Use of food attractants to monitor and forecast Spodoptera frugiperda Smith seasonal abundance in southern China

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Abstract

The fall armyworm (FAW, *Spodoptera frugiperda* Smith) is an important invasive pest of maize crops in Africa, Asia and the Middle East. To enable timely and effective pest management, accurate monitoring and forecasting of *S. frugiperda* populations is essential. In this study, we used food attractants to assess seasonal abundance of *S. frugiperda* in southern Yunnan (China) and determined adult age based upon ovarian development or testes size. During 2020–2021, the seasonal abundance of trapping *S. frugiperda* males with food attractants and sex pheromones were approximately the same at two field sites. Both trapping methods yielded *S. frugiperda* males of different ages – with an identical age structure for both trap types. The proportion of females trapped with food attractants was about 80%, which was significantly higher than that of males. *S. frugiperda* populations at two field sites were composed of immigrants that either originated in central Yunnan or in eastern Myanmar. Based upon field-level recordings of adult reproductive state, models reliably anticipated *S. frugiperda* fecundity dynamics. Next, drawing upon meteorological data and FAW adult age, migration trajectories were established for *S. frugiperda* immigrant populations. Overall, these novel (food-based) monitoring and forecasting tools can improve integrated pest management (IPM) of *S. frugiperda* in China and abroad.

Key Message

- Limited research has been conducted on the role of food-based attractants in *S. frugiperda* population monitoring.
- Adult age can be inferred from the reproductive development state of field-collected male and female *S. frugiperda*.
- In southern Yunnan, *S. frugiperda* adult populations mainly consist of immigrant individuals.
- Meteorological data and adult age are used to simulating *S. frugiperda* migration trajectories.
- These new monitoring and forecasting methods complement the integrated pest management (IPM) toolbox for *S. frugiperda*.

Introduction

The fall armyworm (FAW) *Spodoptera frugiperda* (Smith) is an economically important lepidopteran native to the American (sub-)tropics (Sparks 1979). FAW larvae are voracious consumers of multiple cultivated crops including maize, sorghum, rice, cotton and soybean (Bueno et al. 2011; Hardke et al. 2015; Montezano et al. 2018). Since 2016, *S. frugiperda* has invaded large sections of Africa, Asia and the Middle East and has caused serious losses to local maize crops (Goergen et al. 2016; CABI 2021). In 2019, *S. frugiperda* had spread across 21,135 km^2 in Asia and posed a major threat to the food and nutrition security of several Asian countries (Liu et al. 2021).

Monitoring and forecasting methods are essential to the effective management of invasive and native pests alike (Pedigo et al. 2021; Wu et al. 2021b), and can help to target curative and preventative management interventions. Up till present, *S. frugiperda* field-level populations have been monitored using insect radar and sex pheromone or searchlight trapping (Wolf et al. 1986; Feng et al. 2020; Haftay and Fissiha 2020; Cruz-Esteban et al. 2021). Pheromone-based trapping is widely used, as it constitutes a sensitive, specific, cheap and user-friendly method to monitor *S. frugiperda*. However, as pheromone-based approaches only trap FAW males, they do not shed light upon *S. frugiperda* female abundance or oviposition dynamics. These methods are thus of limited value to anticipate FAW larval abundance or population growth. Also, males will go to females in preference to traps, and pheromone-based trapping regularly do not provide reliable estimates of field-level adult abundance (Kondo and Tanaka 1994).

Upon adult emergence, lepidopteran species such as *S. frugiperda* feed on plant nectar or pollen to enhance their overall fitness (He et al. 2021a). When foraging for plant hosts, adult lepidopterans rely upon volatiles that are constitutively emitted by one or more plant species (Bruce and Pickett 2011; Knolhoff and Heckel 2014; Gallinger et al. 2019). These food-based attractants or kairomones regulate adult foraging behavior (Cai et al. 2018), and constitute environmentally friendly and efficient means to attract (or mass-trap) both female and male individuals (Gregg et al. 2016; Gregg et al. 2018; Justiniano and Fernandes 2020). At present, food lures are used to monitor population dynamics of different lepidopterans e.g., *Helicoverpa armigera*, *Spodoptera exigua* or *Cydia pomonella* L. (Knight et al. 2005; He et al. 2021c; He et al. 2021d). These monitoring tactics are regularly used to generate population forecasts and 'early warning' alerts to farmers (Cha et al. 2018), and are often paired with measurements of reproductive anatomy (e.g., egg load, ovarian maturity) to anticipate adult fecundity and population growth in the field (He et al. 2021c). In China, food-based attractants are commercially available for agricultural pests such as *H. armigera* and *Cnaphalocrocis medinalis* (He et al. 2021a; Zeng et al. 2021). Similar kinds of lures have also been developed for *S. frugiperda*, but their efficacy remains to be tested under field conditions. Moreover, no work has been done integrating monitoring data with reproductive development analysis for this pest.

In this study, we use dissections of the *S. frugiperda* (male and female) reproductive apparatus to establish a relationship between its development status and adult age. Next, we validate the use of food-based attractants for *S. frugiperda* population monitoring and relate the field-level abundance of FAW adults to their reproductive development dynamics. Lastly, we use field monitoring data from southern Yunnan (China) to assess *S. frugiperda* migration patterns and fecundity dynamics. By validating the use of food-based attractants for *S. frugiperda* monitoring and by generating population forecast methods, our work expands the integrated pest management (IPM) toolbox for this invasive pest in China and abroad.

Materials And Methods

Reproductive development analysis

Study insects

In January 2019, *S. frugiperda* larvae were collected from maize fields in Mengmao Mengmao (Ruili city), Yunnan, China (24°14'46"N, 97°31'09"E). Larvae were transferred to the laboratory and fed with maize leaves until pupation. Upon adult emergence and mating, the F1 larval generation was kept in a 22 x 15 x 8 cm plastic container and fed with artificial diet (Liang et al. 1999).

The experimental population was established after multiple generations of laboratory rearing. More specifically, 6th instar larvae were placed into a 22 x 15 x 8 cm plastic container with vermiculite to pupate. Once pupae reached five days of age, female and male pupae were separated following procedures by Dong et al. (2019) and individualized within 12 cm diameter glass Petri dishes. Upon emergence, adults were offered cotton balls soaked in 5% (V/V) honey/water solution (Beijing Baihua Bee Products Technology and Development Co. Ltd., Beijing, China). FAW larvae and adults were kept in the laboratory at 25 ± 1 °C, 75% ± 5% relative humidity (RH) and 16 : 8 L:D photoperiod.

Experimental assays

Following adult emergence, 10 females and 10 males were placed within 35 x 35 x 35 cm screened cages (200 mesh). For adult males and females of ages 1–10 days, reproductive organs were dissected and the reproductive development state of the respective ovaries and testes was assessed following He et al. (2019). At each age (i.e., 1–10 days old), we made recordings on the following number of individuals: 49, 28, 29, 31, 24, 29, 25, 23, 21, 28 (males) and 14, 12, 11, 15, 14, 11, 15, 12, 13 (females). Prior to dissection, body length of 1, 3 and 5-day old adult males was recorded with a vernier caliper (LT-MT518; Leta Industrial Co., Ltd., Shanghai, China). Next, testes were removed and placed within a 3 cm diameter plastic Petri dish filled with saline solution. The Petri dish was placed under a stereoscope (TS-75X; Shanghai Shangguang New Optical Technology Co., Ltd., Shanghai, China) and the major axis length of the testis (i.e., testis size) was measured with an OLD-SGD imaging system. For adult females, ovaries were dissected completely, the index of ovarian development was determined following criteria by Zhao et al. (2019) (Fig. 1) and the number of eggs within the ovarioles (i.e., egg load) was recorded.

Field-level monitoring

Boat and bucket traps (Fig. 2), food attractants and pheromones were provided by Shenzhen Bioglobal Agricultural Science Co., Ltd (Shenzhen, China). The food attractants consisted of a 1:0.5:1 ratio blend of eucalyptus oil, linalool and methylo-anisate, in solid form with 4.5 g active ingredient per package. The *S. frugiperda* sex pheromone was composed of Z9-14:Ac, Z7-12:Ac, Z11-16:Ac and Z9-14:Ac at a 80:2:17.5:0.5 ratio (Jiang et al. 2021), with 12 mg active ingredient provided on a PVC capillary. During field trials, traps (baited with either of the above volatile lures) were positioned at different heights and attached to a 2 m long rod.

Field monitoring assays were conducted in Xundian County (Kunming City) (25°50'34.5"N, 103°7'12.2"E) and Jinghong City (Xishuangbanna Prefecture) (21°56'15.5"N, 100°46'12"E), Yunnan, China. At Xundian, experiments were carried out from September 8 to October 28, 2020 and from April 3 to August 28, 2021. Meanwhile, experiments in Jinghong City were performed from September 20 to November 19, 2021. In 2020, assays were conducted at eight (2000 m^2) maize fields established on flat terrain with identical crop varieties and similar management. Within each field, boat traps (baited with food lures) were spaced at 20 m distances and six traps were placed equidistant in the center of each plot. As such, a total of 48 boat traps were placed. Meanwhile, a bucket trap with sex pheromone was deployed at 50 m distances from the above boat traps. Bucket trap was positioned 1.5 m above the ground. Boat traps were fixed at 20 cm above the maize canopy, and the height was adjusted regularly with the growth of maize. Food and pheromone lures were replaced every 20 or 30 days, respectively. Boat traps (baited with food attractants) and bucket trap (baited with pheromones) had been tested many times before the start of the experiment, which is the best collocation. The blank control experiment without bait in traps (boat trap and bucket trap) was also tested before the start of the monitoring, and the average daily number of *S. frugiperda* trapped by a single trap was less than 0.10, so no analysis was made. In 2021 four maize (2001 m^2) fields were selected in Xundian County and six (2001 m^2) fields were chosen in Jinghong City. According to the field test standard of Xundian in 2020, 24 boat traps (with food lures) and 4 bucket traps (with sex pheromones) were placed in Xundian fields. Meanwhile, 36 boat traps and 6 bucket traps were placed in Jinghong City.

Every morning, we recorded the number of *S. frugiperda* adults per trap and transferred all field-caught individuals to the laboratory for further anatomical recordings and an assessment of reproductive development status. On a daily basis, up to 20 male and female individuals (per type of attractant) were dissected and all of them were dissected if the trapping number was less than 20.

Analysis of migration trajectory and fecundity dynamics

The reproductive development status of field-trapped *S. frugiperda* adults can reflect their migration history. More specifically, the reproductive apparatus of local populations is largely immature while the ovaris and testes of immigrant populations are relatively developed (Zhao et al. 2019). Next, the source location of migrant populations can be determined using trajectory analysis based on the HYSPLIT (Hybrid Single Particle Lagrangian Integrated Trajectory) trajectory analysis model. Trapping locations (i.e., Jinghong and Xundian field sites) were entered as starting points of HYSPLIT trajectory analysis, and 12h backward flight trajectories were computed on peak *S. frugiperda* migration days (i.e., dates of high trap counts). Biological parameters were set as follows: (1) ignoring the active flight ability of *S. frugiperda* (Ge et al. 2021b), migration was assumed to occur downwind; (2) ascent occurred within 1 hour after sunset, while descent and landing occurred 1 hour before sunrise. As such, the respective *S. frugiperda* ascent and descent times were 20:30 and 7:00 for Jinghong and 20:30 and 5:30 for Xundian. (3) FAW could engage in flight over two consecutive nights; (4) flight altitude was set at 200 m, 300 m, 400 m, 500 m, 600 m, 700 m and 800 m. (5) Suitable host plants and crops were assumed to be present along the migration trajectory, facilitating take-off and landing at any location.

Based on the oviposition dynamics of *S. frugiperda* (Ge et al. 2021b), the following relationship was established between age and egg deposition: $y = 0.2359x^4 - 6.6983x^3 + 56.244x^2 - 123.93x + 62.796$ (R^2 = 0.8512) in which y represents the daily egg deposition and x is age. By integrating the function model, the following function integral was obtained:

$\int_a^b 0.2359x^4 - 6.6983x^3 + 56.244x^2 - 123.93x + 62.796dx$, in which a and b refer to the FAW adult age. Using this function integral, the total number of deposited eggs can be computed for *S. frugiperda* females between two different ages. As such, we determined the fecundity i.e., total number of eggs deposited by a given *S. frugiperda* female from the average age of field-trapped individuals (parameter a) until death (parameter b). (6) The total lifespan of the *S. frugiperda* experimental population was assumed to be identical to that of a field population, and the upper limit of integration was thus set at 14 days.

Statistical analysis

For data analyses and model fitting, we used SPSS 26.0 (IBM, Armonk, NY, USA). One-way analysis of variance (ANOVA) was used to compare the ovarian development index, egg load or testis size between *S. frugiperda* (female, male) adults of different ages. As a post-hoc test, we used Tukey's honestly significant difference (HSD) test. A Student's t-test was used to compare (daily) trap counts between traps baited with food attractants and sex pheromones. A chi-square test was used to assess differences in sex ratio of female to male (1:1) and male age structure for individuals caught in traps with food lures or pheromones. Meanwhile, we employed *Spearman* correlation analysis to relate the number of *S. frugiperda* males, adults (males and females) in food-baited traps with males in pheromone-baited traps. *Pearson* correlation analysis were used to relate body length to testis size for 1, 3 and 5-d-old *S. frugiperda* males. Curvilinear models were developed to fit the relationship between female age, egg load and ovarian development index.

Results

Age-dependent reproductive development

In the experimental *S. frugiperda* population, female adults of varying age exhibited different ovarian development indices ($F_{9,107}$ = 179.949, P< 0.001; Fig. 3a) and egg load ($F_{9,107}$=71.233, P< 0.001; Fig. 3b). Ovarian development index increased with increasing *S. frugiperda* female age. Egg load first increased and then decreased with the increasing *S. frugiperda* female age, and reached the maximum (1512.0 ± 63.0) at 4-day old. The functional relationship between ovarian development index, egg load and female age was captured by y = -0.0019x_1 + 1.7872x_2 + 1.2382 ($F_{2,124}$ = 972.723, P< 0.001, R^2 = 0.9414) in which y is age, x_1 is egg load, and x_2 is ovarian development index.

Testis size declined with increasing *S. frugiperda* male age ($F_{9,277}$ = 174.831, P< 0.001; Fig. 3c). This functional relationship was captured by the non-linear function $y = 5.16x^2 - 152.59x + 2606.4$ ($F_{2,7}$ = 179.949, P< 0.001), in which y is testis size and x is age (Fig. 3c). For 1-, 3- and 5-day old FAW males, average body size was 16.5 ± 0.2 mm (n = 49) and 15.6 ± 0.2 mm (n = 18), 16.3 ± 0.2 mm (n = 24) and testis size was 2487.0 ± 18.5 μm, 2157.5 ± 18.7 μm and 1982.8 ± 26.0 μm, respectively. Body size did not correlate with testis size for three ages (1-day old males : r = 0.197, P = 0.167; 3-day old males : r = 0.317, P = 0.200; 5-day old males : r = -0.010, P = 0.965).

Field-level dynamics

At Xundian during 2020, food- and pheromone-based traps yielded the highest (male) adult abundance during mid-September and early October, respectively (Fig. 4a). Meanwhile, in 2021, both trap types resulted in identical seasonal abundance patterns with (male) adult abundance gradually increasing from April onward to reach peak values in late May (Fig. 4b). At Jinghong during 2021, food-based traps yielded peak *S. frugiperda* numbers in early and mid-October, while those baited with sex pheromones yielded the highest abundance of FAW males during late September and mid-October (Fig. 4c). For the two experimental sites and years, the number of males caught in traps with food attractants was correlated with those caught in pheromone-based traps (Xundian 2020: $r = 0.343$, $P = 0.023$; Xundian 2021: $r = 0.255$, $P = 0.003$; Jinghong 2021: $r = 0.489$, $P < 0.001$). A similar pattern was recorded for the total number of (male and female) adults (Xundian 2020: $r = 0.671$, $P < 0.001$; Xundian 2021: $r = 0.242$, $P = 0.005$; Jinghong 2021: $r = 0.502$, $P < 0.001$). Across sites and years, food-based traps caught an average of 0.2 ± 0.0 (Xundian, 2020), 0.7 ± 0.0 (Xundian, 2021) and 0.5 ± 0.1 FAW adults per day (Jinghong, 2021). Meanwhile, pheromone-based traps yielded 125.4 ± 59.6 (Xundian, 2020), 10.0 ± 2.5 (Xundian, 2021) and 8.3 ± 4.8 adults per day (Jinghong, 2021). Pheromone-based trapping thus yielded a higher daily trap capture than food-based approaches (Xundian 2020: $t = -7.459$, $P < 0.001$; Xundian 2021: $t = 3.667$, $P = 0.008$; Jinghong 2021: $t = -2.663$, $P = 0.044$).

Based on the functional model of the age of males and the testis size in the experimental population of *S. frugiperda*, the age of trapping males with food attractants and sex pheromones in the field was analyzed. Taking males trapped at Xundian in 2021 as a sample, 100 males trapped by using food attractants and 100 males trapped by using sex pheromones were randomly selected. Field trapping yielded *S. frugiperda* males of all ages (Fig. 5), with 10-day old males constituting a respective 31% and 21% of the total trap capture for food-based and pheromone-based approaches. Meanwhile, 1-day old males only constituted 0% and 4% for the respective trapping methods. The age structure of field-caught males did not differ between both trapping methods ($\chi^2 = 14.398$, $P = 0.101$). At Xundian, food-based traps yielded a total of 2693 females and 611 males during 2020, and 331 females and 85 males during 2021. During either year, females thus accounted for a respective 82.0% and 78.5% of the total trap capture. At Jinghong, traps baited with food lures caught 742 females and 186 males i.e., 80.0% females. Across sites and years, food-based trapping thus yielded significantly more female *S. frugiperda* adults (Xundian 2020: $\chi^2 = 1383.017$, $P < 0.001$; Xundian 2021: $\chi^2 = 128.98$, $P < 0.001$; Jinghong 2021: $\chi^2 = 333.12$, $P < 0.001$).

In both years and sites, female FAW adults were caught with food attractants and subject to ovarian dissection. Following dissection of 1651 females from Xundian in 2020, the daily ovarian development index ranged between 3.5 and 4.4, and the corresponding age fluctuated between 6.0 and 8.7 days (Fig. 6a). Following dissection of 296 female from Xundian in 2021, the daily ovarian development index ranged between 1.3 and 5.0. The female age was only 2–4 days around May 13 and August 6 i.e., at the lowest FAW abundance level, and gradually increased thereafter (Fig. 6b). The female age was 8–10 d around May 30 and June 28 i.e., at the highest FAW abundance level (Fig. 6b). Therefore, it can be inferred that around May 13 and August 6 may be the peak period of emergence of the local population, so the age of trapping females was lower. About May 30 and June 28 were the peak periods for the migration of immigrant populations. On these days, the daily age of females was higher.

Lastly, following dissection of 709 field-caught females from Jinghong during 2021, the daily ovarian development index ranged between 3.9 and 5.0, and the corresponding age fluctuated between 7.3 and 10.1 days (Fig. 6c). Hence, individuals caught at Xundian (2020), Jinghong (2021) and during peak abundance at Jinghong (2021) primarily originate from migrant populations.

Migration trajectory and reproductive dynamics

To perform trajectory analysis and determine the origin of *S. frugiperda* migrant populations, the dates of peak abundance were recorded for each site and year. At Xundian in 2020, peak abundance was recorded over September 13–20, when the migrant population mainly originated from western parts of Yuxi City (Yunnan; northward migration) and eastern parts of Zhaotong city (Yunnan; southward migration). For a second peak abundance at October 4–11, the migrant population originated from southern parts of Kunming (Yunnan; northward migration) (Fig. 7a). At Xundian in 2021, peak FAW abundance was recorded from May 27 to June 2, when the migrant population mainly originated from western parts of Yuxi City (Yunnan; northward migration) and to lesser extent from northern parts of Xundian County (Yunnan; southward migration). For a second peak abundance at June 23–27, migrant populations originated from the south and east of Kunming City and west of Yuxi City (Yunnan; northward migration). Lastly, during peak abundance from August 16–18, migrant populations originated from the west of Kunming City and the west of Yuxi City (northward migration) (Fig. 7b). At Jinghong in 2021, *S. frugiperda* attained the highest abundance between October 12–21 and the migrant population mainly from Pu'er City and Zhuang-miao Autonomous Prefecture of Wenshan (Yunnan, China; southward migration) or eastern Myanmar (northward migration) (Fig. 7c).

Based on the age of field-caught females at Xundian in 2020, female fecundity was estimated to be highest (784) on September 23 and lowest (226) on September 9 (Fig. 8a). At Xundian in 2021, fecundity was projected to be highest (1167) on August 6 and lowest (24) on June 1 (Fig. 8b). At Jinghong in 2021, fecundity was projected to be highest (505) in mid-September to then decrease over time (Fig. 8c).

Discussion

Integrated pest management (IPM) decision-making is facilitated through a systematic quantification of in-field pest populations (Pedigo et al., 2021) e.g., through physical scouting or by using monitoring aids such as (light, color or volatile) traps. Further, impending pest outbreaks can be anticipated, and crop losses can be averted by gauging seasonal migration dynamics and devising science-based forecasting or early-warning systems. In this study, we validated the use of food attractants to assess field-level populations of the invasive *Spodoptera frugiperda* in China. We equally showed how the reproductive development status of field-caught *S. frugiperda* males and females can inform age structure and egg deposition patterns. Lastly, by integrating the above data with meteorological information (i.e., wind currents), we delineated the migration trajectories for this pest in different sites and years. Our work facilitates the development of effective IPM schemes for this newly invasive pest and aids the design of sustainable, environmentally sound crop protection schemes in China and abroad.

The development of reproductive apparatus affects (male, female) mating and oviposition behaviour, and mediates population growth. Our work showed that *S. frugiperda* adults of varying age exhibited differences in ovarian development index, egg load and testis size, which was similar to that of *H. armigera*, *S. exigua*, *C. medinalis* and other pests (Fan et al. 2019; He et al. 2021c; He et al. 2021d). Meanwhile, male body length did not affect testis size and factors such as photoperiod, flight duration or adult nutrition status only assume a minor role in *S. frugiperda* reproductive development (He et al. 2021a; He et al. 2021b; Ge et al. 2021a). Age-dependent models of *S. frugiperda* reproductive development can thus be a valid approach to infer the age of field-caught adults to predict population build-up.

Field trials showed that food attractants and sex pheromones could be effectively used to trap *S. frugiperda* adults, with the former approach yielding both male and female FAW. There was a significant correlation between the number of males trapped with food attractants and sex pheromones, which proved the feasibility of monitoring *S. frugiperda* with food attractants. Food attractants equally used to track population dynamics of other lepidopteran pests such as *H. armigera*, *S. exigua*, *C. pomonella* L. and *C. medinalis* (Knight and Light 2005; He et al. 2021c; He et al. 2021d; Zeng et al. 2021). On the other hand, pheromone-baited traps caught more FAW adults than food-based ones. However, the markedly lower capture rate of food-based traps may be due to the interference from (ambient) volatiles e.g., as released by (host or non-host) plants in or near the trapping sites (Schröder and Hilker 2008). Indeed, (common) plant-derived volatiles such as methyl salicylate or (E)-alpha-bergamotene act as oviposition attractants for *S. frugiperda*, while geranyl acetate acts either as an oviposition attractant or repellent depending on context (Signoretti et al. 2012; Yactayo et al. 2021). Moreover, by dispensing green leaf volatiles in the field (e.g., by using traps with food attractants), one may alter the volatile emission spectrum of maize plants themselves (von Merey et al. 2011). Lastly, both trapping methods yielded *S. frugiperda* males of different ages – with an identical age structure for both trap types. This possibly can be attained by combining sex pheromone and food lures in order to enhance overall attractiveness and also capture more male adults. For *C. pomonella* L., such combined lures yielded higher number of adults but did not effected on the trapping amount of female individuals. Follow-up research is thus essential and food attractant blends may need to be continually optimized.

In earlier work, traps baited with food attractants yielded *H. armigera* adults of a 1:1 sex ratio (He et al. 2021c), C. *pomonella* L. adults of a 4:1 (female : male) sex ratio (Knight et al. 2011) and a blend of benzyl alcohol and benzaldehyde yielded twice as many *Thysanoplusia orichalcea* F. females than males (Stringer et al., 2008). In our study, food-based traps attracted *S. frugiperda* adults of a sex ratio 4:1(female : male). Previously, electrophysiological studies revealed how *S. frugiperda* males are more responsive to multiple plant volatiles than females (Malo et al. 2004). Therefore, it may be the difference in the volatile components of different food attractants that led to the difference in the number of trapped females and males. Female attraction can thus possibly be enhanced by altering the volatile blend composition, adding oviposition attractants such as methyl salicylate or by modifying the overall dosage. As the development of accurate forecasting models depends upon sufficient numbers of S. *frugiperda* females, improved attractants can make an important contribution to fall armyworm IPM.

Insects' ovarian development status is a key parameter in migration ecology research, and populations are considered to be either local or migratory once their respective ovarian development index is below or above 3. For local populations, ovarian development indices can be 1 during adult emergence peaks and the proportion of individuals with indices above 3 often increases with time (Qi et al. 2011; Zhang et al. 2021). In our study, *S. frugiperda* population that were caught with food-based traps primarily consisted of migrants. Yet, at Xundian in 2021, we recorded the presence of both local and migrant *S. frugiperda* populations, and assessed their relative abundance. Through the analysis of the age of trapping females and seasonal abundance of the population of *S. frugiperda*, we also found out the peak period of emergence and migration of *S. frugiperda*. This information can be used to deploy preventative IPM strategies in a timely and targeted manner, thereby avoiding the expenditures and social-environmental impacts of chemical insecticides.

In our study, in-field monitoring of *S. frugiperda* enabled the delineation of migration trajectories (or population origin) and fecundity dynamics. Key insights were gained on the FAW fecundity dynamics, with female *S. frugiperda* attaining highest fecundity during mid-September in Jinghong and during multiple instances between mid-May and early August at Xundian in 2021. One can readily build upon this information and construct more complex population development models. Our work also unveiled (inter-country) FAW migration patterns. While *S. frugiperda* populations at Jinghong consisted of both north- and south-bound migrants including individuals that originated in Myanmar, those at Xundian primarily migrated northward from the south of Kunming (Yunnan). From March to May, *S. frugiperda* largely enters southwestern Yunnan from Kaye and Shan states in eastern Myanmar. Once the southwest summer monsoon strengthens after May, Myanmar's *S. frugiperda* populations will disperse northeastward and land in central or southern Yunnan (Wu et al. 2019; Wu et al. 2021a). By thus delineating the *S. fruiperda* migration trajectory, other trapping devices can be optimally positioned to reliably predict the onset of pest outbreaks (Wu 2020). Similarly, knowledge of the exact origin of migrant populations can facilitate the local deployment of management tactics (e.g., spray applications of nucleopolyhedrosis virus, NPV) or diversification measures to drastically reduce the initial inoculum size (e.g., Midega et al. 2018; Guo et al. 2020). Given that each trapped *S. frugiperda* female ceases ovipositing and no longer contributes to population growth, (food-based) trapping can also directly to pest management (Gregg et al. 2018). Justiniano et al. (2021) sprayed noctuid food attractants (active ingredients: oleoresins and sugars) with high-efficiency insecticides in corn fields could effectively attract and kill adults of *S. frugiperda* and significantly reduce the damage rate of offspring larvae to corn. During times of high female fecundity (at source locations or landing sites), effective trapping methods can thus reduce oviposition rates, lower larval densities and curb crop losses.

Multiple methods exist to monitor (pestiferous) lepidopterans in agricultural or natural habitats, each with their respective strengths and weaknesses. Light monitoring can provide quantitative estimates of seasonal abundance and unveil the ovarian development status of trapped individuals (Nieminen et al. 2000; Fu et al. 2014), which permits delineating the migration source or gauging the reproductive potential of migratory populations (Qi et al. 2011). Forecasting population fecundity based solely upon the ovarian development index carries drawbacks, as egg load varies with female age, nutrition status, fitness or energy expenditure and population phenology. Sex pheromone monitoring also offers quantitative metrics of population abundance and (male) adult age, but does not provide information on female fecundity (He et al. 2019). Our work demonstrates how food-based monitoring readily complements the above tactics, by generating valuable information on population abundance, reproductive development status, egg load and adult age. This method allows for a reliable assessment of the migration status of resident populations and a robust prediction of population fecundity e.g., based on female age. Food-based trapping thus provides a solid base to develop more comprehensive population development models and inform pest management practice.

In conclusion, this study established food-based trapping as a valid, effective monitoring method for (invasive) *S. frugiperda* populations and generated age-dependent models of FAW reproductive development. These novel monitoring methods further permitted delineating *S. frugiperda* migration trajectories and source areas. Our work helps to advance integrated pest management (IPM) of fall armyworm across its native and invasive range. It helps to unlock the true potential of area-wide pest management by guiding a timely, targeted deployment of non-chemical, preventative measures in FAW source and landing areas – far beyond the confines of individual fields, farms or agro-landscapes.

Declarations

Authors' Contributions

KW conceptualised and designed the work. WH conducted experiments. WH, LW, CL, SG, HZ, SJ and BC interpreted data. WH, XY, KAGW and KM drafted the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials The datasets generated during the current study are available from the corresponding author on reasonable request.

Conflict of interest The authors have declared they have no conflict of interest in this article.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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Figures

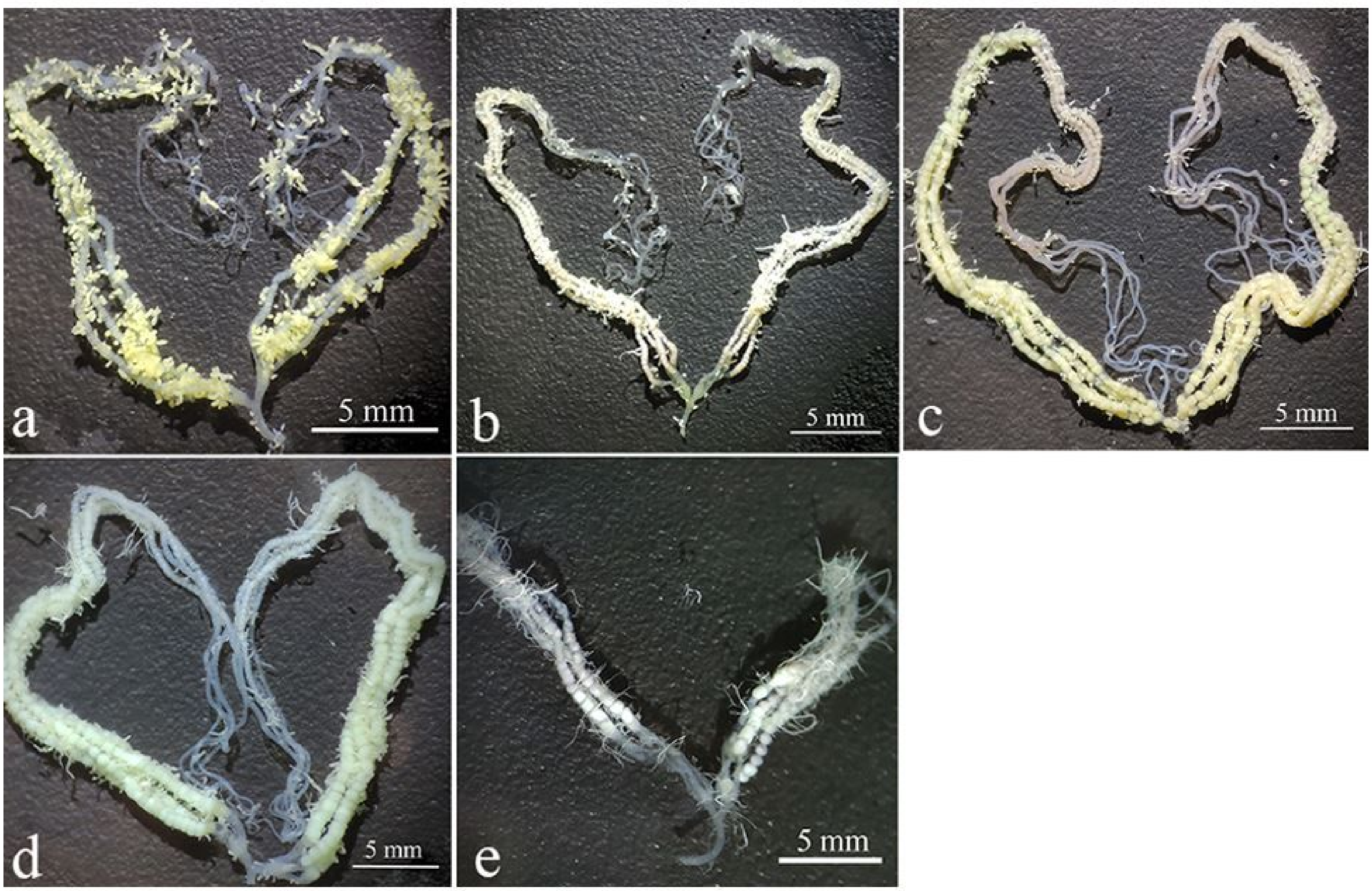

Figure 1

Ovary of *S. frugiperda* adult females at successive levels of development i.e., indices 1 (a), 2 (b), 3 (c), 4 (d) and 5 (e).

Figure 2

Bucket (a) and boat traps (b) used during 2020-2021 in Yunnan province (China) to evaluate different bait types and volatile attractants for *S. frugiperda*.

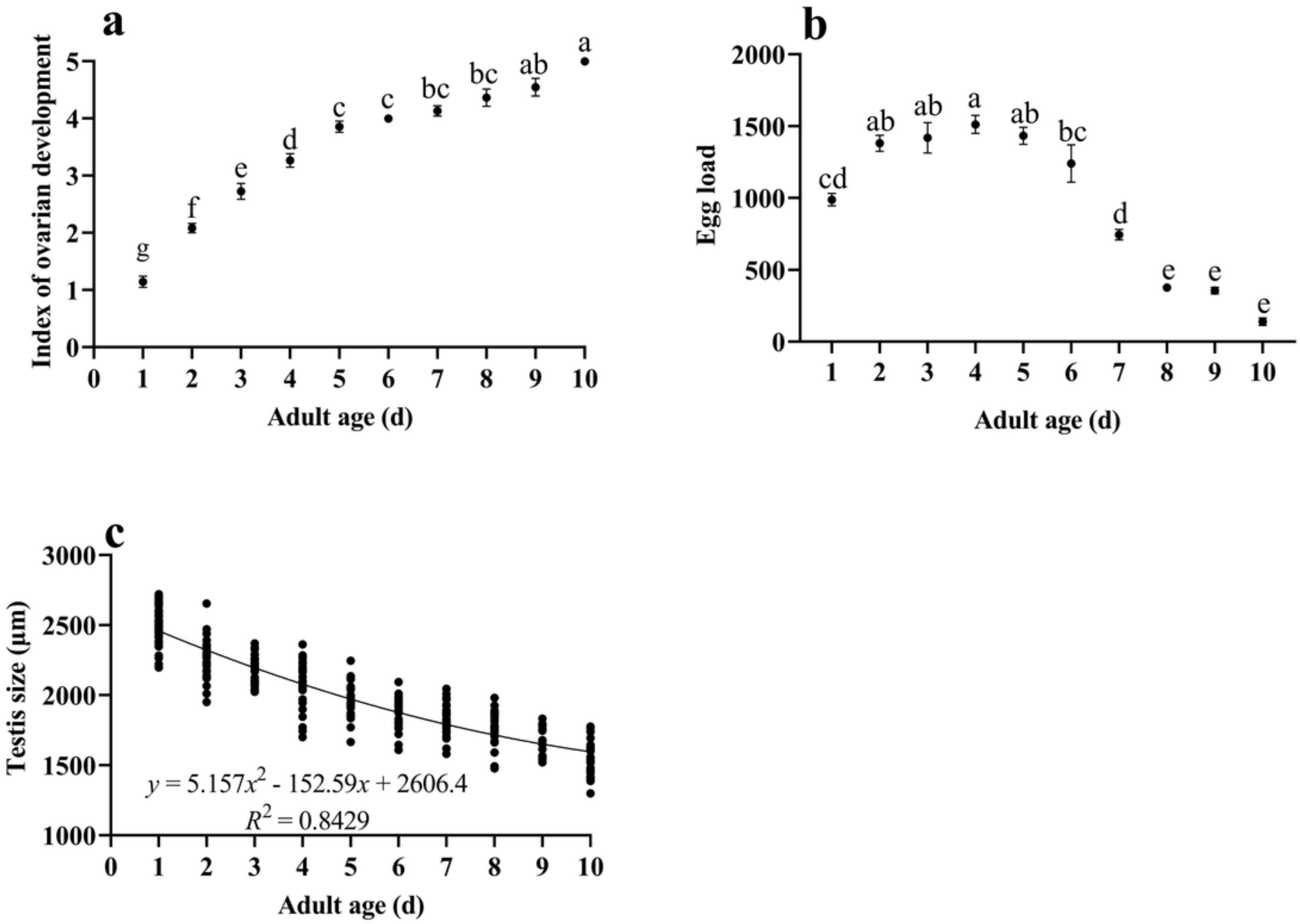

Figure 3

Fall armyworm adults of varying age exhibit different ovarian development indices (a), egg load (b) and testis size (c). Different lowercase letters in panels (a) and (b) are indicative of statistically significant differences (One-way ANOVA; $P < 0.05$).

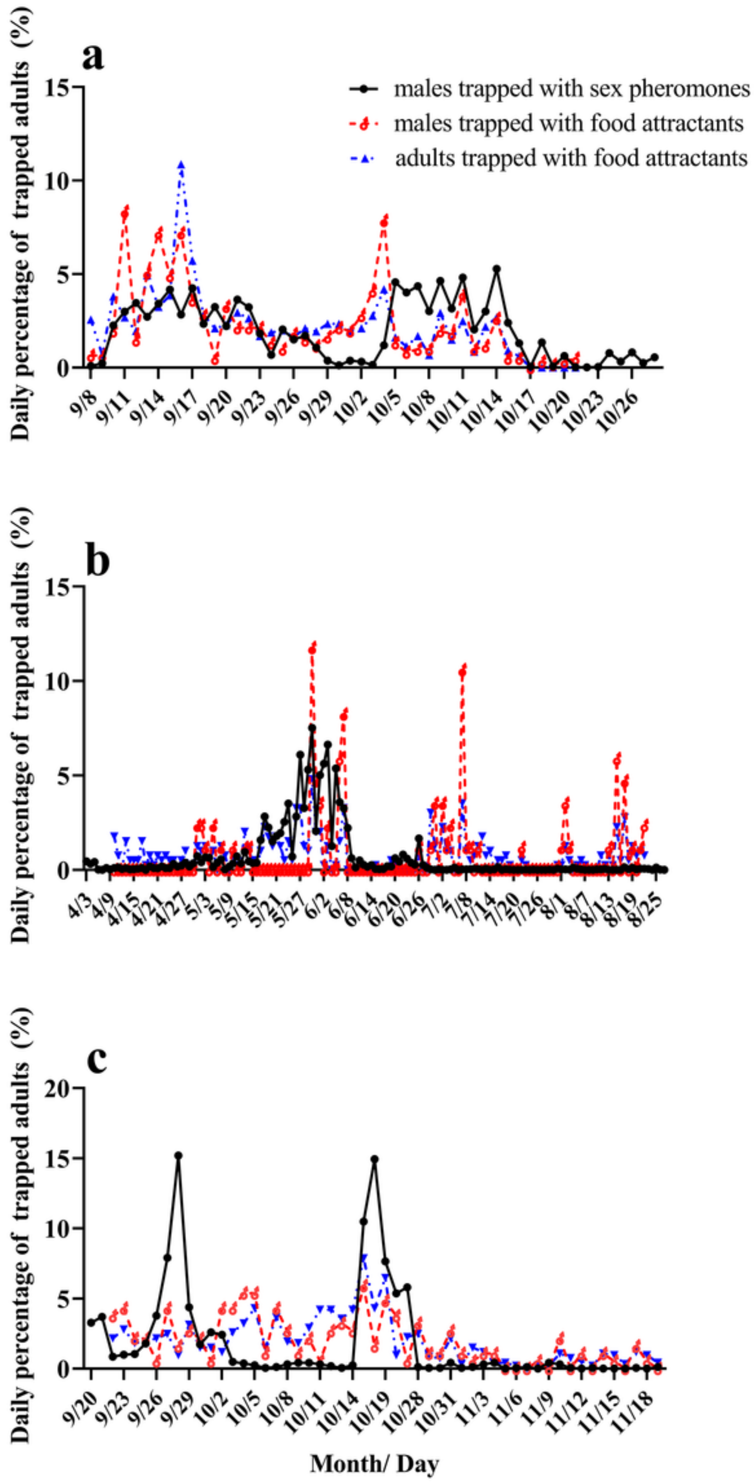

Figure 4

Temporal shifts in *S. frugiperda* abundance, as determined using traps baited with food attractants or sex pheromones. The different panels show trapping patterns at Xundian in 2020 (a) or 2021 (b) and at Jinghong in 2021 (c). “Daily percentage of trapped adults” means the daily proportion of adults caught to the total catch of *S. frugiperda* during the whole monitoring period. Different colors reflect trap type and *S. frugiperda* adult sex.

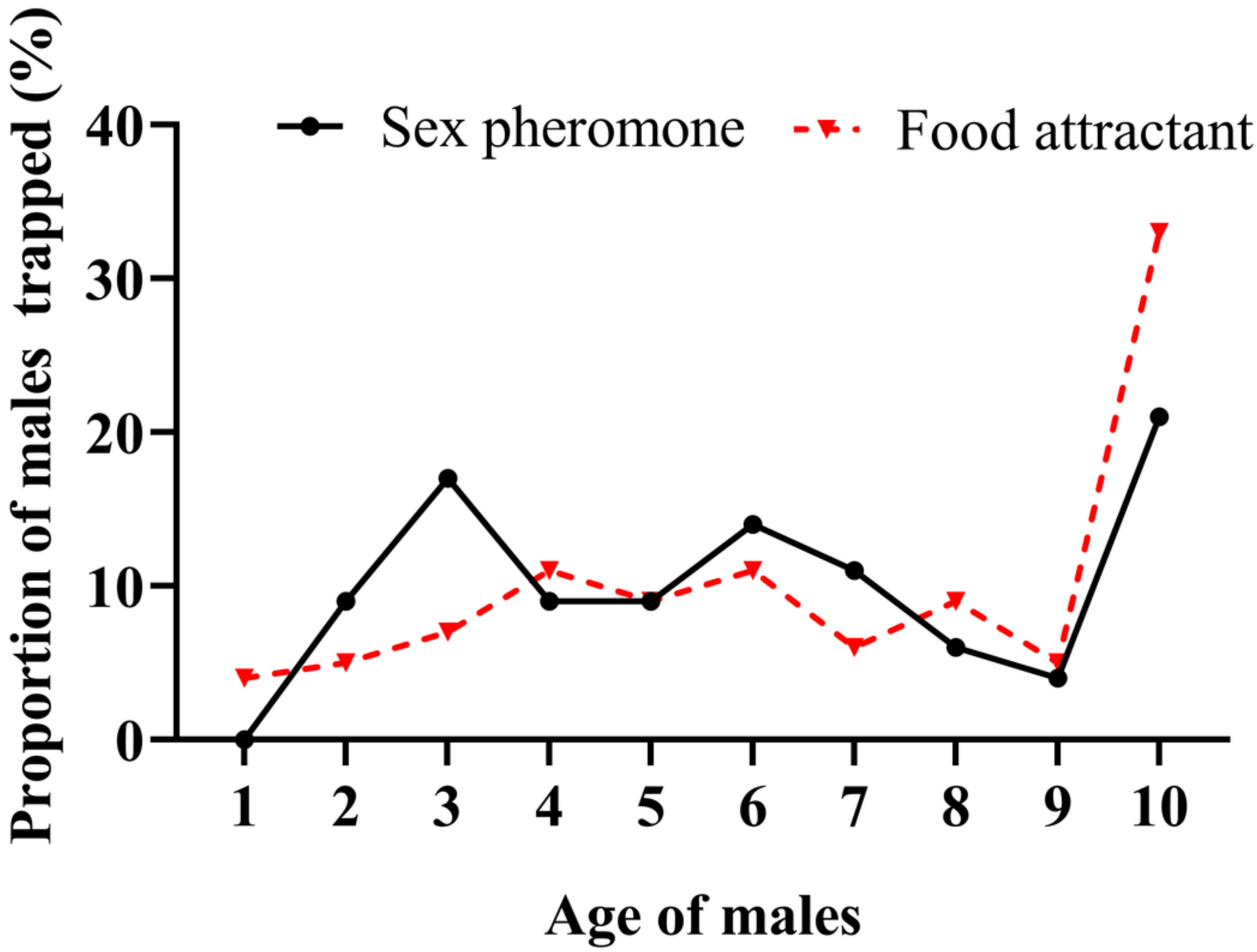

Figure 5

Age structure of *S. frugiperda* males caught using traps baited with food lures or sex pheromones at Xundian in 2021.

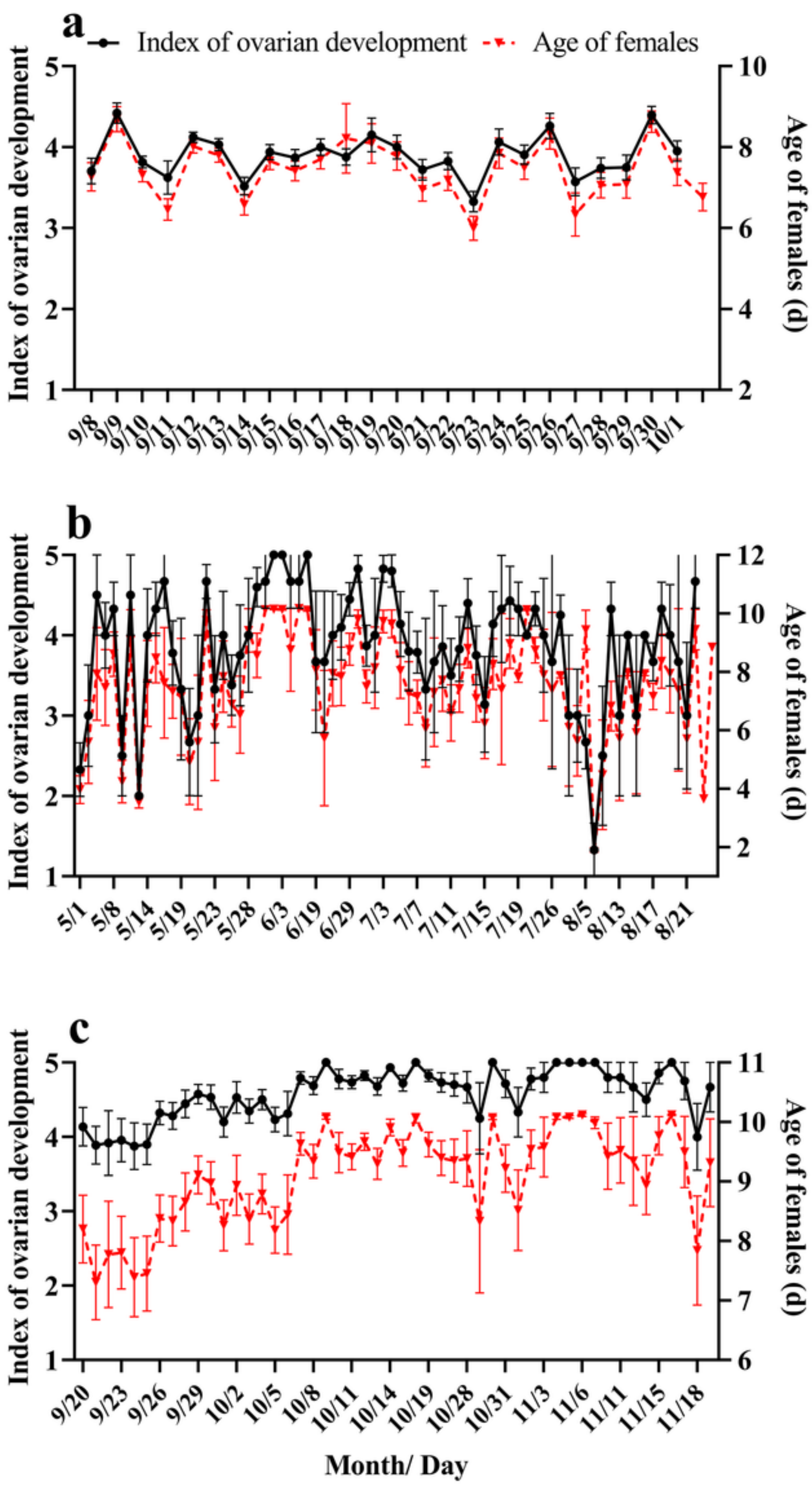

Figure 6

Temporal shifts the ovarian development index and corresponding age of *S. frugiperda* caught with food-based traps at Xundian in 2020 (a) or 2021 (b) and at Jinghong in 2021(c).

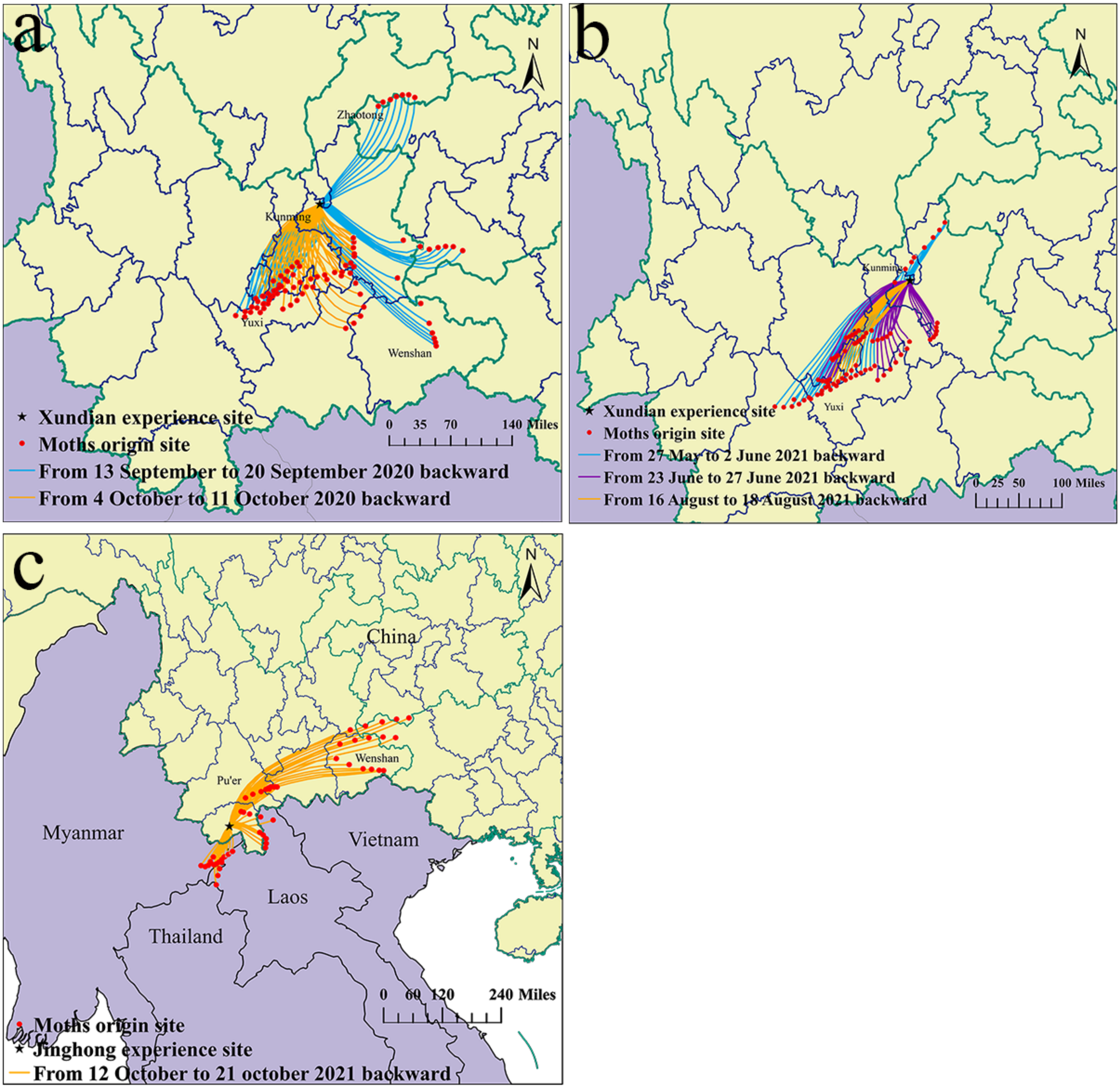

Figure 7

Modeled migration trajectories for dates of *S. frugiperda* peak abundance at Xundian in 2020 (a) and in 2021 (b) and at Jinghong in 2021 (c).

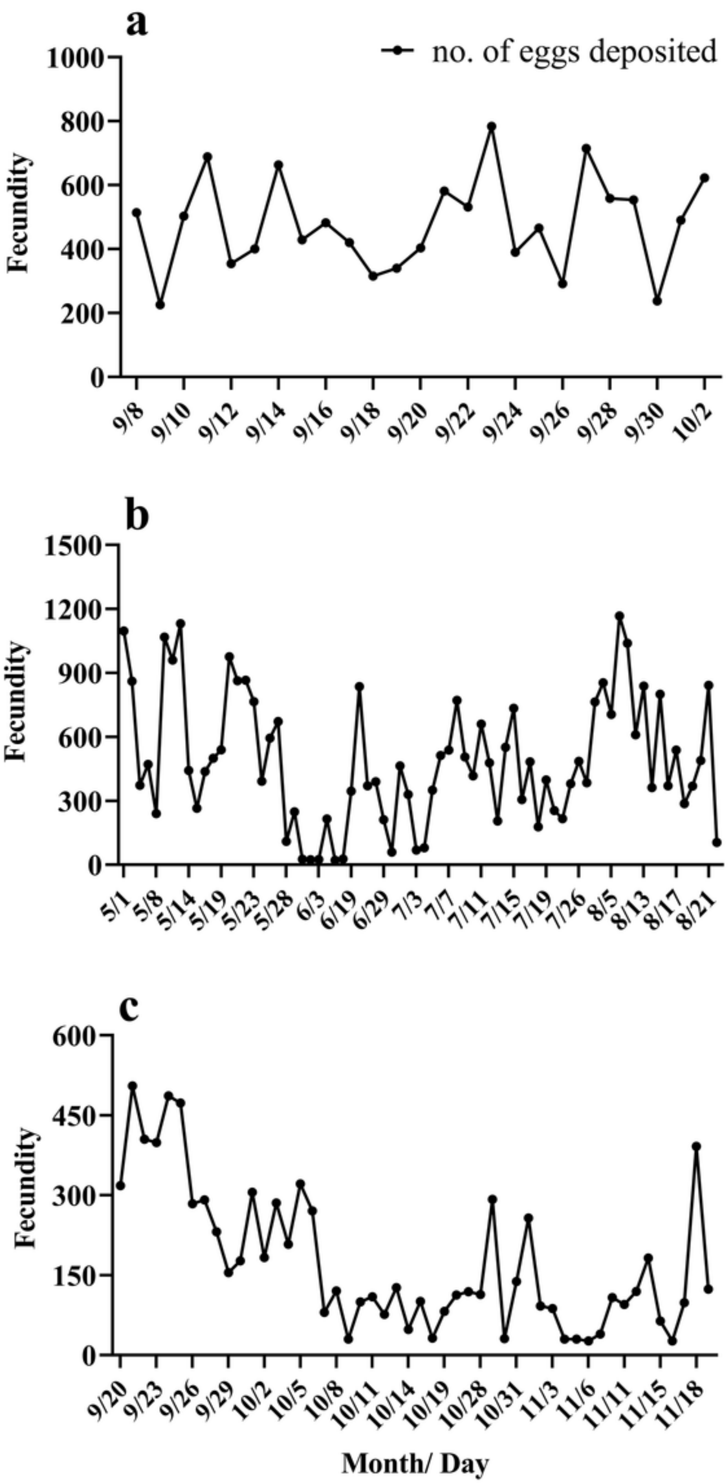

Figure 8

Temporal patterns in (predicted) fecundity of *S. frugiperda* females caught with food-based traps at at Xundian in 2020 (a) and in 2021 (b) and Jinghong in 2021 (c).