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Received: 26 November 2024 | Revised: 31 July 2025 | Accepted: 1 August 2025

DOI: 10.1111/phen.70001

ORIGINAL ARTICLE

Physiological Entomology: How Insects Work - Linking Genotype to Phenotype

Lateralized courtship behaviours and mating success in *Ostrinia furnacalis* (Lepidoptera: Crambidae): A population-level study on maize plants under greenhouse conditions

Sohail Abbas[1] | Aleena Alam[1] | Bilal Ahmad[1] | Muneer Abbas[2] | Weibo Qin[1] | Wu Haichao[1] | Zhang Cong[1] | Ji Yunliang[1] | Dong Hong Yuan[1] | Khalid Ali Khan[3,4] | Hamed A. Ghramh[4,5] | Jamin Ali[1] | Nora Burroni[6] | Menno Schilthuizen[7,8] | Ri-Zhao Chen[1]

[1]College of Plant Protection, Jilin Agricultural University, Changchun, People's Republic of China

[2]Citrus Research Institute, Sargodha, Pakistan

[3]Center of Bee Research and its Products and Research Center for Advanced Materials Science (RCAMS), King Khalid University, Abha, Saudi Arabia

[4]Applied College, King Khalid University, Abha, Saudi Arabia

[5]Biology Department, College of Science, King Khalid University, Abha, Saudi Arabia

[6]Institute of Ecology, Genetic and Evolution of Buenos Aires (IEGEBA-CONICET), University of Buenos Aires-National Council for Scientific and Technical Research, Buenos Aires, Argentina

[7]Naturalis Biodiversity Center, Leiden, The Netherlands

[8]Institute for Biology Leiden, Leiden University, Leiden, The Netherlands

Correspondence
Ri-Zhao Chen, College of Plant Protection, Jilin Agricultural University, Changchun, Jilin, 130118 People's Republic of China.
Email: rizhaochen@jlau.edu.cn

Funding information
People's Government of Jilin Province, Grant/Award Number: 20220203198SF; the Ministry of Science and Technology of China, Grant/Award Number: 2022YFD1500701; the Ministry of Agriculture of the People's Republic of China, Grant/Award Number: 15226025

Associate Editor: Thies Büscher

Abstract

Lateralization, defined as the asymmetric organization of brain functions, is a widely recognized phenomenon observed in an increasing number of insect species. However, knowledge remains limited for *Ostrinia furnacalis* (Guenée), particularly regarding population-level courtship lateralization on maize plants in greenhouse environments. This study investigates the lateralized mating behaviours of *O. furnacalis* on maize plants in controlled greenhouse conditions. Our findings reveal distinct differences in two population-level lateralized mating behaviours (left-biased and right-biased approaches, and 180° turnings), demonstrating for the first time the influence of the host plant environment. Male moths consistently exhibited a right-biased approach and left-biased 180° turning behaviour towards the female during copulation on maize plant leaves, which was associated with a reduced number of mating attempts. In response, female moths on maize leaves exhibited decreased rejection rates and increased receptivity to right-sided approaches and left-biased 180° turnings for intromissive copulation. Males performing ultrasonic courtship songs with left-biased 180° turning, reduced female rejections and lower courtship aggression achieved significantly higher mating success on maize plant leaves than those with right-biased 180° turnings for intromissive copulation. These findings provide the first empirical evidence of host plant-mediated lateralized courtship behaviours in *O. furnacalis* under greenhouse conditions. They offer novel perspective into the adaptive value of behavioural lateralization and highlight its relevance in naturalistic settings. This work advances insect behavioural ecology and has potential implications for developing behaviour-based pest control strategies.

KEYWORDS
greenhouse, lateralization, maize, mating behaviour, *Ostrinia furnacalis*

INTRODUCTION

Lateralization, the phenomenon of asymmetrical organization of brain functions and behaviours along the left–right axis, has intrigued neuroscientists for its implications on cognitive and behavioural processes (Güntürkün et al., 2020; Labache et al., 2023). It represents an intriguing concept in neuroscience, enhancing brain efficiency by enabling the concurrent left–right processing of multiple information streams (David Fernandes & Niven, 2020; Desaunay et al., 2023). It occurs at two levels: individual-level laterality, where an individual shows a consistent preference for one side, and population-level laterality, where a significant portion of individuals within a population exhibit a similar, side-specific behavioural tendency (Chapelain et al., 2015; Versace et al., 2020). In insects, behavioural asymmetries become especially pronounced during various activities, with a notable emphasis on mating phases (Takanashi et al., 2010). These phases encompass the development of premating and mating behaviours, which are characterized by lateralized movements, such as directional turns to the right or left (Boukouvala et al., 2022; Kavallieratos et al., 2023). The impact of these directional variations on mating success is substantial, resulting in marked differences in biological fitness (Dadda et al., 2009; Vallortigara & Rogers, 2005; Vallortigara & Rogers, 2020). While research on lateralized traits has primarily focused on vertebrate animals (Stieger et al., 2023; van Dijk et al., 2023; Wang et al., 2023), an increasing number of studies are shedding light on individual- and population-level brain and behavioural asymmetries in various invertebrate species (Benelli, Romano, Stefanini, et al., 2017; Romano et al., 2017). Notably, the lateralization of courtship and mating behaviour has been examined in several insect species, including hymenopteran parasitoids under laboratory conditions (Romano et al., 2018) (Romano et al., 2020), stored-product beetles (Boukouvala et al., 2021; Boukouvala et al., 2022; Boukouvala et al., 2023; Gidari et al., 2024; Kavallieratos et al., 2023), mosquitoes (Benelli, 2018) and a calliphorid fly (Benelli et al. 2015b). Previously, we investigated the lateralization of courtship and mating behaviours in *Ostrinia furnacalis* (Lepidoptera: Crambidae) under controlled laboratory conditions (Abbas et al., 2024). This study aimed to establish foundational insights into lateralized behaviours in this species. However, the role of lateralization in these behaviours on maize plants, its primary host, under semi-natural conditions such as a greenhouse remains underexplored. This study aimed to confirm the findings of our previous laboratory research by examining the lateralization of courtship and mating behaviours in *O. furnacalis* under greenhouse conditions, providing a more ecologically valid context. By doing so, we seek to determine whether lateralized behaviours, previously documented in the laboratory, exhibit any variations when observed on maize plants in a semi-natural setting.

Ostrinia furnacalis (Asian corn borer) is a highly adaptable seasonal pest that primarily develops on maize (*Zea mays*), its major host plant, which it prefers for complex lateralized courtship and mating behaviour where males exhibit lateralized courtship and mating behaviours (Abbas et al. 2025a; Frolov et al., 2022; Kim et al., 2022; Kojima et al., 2010; Li et al., 2021). Understanding these intricate mating rituals is crucial for effective pest control, as a thorough exploration of its lateralized behaviours on maize can significantly inform management strategies (Abbas et al. 2025a; Alam et al., 2023). The focus of this study is on capturing and quantifying these behaviours in the context of a greenhouse, allowing for the observation of these behaviours in an environment that more closely mirrors the moth's natural habitat. This research builds upon our previous laboratory findings, confirming previously documented lateralized behaviours while also expanding the study to a semi-natural setting. By examining lateralized courtship and mating behaviours on maize under greenhouse conditions, we aimed to validate our prior results, identify potential behavioural variations and assess the impact of these behaviours on male mating success. In moth species, variations in behavioural displays are crucial for mate recognition, copulation and mating success, with these behaviours playing a significant role in influencing evolutionary processes (Arminudin et al., 2020; Takanashi et al., 2010). We hypothesized that lateralized courtship and mating behaviours observed in the greenhouse will show variations compared to those seen in the laboratory, particularly in terms of male mating success and behavioural displays. The primary objectives of this study are to (1) identify population-level patterns of lateralization on maize plants under greenhouse conditions, (2) compare courtship and mating behaviours in a greenhouse setting as compared to our previous study (Abbas et al., 2024) and (3) assess how these lateralized behaviours influence male mating success on maize plants. This comparison is crucial for understanding and confirmation in this setting of the ecological relevance of lateralized traits in *O. furnacalis* and their implications for pest management strategies.

MATERIALS AND METHODS

Experimental site and insect population

Adult moths were obtained from laboratory-maintained populations that were previously used in our study on the exploration of lateralization, which examined the behavioural patterns of *O. furnacalis* in controlled conditions (Abbas et al., 2024). The study was conducted from late January to early February 2024 in the Agricultural Entomology and Pest Control Greenhouse and the Conservation Tillage Pest and Disease Monitoring Base at Jilin Agricultural University, China (43.815° N, 125.398° E).

Maize plants for mating trials

Non-Bt (Yudi-871) maize seeds were cultivated under controlled greenhouse conditions in mesh cloth cages. The greenhouse environment was maintained at 28 ± 2°C with 60 ± 10% relative humidity and a 16 L:8 D photoperiod to closely simulate natural field conditions during the maize-growing season in northeastern China. Maize plants were watered daily, and nutrient levels were regularly monitored to ensure consistent growth. Soil nutrient levels were monitored using the methodology outlined in a previous study (Li et al., 2013). An exhaust fan facilitates air circulation within the greenhouse to prevent overheating and maintain proper airflow (Calatayud et al., 2008). Only healthy, uninfested plants (maize plants at the J3 growth stage), free from any insect damage and treatments, were selected for the experiment to ensure optimal conditions for observing mating behaviours (Calatayud et al., 2008). Each maize plant was individually grown in small pots (5.4 cm diameter, 5.2 cm height) to ensure adequate nutrients and a consistent water supply. Four maize plants were placed together in a single experimental mesh cloth cage (30 cm $\times$ 30 cm $\times$ 30 cm) to facilitate the observation of lateralized mating interactions (see Table 1).

Experimental setup for observation of courtship and mating behaviour on maize plants under greenhouse conditions

Adult *O. furnacalis* were individually housed in ventilated plastic cups (3.5 cm diameter $\times$ 3.5 cm height) upon pupation to prevent premature mating and allow consistent monitoring of adult emergence. Each cup contained a piece of cotton to maintain humidity, prevent dehydration and support adult survival. To ensure consistent physiological conditions, a cotton wick soaked in 10% sucrose solution was also provided as a standardized diet until the start of mating trials. The sugar solution was replenished daily, and no additional food sources were present inside the experimental cages during behavioural observation. Male and female moths were identified based on body size, abdominal structures and other morphological characteristics (Alam et al., 2024; Frolov et al., 2007; Wang & Chen, 2024). Only newly emerged (≤1 day old), healthy and active male–female adults were selected for the trials. All the mating trials were conducted between 14:00 and 21:00 (Da Silva et al., 2013; Iwaizumi et al., 2010; Silvegren et al., 2005). After emergence, adults were allowed to acclimatize for a maximum of 16 hours before being introduced into the experimental cages (30 cm $\times$ 30 cm $\times$ 30 cm) for lateralized behavioural observation. One male–female pair of adults was introduced into an experimental arena (single mesh cloth cage) to study courtship and mating behaviours, focusing on four maize plants (Figure 1). The greenhouse was fully enclosed with black shading material to eliminate all external light sources, thereby ensuring a visually uniform and controlled environment. Illumination was provided exclusively by the greenhouse's pre-installed overhead artificial lighting, which remained continuously active during all observation sessions. The light source was fixed at a constant height (1.8–2.4 m) above the experimental area and emitted diffuse, uniform illumination, minimizing directional shadows and eliminating light gradients that could bias behavioural observations. To minimize direct light exposure on moths, one side of the cage facing the direct light source was partially covered with translucent filter paper (Whatman No. 1), which diffused the incoming light while maintaining clear visibility for accurate behavioural observation. Temperature (28 ± 2°C) and relative humidity (60 ± 10%) were maintained using standard greenhouse monitoring and control practices. All environmental parameters including lighting, temperature and humidity were consistently maintained across all trials. These conditions were selected to closely simulate the average environmental conditions during the maize-growing season in northeastern China. Although the region typically experiences a cold climate, average temperatures during the active mating period of *O. furnacalis* align with these settings. This approach ensured ecological relevance and allowed for realistic behavioural observations under semi-controlled conditions. No external disturbances or environmental variability interfered with observations, ensuring the reliability and reproducibility of data on lateralized courtship and mating behaviours under semi-natural greenhouse conditions. Lateralized courtship and mating behaviours were recorded for 107 male–female pairs, observed visually tracking them by a trained observer (S. Abbas) for 10 min, or until the end of the sexual interaction, if any (Benelli et al. 2017b). Out of the 107 initial pairs, 48 were excluded from the analysis because they did not exhibit mating behaviour on the host maize plants, including instances where pairs showed no interaction, appeared lethargic, or experienced premature death. A total of 59 male–female pairs displaying courtship and mating behaviours on maize plants were observed and included in the behavioural analysis. Among them, 54 pairs successfully achieved intromissive copulation following directional

TABLE 1 Behavioural displays observed during courtship and mating behaviour of *O. furnacalis*.

Behavioural displays	Observations (units)
Mate recognition	The time taken by the male to recognize the female for mating (s)
Male ultrasonic courtship song	The time spent by the male on ultrasonic courtship songs until intromissive copulation (s)
Male aggression towards female	The number of male aggressive frequency on the female for mating (n)
Antennal tapping by male on the female	The time spent by the male performing antennal tapping on the female (s)
Male antennal contact with the posterior of a female	The time spent by the male touching with its antennae on the posterior of the female's abdomen (s)
Number of male copulation attempts	The number of male copulation attempts (n)
Female courtship rejection/escape	The number of female rejections/escapes from the male to avoid mating (n)
Female motionless in response to male ultrasonic courtship songs	The number of female motionless responses to male ultrasonic courtship songs to accept mating (n)
Duration of intromissive copulation	The time from the insertion of the male's aedeagus into the female's genital chamber until genital disengagement (min)
The male mating success	The number of copulations that were successful (n)

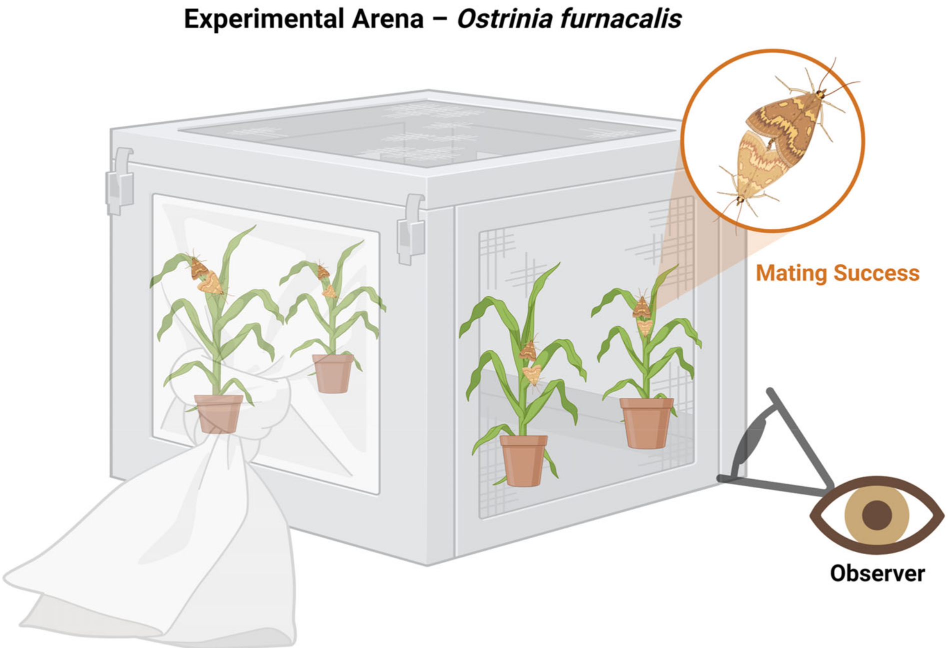

FIGURE 1 Experimental arena for observing lateralized courtship and mating behaviours in *O. furnacalis*.

approaches. However, this number further decreased to 45 pairs when only those males that performed a directional turning leading to confirmed genital engagement were considered. Only mating interactions that occurred in clearly visible positions on the maize plants such as exposed leaf surfaces were recorded. Observations were excluded from analysis if plant material obstructed visibility, preventing accurate documentation of behaviour. Lateralized courtship and mating behaviours of *O. furnacalis* were observed under greenhouse conditions on maize plants to capture natural behavioural patterns. All experimental pairs were consistently exposed to the same greenhouse conditions (Fattoruso et al., 2021) to ensure consistent behavioural observations. Although the absence of a control group limits certain comparisons, the key focus of this study was to expand upon previous laboratory-based research (Abbas et al., 2024; Romano et al., 2022) and observe how these behaviours manifest in a semi-natural environment.

Lateralized behavioural observations

After observing behavioural displays, the following lateralized behaviours were recorded: (i) directional approaches (right-biased and left-biased approaches) and (ii) directional turnings (right-biased and left-biased 180° turnings). Directional approaches refer to the male's selection of a side when approaching the female's posterior. Directional turnings involve the specific side (left or right) chosen by the male from the female to perform a 180° turning, positioning his abdomen for successful intromissive copulation. This turning manoeuvre is critical for establishing end-to-end genital linkage and initiating intromissive copulation. If no copulation occurred within the 30-minute observation window, the interaction was classified as unsuccessful (see Table 1; Figure 2).

Statistical analysis

The impact of lateralization on courtship and mating behaviours, including variation in mean duration and/or frequency was analysed using Origin Pro 2025b (Northampton, Massachusetts, USA). Non-parametric statistical methods were employed due to the non-normal distribution of data, as confirmed by the Shapiro–Wilk test ($p < 0.05$), and the presence of non-homoscedasticity, as indicated by Levene's test ($p < 0.05$). Non-parametric tests are particularly appropriate for data that do not meet the assumptions of normality or homogeneity of variances. Significance was set at $p < 0.05$. Differences in laterality, specifically the number of males approaching the left or right side of the female and the direction of their 180° turnings during courtship, were assessed using the chi-square test with Yates' correction ($p < 0.05$). Directional turning behaviours were compared using the Kruskal–Wallis test ($p < 0.05$), and directional approaches were compared using the Wilcoxon test ($p < 0.05$). The impact of male behavioural displays on mating success was analysed using the Mann–Whitney U test ($p < 0.05$) for two independent groups (successful vs. unsuccessful mating; Loriaux, 1971). The chi-square test results were interpreted in terms of biological significance by examining the strength of the observed differences in laterality, specifically focusing on whether males exhibited a consistent directional bias (left or right) when engaging in courtship behaviours.

To assess inter-rater reliability for the coding of lateralized courtship and mating behaviours, a randomly selected subset (~20%) of

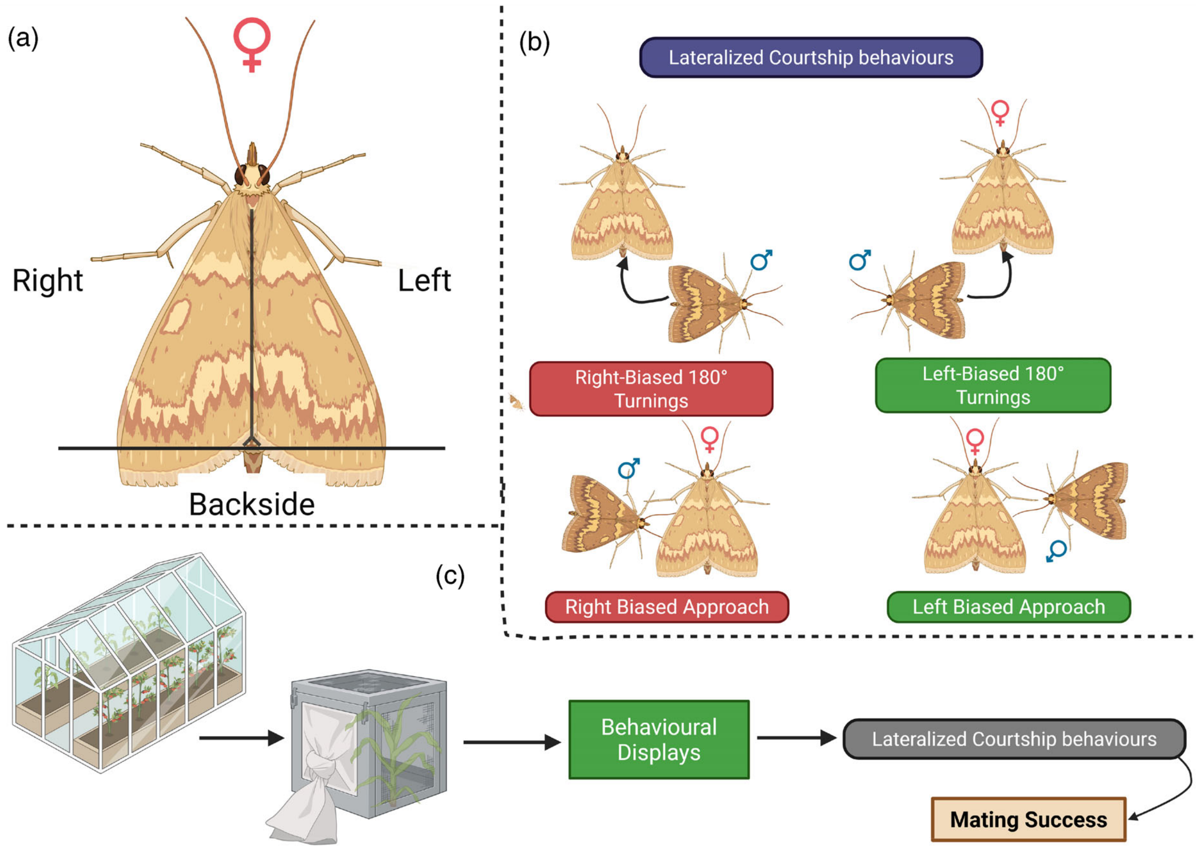

FIGURE 2 The mating sequence of *O. furnacalis* adults. (a) Male's choice of approach side relative to the female. (b) Directional biases in male approaches and turnings leading to intromissive copulation. (c) Transition from precopulatory to copulatory phases.

the observed pairs was independently re-analysed by two trained observers who were blinded to the experimental conditions, following the approach of Bisazza et al. (2001). The subset included representative cases of lateralized approach direction, 180° turnings and copulation behaviours. Inter-rater reliability was quantified using Cohen's kappa (Cohen, 1960) and the concordance index (Gwet, 2014; Romano et al., 2016). The concordance index yielded a value of 0.89, indicating almost perfect agreement, while Cohen's kappa was 0.841, reflecting substantial agreement between observers. The remaining dataset was analysed by the primary observer (S. Abbas) using the same validated behavioural coding criteria.

RESULTS

Mating behaviour sequence

The courtship sequence typically began with male directional approaches (from either the left or right side), followed by the production of ultrasonic signals via wing vibrations, antennal palpation, agonistic interactions and rotational alignment often involving a 180° body turn relative to the female. This behavioural progression commonly culminated in female immobility, a well-established indicator of sexual receptivity. While the observed patterns remained consistent, the specific behavioural differentiation showed notable deviations from those previously reported under controlled laboratory conditions (Abbas et al., 2024) and are therefore not detailed further in this study. In the results, 40% of males exhibited left-biased approaches, with 12% performing right-biased 180° turnings; however, only 18% of these pairs ultimately achieved successful mating on maize plant leaves. By contrast, 60% of males displayed right-biased approaches, and 55% performed left-biased 180° turnings, resulting in a significantly higher mating success rate of 58%, compared to the left-biased approach/right-biased turning combination (Figure 3).

Impact of lateralized approaches and behaviours on mating success in *O. furnacalis*

Mating success was higher when *O. furnacalis* males approached females from the right side during sexual interactions, whereas left-side approaches did not affect mating outcomes (Figure 4). Males that turned 180° to the left while attempting copulation also showed greater mating success compared to those exhibiting right-biased turnings (Figure 4; Table 2; Table 3).

Several behavioural traits were significantly associated with mating success, including mate recognition, ultrasonic courtship songs, male aggression, female rejection or escape and the number of male

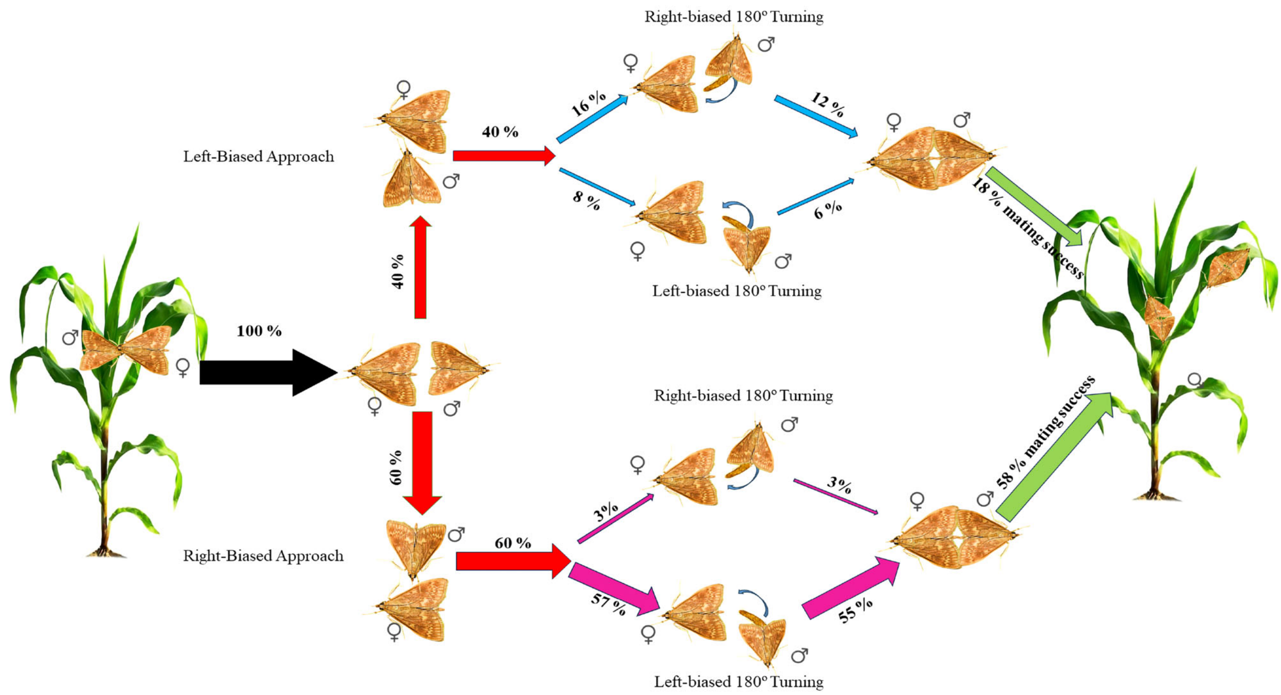

FIGURE 3 Ethogram depicting the courtship and mating sequence of the *O. furnacalis* on maize plants under greenhouse conditions. The proportion of adults displaying each behaviour is indicated by the thickness and percentage of each arrow ($n = 59$ observed mating pairs).

copulation attempts. By contrast, antennal tapping and antennal contact with the female's posterior did not influence mating success (Table 4).

When comparing left- and right-biased approaches with males, no substantial differences were found in the duration of mate recognition, antennal contact with the female's posterior, or copulation duration. However, left-biased males generally performed more copulation attempts, induced less female rejection and evoked stronger female receptivity (Table 2). Similar trends were observed when comparing left- and right-turning males during courtship sequences (Table 3).

Left-biased 180-degree turnings were associated with more frequent copulation attempts, reduced female rejection or escape behaviour and increased female motionlessness, indicating enhanced receptivity. Males approaching from the left also displayed lower levels of aggression and performed longer ultrasonic courtship songs compared to right-biased males (Table 2). Similarly, males performing left-biased 180° turnings made fewer copulation attempts and triggered less female rejection while also producing longer ultrasonic courtship songs and showing less aggression than right-turning males. These patterns suggest that left-biased approaches and turnings facilitate more efficient courtship behaviour and greater mating success in *O. furnacalis* (Table 3).

DISCUSSION

In the context of lateralized courtship and mating behaviours in *O. furnacalis*, several key lateralized actions play a crucial role in ensuring successful mating. Our recent study, conducted in the laboratory with several previous studies on some pests, strongly supports the significance of host plants under greenhouse conditions in enhancing mating success (Abbas et al., 2024; Calatayud et al., 2008; Fattoruso et al., 2021; Sun et al., 2023). Our research has revealed significant variations in the lateralized mating behaviours of *O. furnacalis* adult male and female moths on their primary host, maize plants, compared to previous studies (Abbas et al., 2024; Abbas, Alam, Ahmad, Abbas, Feng, et al., 2025). These findings not only reinforce but also expand upon earlier observations of lateralized behaviours, now confirmed under controlled greenhouse conditions. Upon encountering a female, males follow a distinct sequence of actions, as detailed in the results. These ethological units align with earlier studies on *O. furnacalis*, underscoring the consistency of courtship and mating patterns within this genus. Notably, the role of male ultrasonic courtship songs, a key factor in mating success, remains a constant across studies (Nakano et al., 2010; Nakano et al., 2013; Nakano & Nagamine, 2019; Rizvi et al., 2021; Zweerus et al., 2021). However, this study offers a novel contribution by demonstrating how these lateralized behaviours are modulated by the host plant environment, an element previously unexplored in laboratory studies (Benelli, 2018; Benelli et al. 2015a; Benelli et al. 2015b; Hunt et al., 2018; Kavallieratos et al., 2023; Zaynagutdinova et al., 2022; Zeni et al., 2024). Additionally, we observed a novel leg-kicking behaviour exhibited by females among successfully mated pairs, which appeared to signal female aggression or an attempt to terminate or separate from copula (Abbas, Alam, Ahmad, Abbas, Feng, et al., 2025). This behaviour has not been previously investigated and warrants further

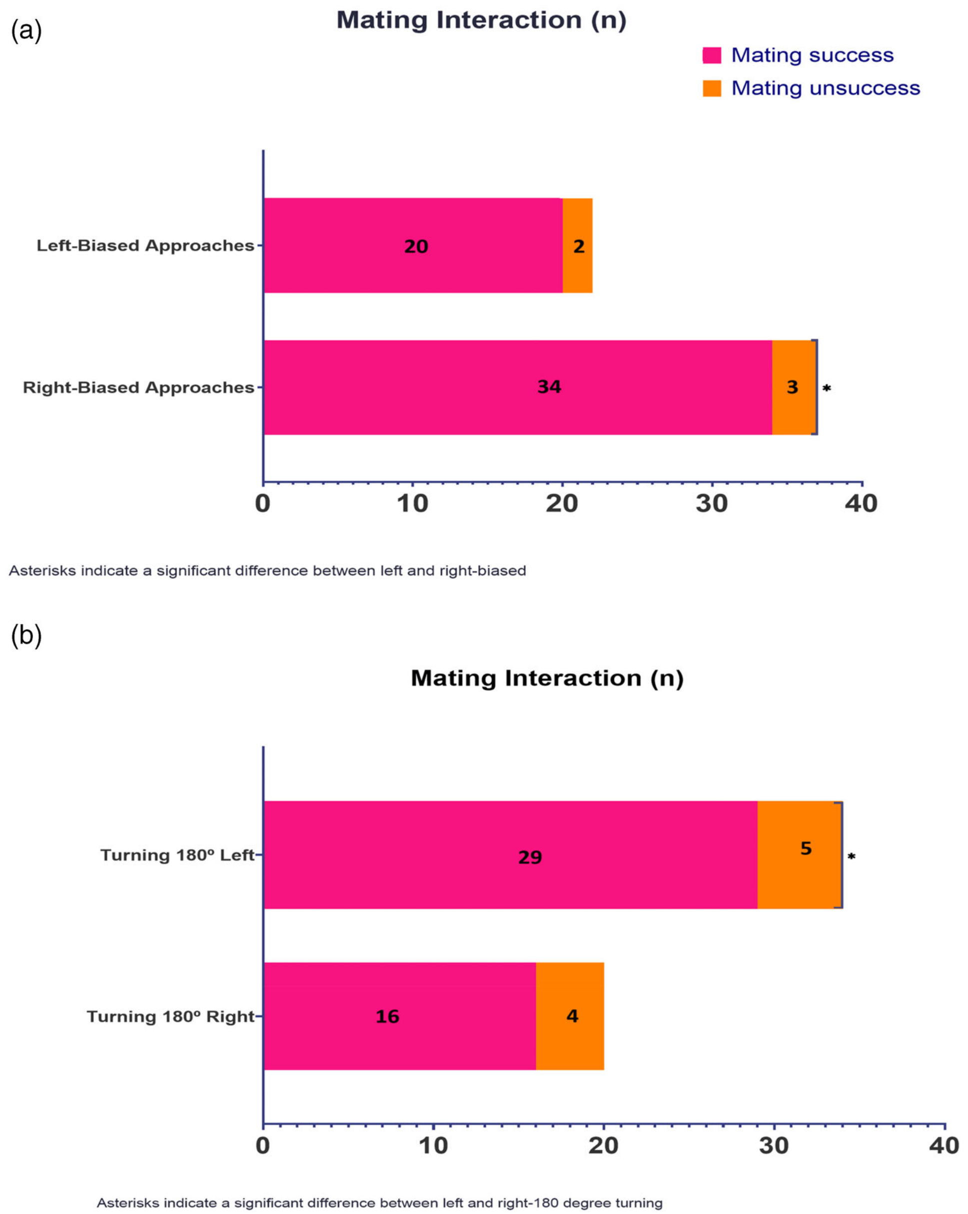

FIGURE 4 Mating success of *O. furnacalis* males showing (a) left- or right-biased approaches to the female and (b) left- or right-biased turning displays; asterisks indicate a significant difference between left- and right-biased acts (χ^2 test with Yates' correction, p < 0.05).

investigation to understand its role in mating success and its potential significance within the courtship dynamics of *O. furnacalis*. Overall, our alignment with existing literature not only underscores the generalizability of our findings within the broader context of insect behaviour but also emphasizes our study's objectives and novelty. By focusing on the lateralized mating behaviours of *O. furnacalis* in a controlled greenhouse setting on maize, we provide fresh insights into how these behaviours are modulated by environmental factors. Our research expands the understanding of courtship dynamics and highlights the critical role of male ultrasonic courtship songs, advancing knowledge by exploring the intersection of lateralization and mating success in a more naturalistic context.

The preference for right-sided approaches and left-biased turning behaviours in our study strongly supports the hypothesis that lateralization in mating behaviours confers adaptive advantages in *O. furnacalis* (Abbas et al., 2024) and has also been reported in previous studies on host plants under greenhouse conditions on *Spodoptera frugiperda* (Block et al., 2021). Specifically, left-biased approaches improve alignment between male and female genitalia, resulting in fewer copulation attempts and enhanced mating efficiency. Males initiating copulation from the left side required significantly fewer attempts to insert their aedeagus into the female's genital chamber, demonstrating a clear behavioural advantage as studied in previous insects (Benelli et al. 2015b; Chivers et al., 2017; Kiss et al., 2020; Romano et al., 2022). Furthermore, in our study, females responding to left-sided approaches exhibited fewer rejections, while males turning left showed reduced aggression and overall fewer copulation attempts. In stark contrast, males employing right-biased

TABLE 2 Courtship behavioural displays of *O. furnacalis* showing directional approaches towards females.

Behavioural displays	Right-biased approaches	Left-biased approaches	Tested adults (*n*., right ± Left-biased adults)	χ^2	df	*p*-value
Mate recognition (s)	36.334 ± 0.12[a]	33.134 ± 2.01[a]	37 ± 22 = 59	0.032	1	0.782
Male ultrasonic courtship song (s)	35.33 ± 2.12[a]	48.34 ± 2.76[b]	37 ± 22 = 59	4.842	1	0.0512
Male aggression towards female (n)	26.34 ± 3.34[a]	3.783 ± 2.43[b]	37 ± 22 = 59	4.244	1	0.0478
Antennal tapping (s)	13.32 ± 1.75[a]	20.17 ± 0.96[a]	37 ± 22 = 59	0.786	1	0.802
Antennal contact with female's posterior (s)	19.44 ± 1.16[a]	20.02 ± 1.76[a]	37 ± 22 = 59	0.021	1	0.820
Copulation attempts (n)	3.18 ± 1.45[a]	6.44 ± 2.66[b]	37 ± 22 = 59	8.187	1	<0.0001
Female rejection/escape (n)	28.13 ± 3.43[a]	4.32 ± 1.34[b]	37 ± 22 = 59	5.996	1	0.049
Female motionlessness (n)	30.43 ± 2.76[a]	18.56 ± 0.17[b]	37 ± 22 = 59	4.029	1	0.052
Duration of intromissive copulation (min)	68.24 ± 2.25[a]	70.19 ± 3.11[a]	34 ± 20 = 54	0.026	1	0.876

Note: Values are means followed by standard errors (SE) within each row; similar letters indicate no significant differences between side-biased parameters (Wilcoxon test, $p < 0.05$).

TABLE 3 Courtship and mating behavioural displays of *O. furnacalis* showing lateralized directional turning behaviour.

Behavioural displays	Right-biased 180° turning	Left-biased 180° turning	Tested adults (*n*., right ± left-biased adults	χ^2	df	*p*-value
Mate recognition (s)	41.67 ± 0.12[a]	38.342 ± 2.01[a]	37 ± 22 = 59	0.001	1	0.902
Male ultrasonic courtship song (s)	40.44 ± 1.68[a]	31.23 ± 1.20[b]	37 ± 22 = 59	10.842	1	<0.0001
Male aggression (n)	18.24 ± 2.02[a]	6.76 ± 1.89[b]	37 ± 22 = 59	6.984	1	0.042
Antennal tapping (s)	22.12 ± 1.23[a]	21.32 ± 2.67[a]	37 ± 22 = 59	0.785	1	0.801
Antennal contact with the female's posterior (s)	22.07 ± 1.59[a]	18.32 ± 1.34[a]	37 ± 22 = 59	0.021	1	0.820
Copulation attempts (n)	6.35 ± 0.34[a]	1.43 ± 1.21[b]	37 ± 22 = 59	10.262	1	<0.0001
Female rejection/escape (n)	20.56 ± 1.69[a]	4.46 ± 1.57[b]	37 ± 22 = 59	6.218	1	0.039
Female motionlessness (n)	18.53 ± 2.82[a]	10.34 ± 0.46[b]	37 ± 22 = 59	4.675	1	0.050
Duration of intromissive copulation (min)	69.01 ± 1.28[a]	68.34 ± 2.58[a]	29 ± 16 = 45	0.039	1	0.891

Note: Values are means followed by standard errors (SE); within each row, different letters indicate significant differences among side-biased parameters (Kruskal–Wallis test, $p < 0.05$).

approaches faced lower mating success, characterized by increased copulation attempts and delayed initiation. These findings support the hypothesis that lateralization may play a role in optimizing motor coordination during copulation even in its host environment (Benelli et al. 2015b; Benelli et al. 2017b; Boukouvala et al., 2020; Boukouvala et al., 2022; Møller & Swaddle, 1997; Romano et al., 2022; Vallortigara, 2006). The physiological or neurological basis for this lateralized preference remains unclear, but it may relate to asymmetric brain function or motor control in *O. furnacalis*, as observed in other stored-product pests, mosquitoes and bugs (Benelli et al. 2015a; Benelli et al. 2017a; Benelli et al. 2017b; Filice et al., 2021; Font et al., 2023; Frasnelli, 2017; Frasnelli et al., 2012; Frasnelli & Vallortigara, 2018). Our findings also emphasize the critical role of specific courtship behaviours, such as ultrasonic songs and antennal tapping, in eliciting female receptivity. Unlike previous studies that deemed these behaviours insignificant in laboratory settings (Abbas et al., 2024), our results indicate that mating success was significantly influenced when males performed ultrasonic courtship songs and exhibited courtship aggression, particularly on the host plant, maize. The absence, inconsistency, or weak expression of these behaviours appeared to negatively affect mating success (Table 3). This highlights the behavioural differences observed in a natural context compared to laboratory conditions and underscores the novelty of our study.

Our study demonstrated a significant correlation between mating success and lateralization in *Ostrinia furnacalis*, showing that males approaching females from the right side and exhibiting leftwards turning behaviours achieved higher mating success rates. This represents the first evidence of consistent population-level lateralized mating traits in *O. furnacalis* on its primary host, maize, under greenhouse conditions. While previous research has primarily focused on motor biases, our findings validate the existence of lateralized courtship and mating behaviours, supporting the broader trend of lateralization

TABLE 4 Male behavioural displays influencing mating success in *Ostrinia furnacalis*.

Behavioural trait	Successful mating	Unsuccessful mating	χ^2	df	*p*-value
Mate recognition (s)	40.45 ± 0.18	60.77 ± 2.92	16.342	1	<0.0001
Ultrasonic courtship song (s)	34.23 ± 4.21	68.32 ± 3.86	20.688	1	<0.0001
Male aggression (n)	3.50 ± 0.12	0.60 ± 0.42	8.4221	1	0.0211
Male Antennal tapping (s)	21.00 ± 2.15	22.30 ± 1.54	0.7862	1	0.8022
Antennal contact (s)	20.80 ± 1.33	20.00 ± 1.23	0.8024	1	0.7711
Copulation attempts (n)	2.10 ± 0.28	7.90 ± 0.71	6.3781	1	0.0211
Female rejection/escape (n)	1.60 ± 1.32	5.10 ± 0.38	5.6162	1	0.0412

Note: Male courtship behaviours between successful and unsuccessful mating outcomes in *O. furnacalis*. Statistically significant values (Mann–Whitney U test $p < 0.05$) indicate behaviours contributing to mating success. Values are presented as mean ± standard error (SE).

observed across various insect species such as *Apis mellifera* (Anfora et al., 2010; Sakurai & Ikeda, 2022). Recent studies have reported lateralized traits related to courtship, mating and genital morphology (Boukouvala et al., 2022; Calla-Quispe et al., 2023; Kamimura et al., 2021; Romano et al., 2018; Romano et al., 2021; Schilthuizen, 2013). This research enhances our understanding of behavioural adaptations in *O. furnacalis* by demonstrating lateralization in a semi-natural environment on its major host plant, as opposed to controlled laboratory conditions without host plants. It further reveals how these behaviours may vary under different environmental and host conditions, highlighting the species' adaptability. Importantly, the study offers authentic evidence of how lateralized courtship and mating behaviours operate within the context of the species' primary host, thus enriching our knowledge of their reproductive strategies in real-world settings.

Theoretical models suggest that population-level lateralization is more likely to emerge in social species due to its potential benefits in coordination, communication and social cohesion (Frasnelli & Vallortigara, 2018; Ocklenburg et al., 2023; Rogers et al., 2013; Tonello & Vallortigara, 2023). Insects, especially those with frequent interactions like *O. furnacalis*, may exhibit lateralized behaviours as an adaptive strategy during mating (Casanova, 2020; Manns, 2022). While much research has focused on controlled environments to study lateralization (Manns, 2021; Romano et al., 2022). Our previous study also highlighted that environmental conditions, along with the origin of the population whether derived from different geographical sites or laboratory versus field environments can have a significant impact on the biological processes and mating behaviours of *O. furnacalis* (Alam et al., 2025). The novelty of our study lies in demonstrating that lateralized courtship behaviours are not only present in *O. furnacalis* but also potentially amplified when observed on maize plants under greenhouse conditions. This suggests that the natural environment, specifically the host plant, may play a critical role in shaping these behaviours. This finding opens up new avenues for exploration in both pest management and behavioural ecology.

In conclusion, this study provides the first comprehensive evidence of population-level lateralized mating behaviours in *O. furnacalis* on maize plants under greenhouse conditions. These results confirm lateralization in a more natural host environment, highlighting left-sided approaches and turning during mating interactions. Moreover, behavioural changes observed under greenhouse conditions indicated more efficient mating success compared to laboratory settings. By examining these behaviours in a semi-natural setting, this research expands our understanding of lateralization beyond the controlled conditions typically used in laboratory studies. The consistent lateralized courtship behaviours observed suggest potential applications in behaviour-based pest control. Specifically, directional biases, such as right-sided approaches and left-biased 180° turns, could be utilized to optimize the design of pheromone traps or mating disruption systems, thereby enhancing pest management strategies. While further field validation is needed, these findings provide a foundation for developing pest control methods that exploit natural asymmetries in mating behaviours. Finally, this study opens avenues for future comparative research across insect species, enhancing our understanding of the evolutionary and ecological significance of lateralization in mating behaviours.

AUTHOR CONTRIBUTIONS

Sohail Abbas: Conceptualization; investigation; writing – original draft; writing – review and editing; methodology; validation; visualization; software; formal analysis; data curation; resources; project administration. **Aleena Alam:** Writing – review and editing; investigation. **Bilal Ahmad:** Writing – review and editing; resources. **Muneer Abbas:** Data curation; writing – review and editing; software. **Weibo Qin:** Writing – review and editing. **Wu Haichao:** Writing – review and editing; resources. **Zhang Cong:** Writing – review and editing. **Ji Yunliang:** Writing – review and editing. **Dong Hong Yuan:** Writing – review and editing. **Khalid Ali Khan:** Writing – review and editing. **Hamed A. Ghramh:** Writing – review and editing. **Jamin Ali:** Writing – review and editing. **Nora Burroni:** Writing – review and editing; validation; visualization; data curation. **Menno Schilthuizen:** Validation; visualization; writing – review and editing; data curation. **Ri-Zhao Chen:** Funding acquisition; writing – review and editing; supervision; resources; methodology; project administration.

ACKNOWLEDGEMENTS

We extend our gratitude to the Conservation Tillage Pest and Disease Monitoring Research Base (GPS: E125.398 N43.815, No. JLP-BCC- 21-31-CC-01) of Jilin Agricultural University for their assistance with lateralized behavioural research. We extend our appreciation to the Deanship of Scientific Research at King Khalid University, Saudi Arabia, for funding this work through the Large Groups Project under grant number R.G.P.2/396/46. We are thankful to Dr. Romano Donato for providing suggestions on the manuscript.

FUNDING INFORMATION

We thank the People's Government of Jilin Province (20220203198SF), the Ministry of Science and Technology of China (2022YFD1500701), and the Ministry of Agriculture of the People's Republic of China (15226025).

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad Digital Repository (Abbas et al. 2025) at https://doi.org/10.5061/dryad.zkh1893nc.

ORCID

Sohail Abbas https://orcid.org/0000-0001-8909-5955
Ri-Zhao Chen https://orcid.org/0000-0001-8866-6648

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How to cite this article: Abbas, S., Alam, A., Ahmad, B., Abbas, M., Qin, W., Haichao, W. et al. (2025) Lateralized courtship behaviours and mating success in *Ostrinia furnacalis* (Lepidoptera: Crambidae): A population-level study on maize plants under greenhouse conditions. *Physiological Entomology*, 1–12. Available from: https://doi.org/10.1111/phen.70001