacia nectar, the oviposition period was longer than on other diets. Females deposited the most eggs on diets of rose pollen, followed by motherwort pollen, acacia nectar and rapeseed pollen. The shortest oviposition period and the fewest eggs deposited per female were recorded for pine pollen. No significant correlation was recorded between the longevity and fecundity of female *A. lepigone* moths (Pearson's $r = 0.361$, $p > 0.05$).

Hadula trifolii

Diets also affected oviposition period ($F_{10,\ 331} = 4.030$, $p < 0.001$), mating frequency ($F_{10,\ 331} = 2.424$, $p = 0.009$) and number of eggs deposited per female ($F_{10,\ 331} = 8.760$, $p < 0.001$; **Figure 4D** and **Table 5**). On acacia nectar, females attained the longest oviposition period, the highest mating frequency and most eggs deposited per female, while fecundity was the lowest on schisandra pollen. Overall, fecundity was positively correlated with the survival of female moths; the longer the longevity, the more eggs were deposited (Pearson's $r = 0.781$, $p < 0.01$). Diets did not affect the pre-oviposition period ($F_{10,\ 331} = 1.408$, $p = 0.175$).

Summary

Overall, nectar and pollen diets had no significant effect on the ratio of oviposition period ($F_{9,\ 30} = 1.972$, $p = 0.079$; **Figure 4E**) or fecundity ($F_{9,\ 30} = 1.947$, $p = 0.083$; **Figure 4F**) for the four species of noctuid moths.

Reproductive physiology

Mythimna separata

Male testis size was significantly affected by diet ($F_{8,\ 3149} = 29.318$, $p < 0.001$), age ($F_{11,\ 3149} = 747.698$, $p < 0.001$) and interaction between diet and age ($F_{88,\ 3149} = 3.199$,

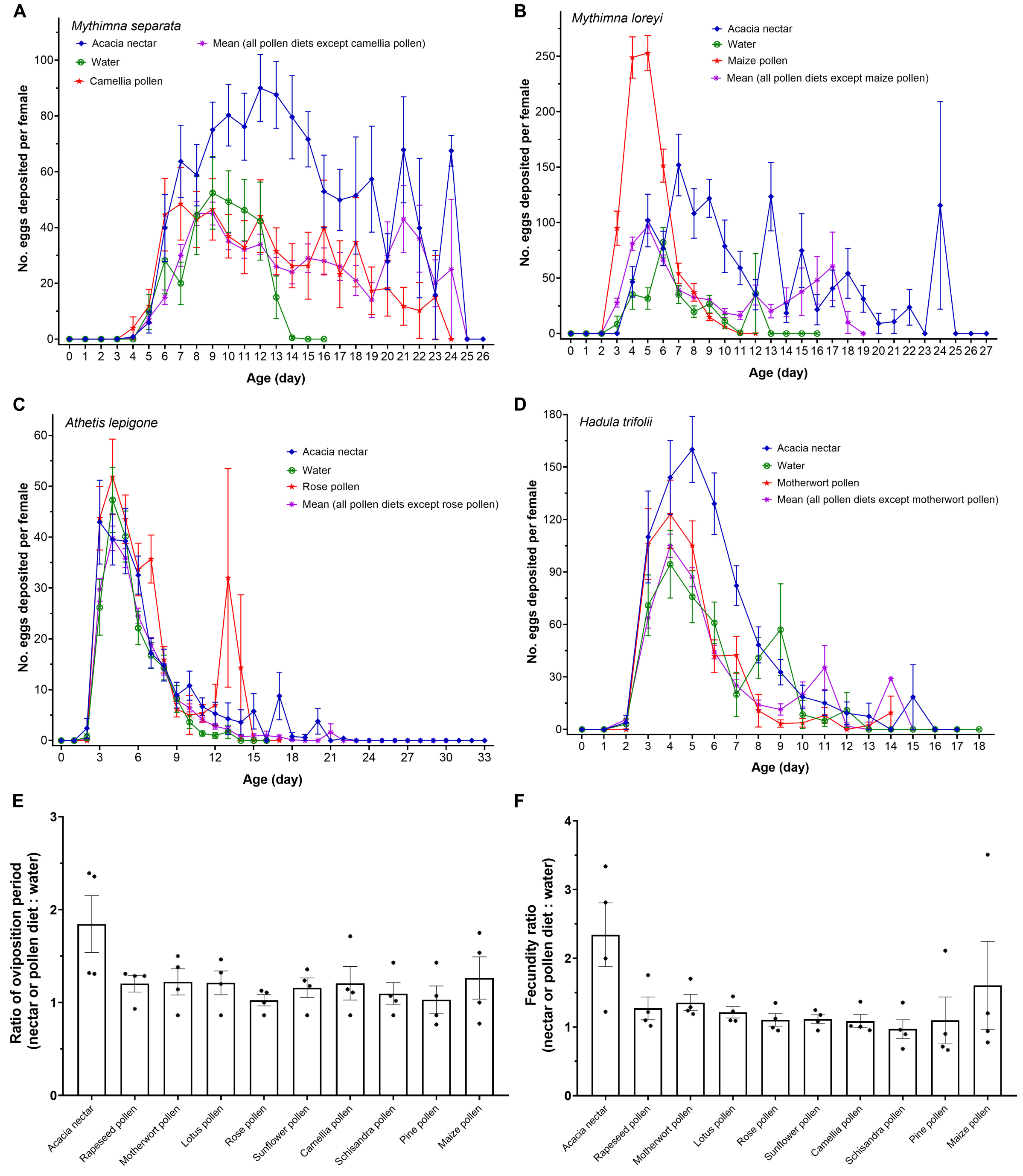

FIGURE 4
Mean (± SE) daily average fecundity curves of female adults of *Mythimna separata* **(A)**, *Mythimna loreyi* **(B)**, *Athetis lepigone* **(C)** and *Hadula trifolii* **(D)** and the ratio of oviposition period **(E)** and fecundity **(F)** for females on different diets. Asterisks for each diet indicate the actual ratio for each species of noctuid moths.

$p < 0.001$) (**Figure 5A**). Male testis size decreased significantly with increasing age (**Figure 5C**). Compared with 1-day-old males, testis size of 12-day-old males was 42.41% lower. Testes were longest on acacia nectar + pine pollen, followed by acacia nectar + rapeseed pollen, and maize pollen, and shortest on rose pollen. On diets containing nectar and pollen (i.e., acacia nectar + pine pollen, and acacia nectar + rapeseed pollen), testis length was 5.53%, 4.80%, and 3.26~9.32% longer, respectively, than on water, acacia nectar, or pollen only (**Figure 5E**).

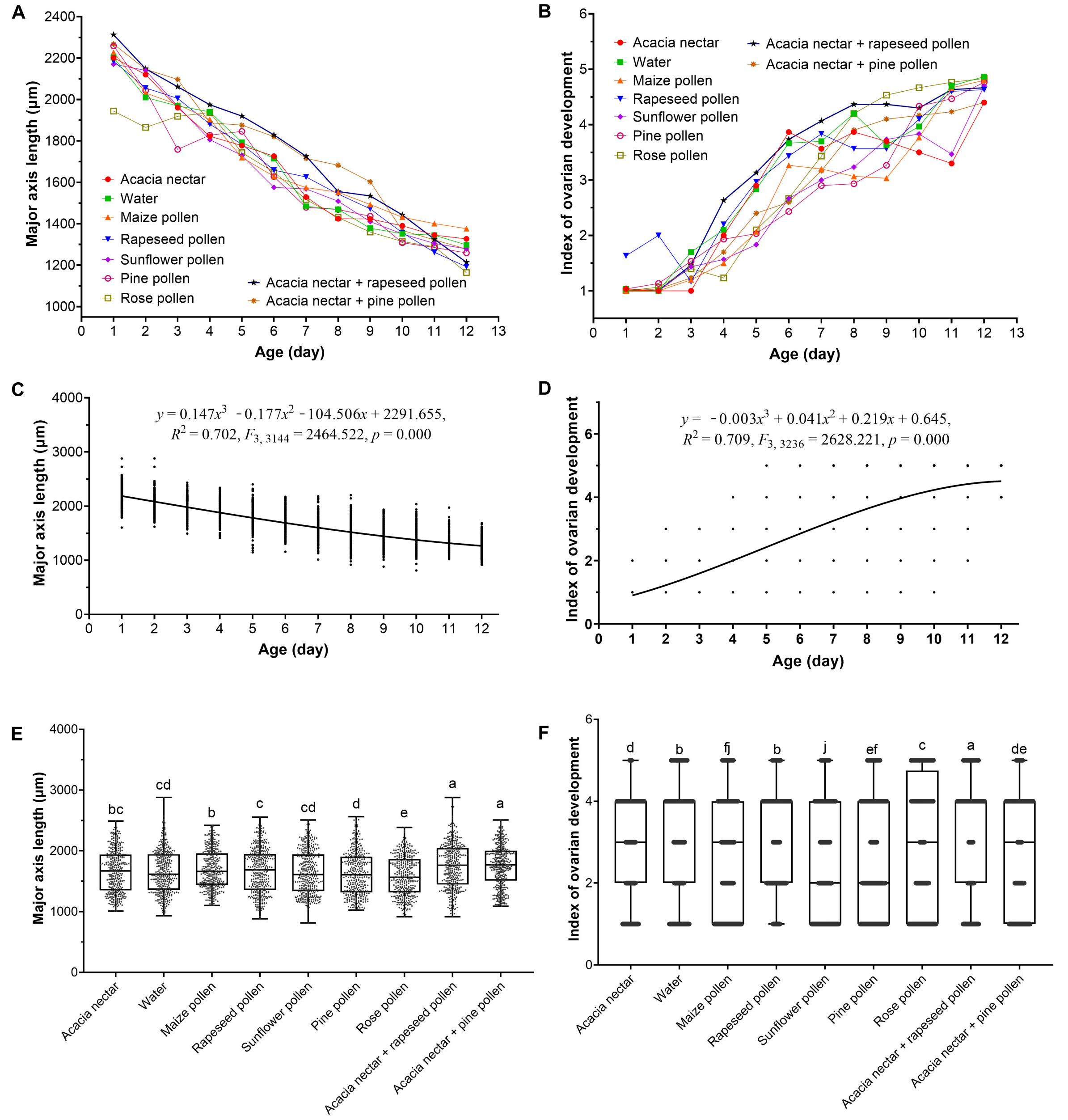

FIGURE 5

Effect of age and diet on testis size **(A,C,E)** and ovarian development level **(B,D,F)** of *Mythimna separata*. In **(C,D)**, means ± SE are shown. In **(E,F)**, the bottom and top of the black box indicate the first and third quartile values, respectively; the horizontal solid line shows the median for each category; bars indicate the maximum and minimum. Different lowercase letters above the bar indicates a significant difference (two-way ANOVA, Duncan's MRT; $p < 0.05$).

Ovarian development also was significantly affected by diet ($F_{8,\ 3240} = 40.559$, $p < 0.001$), age ($F_{11,\ 3240} = 1002.519$, $p < 0.001$) and the interaction between diet and age ($F_{88,\ 3240} = 8.813$, $p < 0.001$) (Figure 5B). Ovarian development level increased significantly with increasing age (Figure 5D). Index of ovarian development was greatest on acacia nectar + rapeseed pollen, followed by rapeseed pollen, then water, and lowest on sunflower pollen (Figure 5F).

Mythimna loreyi

Testis size of *M. loreyi* was significantly affected by diet ($F_{8,\ 2901} = 82.064$, $p < 0.001$), age ($F_{10,\ 2901} = 636.957$, $p < 0.001$) and the interaction between diet and age ($F_{80,\ 2901} = 6.357$, $p < 0.001$) (Figure 6A). Testis size decreased significantly with increasing age (Figure 6C). Compared with 1-day-old males, 11-day-old males had testes that were 37.33% smaller. The longest testis developed on

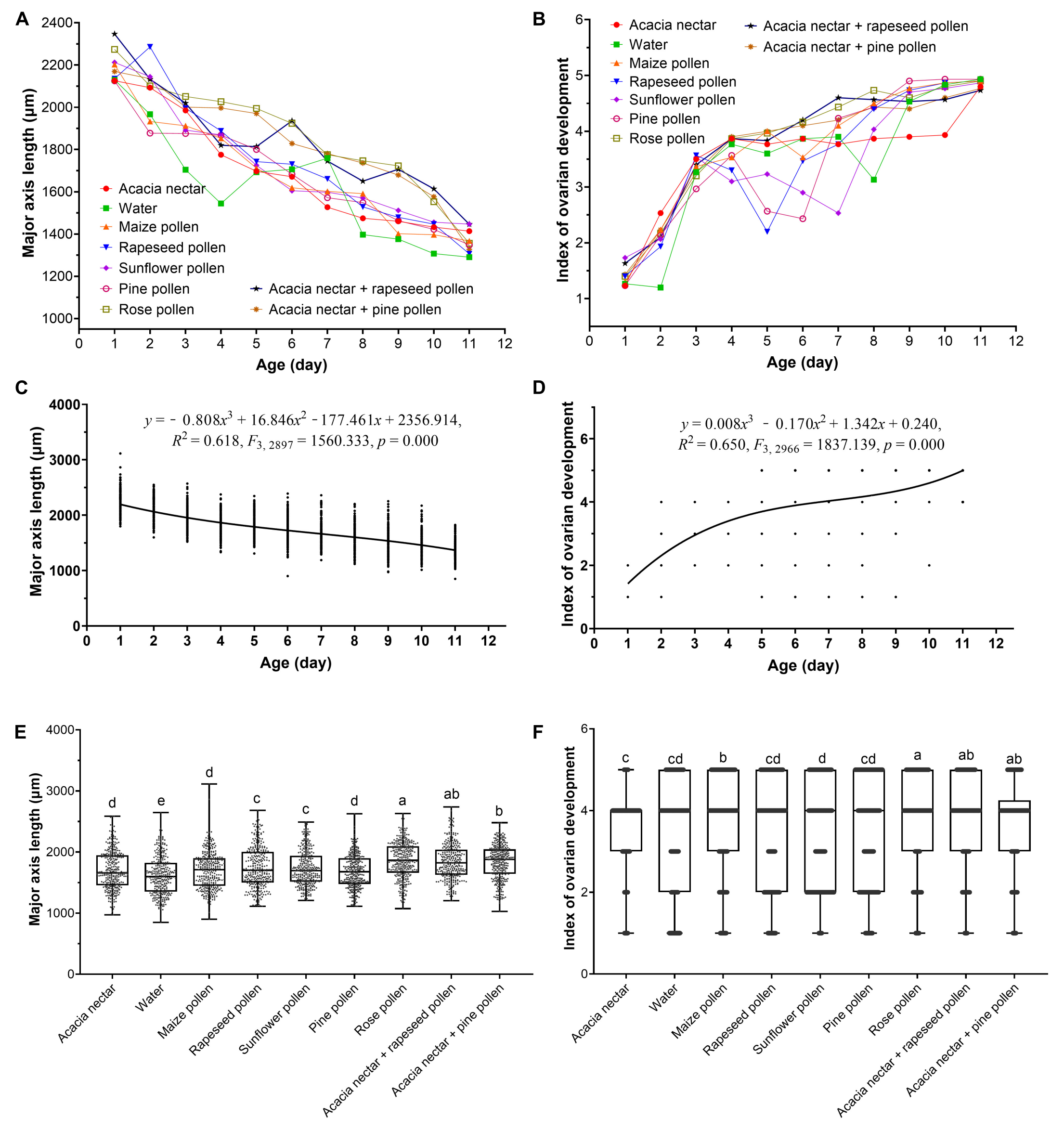

FIGURE 6

Effect of age and diet on testis size **(A,C,E)** and ovarian development level **(B,D,F)** of *Mythimna loreyi*. In **(C,D)**, means ± SE are shown. In **(E,F)**, the bottom and top of the black box indicate the first and third quartile values, respectively; the horizontal solid line shows the median for each category; bars indicate the maximum and minimum. Different lowercase letters above the bar indicates a significant difference (two-way ANOVA, Duncan's MRT; $p < 0.05$).

rose pollen, followed by acacia nectar + rapeseed pollen, and acacia nectar + pine pollen, and the shortest was obtained on water. In diets containing nectar and/or pollen, testis length was 4.00~9.32% longer than on water (**Figure 6E**).

Female ovarian development also was significantly affected by diet ($F_{8,\ 2970} = 26.053$, $p < 0.001$), age ($F_{10,\ 2970} = 877.148$, $p < 0.001$) and the interaction between diet and age ($F_{80,\ 2970} = 13.353$, $p < 0.001$) (**Figure 6B**). Ovarian development level increased significantly with increasing age (**Figure 6D**). Index of ovarian development was greatest on rose pollen, followed by acacia nectar + rapeseed pollen, and acacia nectar + pine pollen and lowest on sunflower pollen, followed by water (**Figure 6F**).

Discussion

Our previous study found that noctuid insects visit a variety of plants during migration process and feed on their nectar and/or pollen (Liu et al., 2016, 2017a; Chang et al., 2018; He et al., 2022). Many literatures report the effect of nectar or honey on the reproduction and longevity noctuid adults, but knowledge on pollen-diets for the noctuid adults of is rather scarce. In this study, we use laboratory assays to demonstrate how various plant-derived foods enhance development and reproduction of *M. separata*, *M. loreyi*, *A. lepigone,* and *H. trifolii*. The testes sizes are good indicators of the effect of diets on development of the male reproductive system in noctuid moths. The testis size of *M. separata* and *M. loreyi* decreased significantly with increasing age and was further affected by diet. Rapeseed pollen, maize pollen and nectar-containing diets resulted in larger testes for *M. separata*, and nectar and/or pollen-containing diets resulted in larger testes for *M. loreyi*. Thus, those food items may help slow testis decay, similar findings were reported for *Ostrinia nubilalis* Hübner, *Cnaphalocrocis medinalis* Guenée and *S. frugiperda* (Milonas and Andow, 2010; Chen et al., 2017; He et al., 2019, 2021a). Meanwhile, ovary status showed that *M. separata* and *M. loreyi* continuously develop eggs, which is further enhanced through supplementary nutrition, in line with a previous study for *S. frugiperda* (He et al., 2021a). Given that *M. separata* and *M. loreyi* ovaries were poorly-developed on sunflower pollen, the type of pollen is likely important in ovary maturation.

The type of pollen and nectar also affects the longevity and reproductive and flight abilities of insects (Liu et al., 2017b; He et al., 2021a). Here, we revealed that life history traits and reproductive physiology of *M. separata*, *M. loreyi*, *A. lepigone* and *H. trifolii* moth were favored by sugar-rich (nectar) or floral-derived (pollen) diets. The lifespan and reproductive traits spanned a range of variabilities among these four species of noctuid moths in our laboratory conditions. Adult feeding on nectar prolonged longevity and enhanced fecundity, which is in line with previous studies for *A. lepigone*, *H. armigera*, *S. frugiperda*, *S. exigua* and *S. litura* (Jiang et al., 2015; Liu et al., 2017b; Zhou et al., 2019; He et al., 2021a). However, the four species differed in their fitness on the pollen diets. On 5% acacia nectar, the longevity of female adults for four noctuid moths increased with 2.4 to 5.0 days compared to distilled water. Similarly, on 5% acacia nectar, the longevity of male adults of four noctuid moths increased with 3.2 to 10.9 days compared to distilled water. Pollen solutions slightly increased adult longevity of *M. separata* and *A. lepigone* compared to distilled water. Similar findings were made for *S. frugiperda* and *S. exigua* (Liu et al., 2017b; He et al., 2021a).

The fecundity of four noctuid moths fed on 5% acacia nectar was 1.22 to 3.34 times as much as water-fed individuals, similar to previous studies for other noctuid moth (Wu and Guo, 1997; Jiang et al., 2015; Liu et al., 2017b; Zhou et al., 2019; He et al., 2021a). While the fecundity of four species for noctuid moth varied in different pollen diets. On suitable pollen diets (e.g., *M. separata*: motherwort, lotus, camellia and maize pollen solution; *M. loreyi*: rapeseed, motherwort, lotus, sunflower, schisandra, pine and maize pollen solution; *A. lepigone*: rapeseed, motherwort, rose and sunflower pollen solution; *H. trifolii*: rapeseed, sunflower, motherwort and lotus pollen solution), the fecundity of female moths increased with 8.12 to 250.84% as compared to water-fed individuals. On 1% pine pollen, the fecundity of female *M. separata*, *A. lepigone* and *H. trifolii* moths was decreased with 10.06% to 33.52% as compared to water-fed individuals. On the contrary, female fecundity for *M. loreyi* on 1% pine pollen was 2.11 times greater than for water-fed individuals, similar to previous studies on *H. armigera*, *S. exigua* and *S. frugiperda* (Liu et al., 2017b; He et al., 2021a). Overall, the fecundity of *M. separata* and *H. trifolii* moths were positively correlated with the survival of female adults in line with an earlier study that showed that enhanced survival is likely to translate into increased fecundity (Rosenheim, 2011). Similar findings were made for *H. armigera* and *S. frugiperda* (Zhou et al., 2019; He et al., 2021a), underlining how sugar-rich (nectar) or floral-derived food items contribute to population build-up, foraging and migration, ultimately enhancing a species' adaptability to variable or unpredictable environments.

In this study, adult longevity of four noctuid moths was significantly affected by interaction between sex and diet/access to acacia nectar; ovarian development and testis size were significantly affected by interaction between diet and age. These findings indicated that the developmental and reproductive parameters of noctuid moths are not only affected by gender, age, and food diets, but also by the combined effects of gender/age and food diets, which may be due to the different nutritional requirements and/or host preferences of noctuid adults between females and males or among varying age. Previous studies have shown that the host plant species among the different species of noctuid moths differed on their migratory individuals (Liu et al., 2016, 2017a; Chang et al., 2018; He et al., 2022). The larvae of four noctuid moths tested usually feed on angiosperms such as gramineous species (maize and wheat) and exhibit varying fitness performance (**Table 1**). The reports of noctuid larvae feeding on gymnosperms (*Pinus* spp.) is rather scarce. While migratory noctuid moths not only feed on flowers of herbs such as maize and rice but also visit pine flowers and consume their nectar and/or pollen (Liu et al., 2016, 2017a; Chang et al., 2018; He et al., 2022). These studies indicate the host plant range of adults differs from that of larvae. Our findings provide preliminary evidence that pollen-diets affects reproduction and longevity of four noctuid moths, as also found for *S. frugiperda* (He et al., 2021a). As mentioned above, the development and reproduction of insects are affected by a variety of internal or external factors such as age, sex, and diets, thus further study is need to explore host-plant feeding preferences of adult noctuid moths and assess the effects on population dynamics.

Generally, flower-visiting and nectar-feeding insects exhibit marked preferences for pollen or nectar from certain plant species and can be attracted by floral volatile compounds (Andrade et al., 2018; Haber et al., 2018; Kessler et al., 2019).

Floral volatiles have been used to trap noctuid moths and monitor and forecast their populations (Tingle and Mitchell, 1992; He et al., 2021b). Migrating moths of *M. separata* and *H. trifolii* are often contaminated with pollen of Amaranthaceae, Compositae, Pinaceae, Poaceae and Rosaceae (Liu et al., 2017a; Guo et al., 2018; He et al., 2022). Our findings that rapeseed, maize, motherwort, rose and pine pollen enhanced fitness and fecundity of several species of noctuid moth reveal that particular types of pollen may be highly attractive to *M. separata*, *M. loreyi*, *A. lepigone* and *H. trifolii* and can be used to develop and design nutritional attractants for eventual incorporation in monitoring, "attract-and-kill" systems and "push-pull" strategy (Miller and Cowles, 1990; Gregg et al., 2018).

Our work demonstrated that the nectar diet commonly slowed testis decay, prolonged the oviposition period and lifespan, and raised fecundity for noctuid pest insects. However, different species of noctuid moths differed in their fitness on the pollen diets, and certain pollen, just like nectar, enhanced fecundity of different moths. The valuable information on nutritional ecology of these noctuid will aid the development and design of nutritional attractants in cropping systems and provide a basis for developing effective, targeted management practices against global noctuid pests.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

LH and KW conceived and designed the experiments and wrote the manuscript. LH performed the experiments and analyzed the data. SZ and WH revised the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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