Lateralized differences in ultrasonic courtship songs and their impact on reproductive strategies in *Ostrinia furnacalis* (Lepidoptera: Crambidae)

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Abstract

BACKGROUND: Lateralized courtship behaviors in *Ostrinia furnacalis* (Guenée) play a pivotal role in reproductive success. However, the variation in ultrasonic courtship sounds produced by males during these lateralized displays, and their subsequent impact on mating success, remain unexplored. To address this gap, this study examined differences in the ultrasonic courtship song characteristics of left- and right-biased courtship displays and their influence on mating outcomes. Mating trials were conducted to record and analyze variations in ultrasonic courtship songs behaviours and associated acoustic parameters, including dominant frequencies, pulse durations, pulse intervals, and the number of pulses emitted during left- and right-biased displays, as defined by the male's turning direction during copulation attempts.

RESULTS: Our findings revealed that left-biased ultrasonic songs featured shorter pulse durations, tighter inter-pulse intervals, and dominant frequencies between 55 and 65 kHz. These acoustic traits closely matched profiles observed in successful mating events, whereas right-biased emissions (65–80 kHz) were frequently associated with unsuccessful mating attempts. Left-biased songs of shorter duration (28–38 s) were positively correlated with greater mating success, whereas the longer durations observed in right-biased displays (40–60 s) were linked to lower mating success. Moreover, males exhibiting left-biased courtship behavior required fewer mating attempts to achieve successful copulation.

CONCLUSIONS: This study provides the first clear evidence of lateralized ultrasonic courtship behavior in *O. furnacalis*, with left-biased displays conferring a reproductive advantage. The findings highlight the ecological and evolutionary importance of acoustic lateralization in moth communication. Future research should investigate how ecological factors such as predator-driven selection, habitat structure, and female sensory biases influence these lateralized courtship behaviors. Such understanding can directly support more effective, behaviorally informed pest control strategies. These results contribute to the development of targeted approaches, such as pheromone traps and acoustic interference.
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1 INTRODUCTION

Lateralization, the preferential use of one side of the body or brain for specific tasks, is a widespread phenomenon in the animal kingdom. It influences various behavioral and cognitive processes, including foraging, predator avoidance, and social interactions. In the context of reproduction, lateralization plays a critical role in courtship behaviors, often enhancing mate attraction and reproductive success. For instance, lateralized behaviors, such as asymmetric vocalizations or visual displays during courtship, allow insects to more effectively signal their suitability as mates.[1–4] Lateralized displays have been observed across a wide range of taxa, including insects, birds, and mammals, where asymmetries in courtship behaviors significantly influence mate choice and reproductive fitness.[5–8] The neural mechanisms underlying such behaviors are often associated with functional specialization of the left and right hemispheres of the brain, where one hemisphere may be preferentially involved in communication, specifically mating rituals.[4,8] Such lateralization may facilitate neuromuscular coordination, minimize interhemispheric interference, and enhance the precision of signal generation by enabling hemispheric specialization in executing courtship motor patterns[9,10] and lateralization in male ultrasonic courtship songs,[11] thereby optimizing mating efficiency and reproductive success. This provides a theoretical basis for our hypothesis that left-biased behaviors may be more reproductively advantageous.

Ultrasonic communication is a well-documented form of acoustic signaling in insects, especially during mating phases.[12–14] Male insects produce species-specific sounds, including ultrasonic pulses, to attract females, assert dominance, or demonstrate reproductive fitness.[15,16] In moths, ultrasonic signals are generated during wing fanning and serve as critical signals for mate recognition and female preference. These courtship songs vary in acoustic parameters such as frequency, pulse duration, pulse interval, and chirp rate.[17,18] Female moths often show a preference for males whose courtship calls align closely with the species-specific frequency range and exhibit precise temporal patterns, such as shorter pulse durations and consistent pulse intervals.[19,20] These preferences are believed to reflect the underlying male quality or genetic fitness, with ultrasonic courtship calls acting as honest indicators of male viability.[21] Beyond mate attraction, ultrasonic signals can also function in competitive interactions, such as repelling rival males.[22,23] While these acoustic features have been extensively studied concerning mating success, the potential influence of lateralized differences in ultrasonic signal production remains largely uninvestigated. Understanding how lateralized courtship behaviors interact with acoustic signaling could elucidate the mechanisms of sexual selection.

The Asian corn borer, *Ostrinia furnacalis* (Lepidoptera: Crambidae), is a major seasonal pest of maize crops across Asia, causing significant economic losses in agriculture.[24–26] Adult moths of *O. furnacalis* engage in ultrasonic courtship during lateralized courtship behaviors, in which males produce high-frequency calls during wing fanning (also called ultrasonic courtship songs) to attract females. These ultrasonic signals vary between individuals in parameters such as frequency, duration, acoustic characteristics, and temporal structure, which are critical for mate recognition and successful copulation.[27,28] *O. furnacalis* females preferentially respond to males whose signals fall within optimal frequency ranges and exhibit consistent acoustic patterns. For instance, specific frequency ranges, ultrasonic courtship durations, and precise pulse intervals can be associated with greater mating success.[29,30] Although the acoustic signaling of *O. furnacalis* has been studied in the context of mate recognition, the influence of lateralized courtship behaviors on these signals and their effect on reproductive outcomes remains unexplored. This gap limits our understanding of the behavioral adaptations that shape mating strategies in this species and their implications for ecological interactions and population dynamics.

This study focuses on the lateralized courtship behaviors of *O. furnacalis*, specifically examining the differences in ultrasonic signal characteristics produced during left- and right-biased displays and their influence on mating success. Recent studies on lateralization in other taxa have shown that asymmetric behaviors can enhance the efficiency of mating displays and improve reproductive outcomes.[31–33] Our previous studies on *O. furnacalis* have shown that males with left-biased displays achieve greater mating success than those with right-biased displays.[34,35] However, the relationship between the lateralization of male displays during copulation and differences in ultrasonic courtship song features between left- and right-biased displays, particularly in terms of why left-biased displays result in more successful intromissive copulations, has not been thoroughly investigated. We hypothesize that this advantage may be linked to differences in ultrasonic courtship song characteristics, with left-biased males producing signals that more closely match female acoustic preferences, an idea rooted in theories of hemispheric specialization and efficient signal production. To date, no research has systematically examined whether such lateralized behaviors in moths, particularly in ultrasonic communication, confer similar advantages. Investigating the ultrasonic courtship differences between lateralized courtship behaviors in *O. furnacalis* could advance understanding of how acoustic signaling and behavioral asymmetries contribute to sexual selection in this pest species. The objectives of this study are to explore variations in ultrasonic courtship song acoustic parameters (chirp duration, chirp interval, chirp rate, pulse duration, pulse interval, pulse rate, and the number of pulses per chirp) between left- and right-biased courtship displays in *O. furnacalis*. We investigated the differences in male mating attempts, ultrasonic courtship song duration, frequency, pulse interval, and pulse duration, and assessed their impact on mating success in males exhibiting left-biased and right-biased behaviors. In addition, we identified the specific ranges of these acoustic parameters in males with left- and right-biased displays that are crucial for mating success. A further objective was to assess the overall quantification of lateralized courtship behaviors and their impact on mating success, specifically by quantifying the number of males exhibiting left-biased and right-biased displays. By

addressing these objectives, this study clarifies how lateralized courtship signals influence reproductive success in *O. furnacalis*, emphasizing their evolutionary relevance and potential utility in integrated pest management strategies, such as mating disruption via targeted acoustic interference or pheromone manipulation to reduce copulation success in pest populations, with future applications potentially extending to field-level control.

2 MATERIALS AND METHODS

2.1 Study species and experimental design

This study investigates the lateralized courtship behaviors of *O. furnacalis* from a laboratory population maintained at the Insect Behavioural and Ecology Laboratory, Jilin Agricultural University, China. The moths used in this study were selected from a well-established colony that has been maintained for approximately ten generations under controlled conditions. The colony was inbred to ensure genetic homogeneity, which was essential for minimizing genetic variation and maintaining consistency in experimental conditions. Detailed information on the population selected for this study, including rearing and collection methods, is provided in our previous studies.[34,35] Upon eclosion, adult moths were provided with a 10% sugar solution on cotton pads to ensure adequate nourishment and facilitate sexual maturation. All moths were reared under controlled environmental conditions (25 ± 2 °C, 12:12 h light/dark cycle) to minimize potential confounding factors that could affect mating behavior. To prevent premating interactions and ensure all individuals remained virgin, males and females were separated upon pupal emergence into small cups (5 cm × 5 cm) before the trials. Sex determination was performed by examining the external genitalia and morphological traits. Males were characterized by smaller body size and fan-like antennae, and females were distinguished by their larger body size and broader abdomens.[35] Although the diet was not expected to influence the trial outcomes significantly, the 10% sugar solution was consistently provided throughout the experimental trials to minimize any potential impact on the results.[34]

2.2 Recording device and setup

Ultrasonic recording is essential for studying *O. furnacalis*, because these moths produce high-frequency sounds during courtship displays that are beyond the detection range of conventional microphones. The Ultramic384K_EVO, with its ability to record frequencies from 20 to 384 kHz, aligns perfectly with the study's objectives by providing the necessary sensitivity to capture these ultrasonic signals with high precision. Recordings were conducted in a controlled environment to minimize ambient noise and reduce interference from external sounds. The temperature was maintained at approximately 25 °C, with a relative humidity of 60%, simulating the natural conditions experienced by *O. furnacalis* in the wild (Fig. 1).

2.3 Microphone positioning and directional sensitivity

For each trial, the Ultramic384K_EVO microphone was positioned approximately 2.5 cm from the male moth, using a magnetic cone to focus sensitivity on the ultrasonic courtship songs. The device was connected to a laptop running GoldWave software with a connecting USB cable (approximately 2 m long; Fig. 2), allowing for real-time monitoring and precise control over the recording process. For further enhancement of directional sensitivity, the microphone was fitted with a magnetic cone, which isolated the ultrasonic signals while reducing ambient noise (Fig. 2).

2.4 Optimizing recording sensitivity

To ensure optimal recording sensitivity, the Ultramic384K_EVO (Fig. 2-(c)) was equipped with a 4-position hardware amplification switch. This switch allows for fine-tuning the gain, adapting the microphone's sensitivity for different sound intensities. Moreover, the device's low-noise circuitry minimizes background noise, ensuring that the captured signals are clear and accurate. In addition to these advanced features, a magnetic cone (Fig. 1) was used further to enhance the directional sensitivity of the Ultramic384K_EVO microphone. This cone is placed around the microphone and secured by two neodymium magnets, offering easy removal and repositioning during data collection. The cone serves to focus the microphone's sensitivity in a specific direction, isolating the ultrasonic sounds produced during courtship displays and reducing the capture of ambient noises. This modification significantly improves the precision of sound recordings, especially in controlled environments where multiple males may be present, ensuring that the courtship signals are accurately captured.

2.5 Recording formats and pre-processing

The recordings were made at a sampling rate of 384 kHz, ensuring high-resolution capture of the ultrasonic signals. Audio files were saved in WAV format to facilitate post-recording manipulation and analysis. Pre-processing steps, including noise reduction and filtering, were automatically applied by the Ultramic384K_EVO to enhance the signal-to-noise ratio.

2.6 Acoustic feature extraction and validation

Automated Python scripts were used to extract key acoustic features from the recordings, based on parameters identified in previous studies. Manual annotations were then used to validate and refine the automated identification of these features during analysis. This combination of automated and manual methods ensured the accurate identification of key courtship behaviors.

2.7 Calibration and control trials

To ensure the accuracy of the recording system, calibration trials were conducted using known reference sounds. These trials confirmed that the Ultramic384K_EVO was performing optimally and accurately capturing the desired frequency range for the study. Calibration ensured the precision of the recordings, providing confidence in the subsequent analysis.

2.8 Technical specifications of the Ultramic384K_EVO

The Ultramic384K_EVO is a high-performance digital microphone equipped with a dual omni-directional microphone system, incorporating a dual-sensor design that allows for the simultaneous detection of both audible and ultrasonic sounds with exceptional sensitivity. The device was purchased from Italy (https://www.dodotronic.com/product/ultramic-384k-evo/). The microphone interfaces with the recording system via a USB 2.0 cable (2 m long), providing a straightforward plug-and-play setup with no need for additional drivers, facilitating ease of use.[36–38] With this setup, the Ultramic384K_EVO was capable of recording ultrasonic signals in the 20–384 kHz frequency range,[38,39] which is typical for *O. furnacalis* courtship songs. The addition of the magnetic cone provided an enhanced ability to detect subtle differences in the ultrasonic courtship song behaviors exhibited by left- and right-biased males.

2.9 Experimental setup for mating trials and courtship display observation

The study was conducted under controlled greenhouse environment conditions and the experimental setup was housed in a subdivided room (400 × 400 cm), ensuring a controlled space for observation. Lateralized courtship behaviors were recorded within a small experimental enclosure made of acrylic sheets (50 × 50 cm), which contained a mesh cloth cage (15 × 15 cm) designed to house the moths while minimizing interference from external and background noise. To minimize disruption to the moths' natural behavior, the room was illuminated with red light (0.2 lx), which is less likely to interfere with their activity (Fig. 1). To reduce variability, all male adults used in the study were selected to have similar body size and wing morphology. Furthermore, all adults were no more than 1 day old (virgin) at the time of the experiment, ensuring they were at their peak mating period. This age selection was informed by data from multiple previous trials, which demonstrated that moths of this age exhibited optimal mating behavior and were fully sexually mature.

2.10 Trial procedure and behavioral displays observation

During the late scotophase (dark period), five to seven virgin females were released into the mesh cloth cage. In some trials, 12 females were introduced to ensure that at least one female was actively calling at any given time, thereby encouraging male lateralized courtship displays.[28] Male moths initiated lateralized courtship behaviors in response to female calling, allowing for the recording and subsequent analysis of their ultrasonic courtship songs. Throughout these trials, special attention was paid
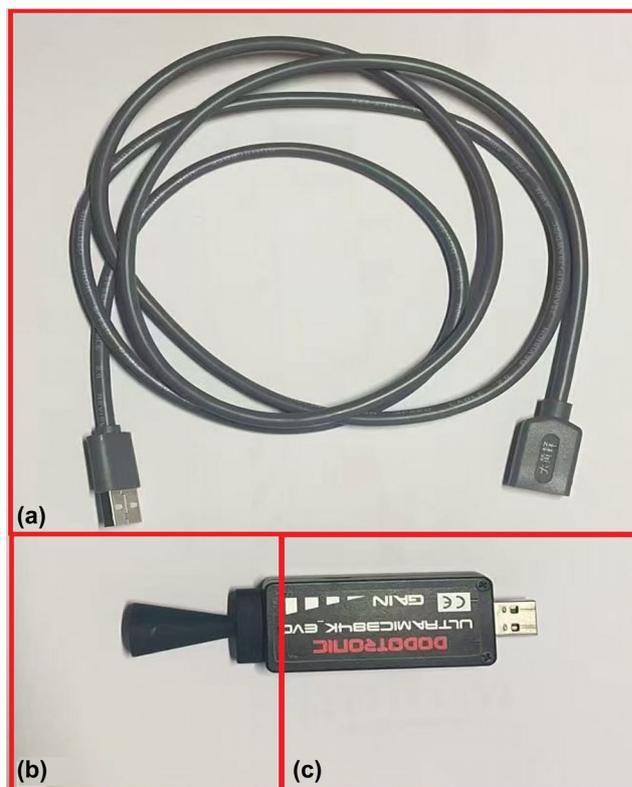

Figure 2. Ultramic384K_EVO. (a) USB cable, (b) and magnetic cone and (c) Ultramic384K_EVO device.
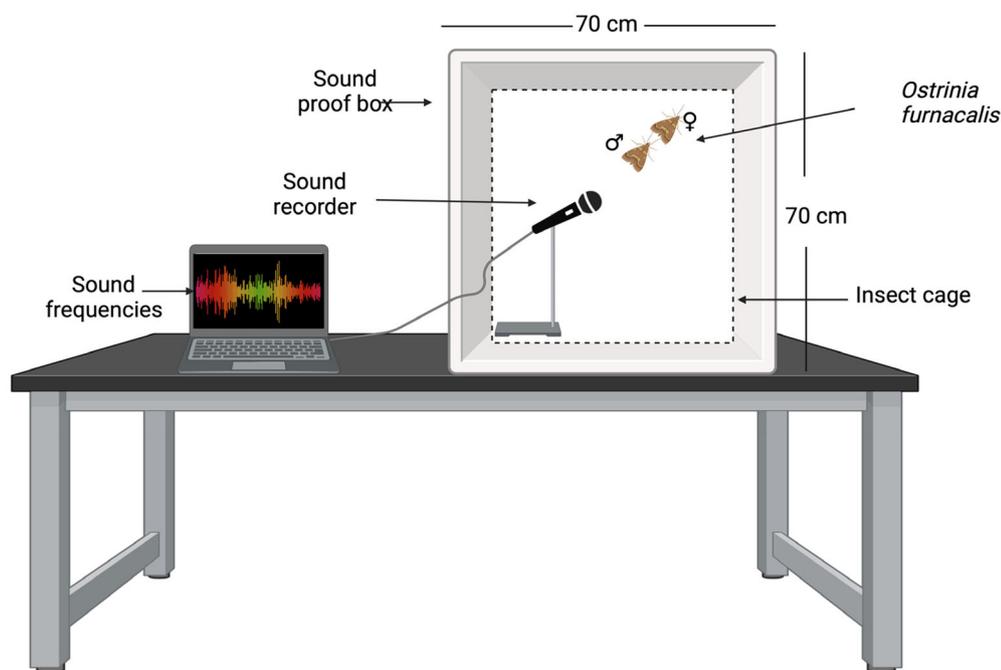

Figure 1. Experimental setup used to record ultrasonic courtship songs in *Ostrinia furnacalis*. The setup includes a soundproof chamber equipped with ultrasonic microphones positioned above a mating arena to capture wing-generated courtship sounds. A pheromone-releasing female is introduced to stimulate male courtship behavior, while synchronized video and audio recordings document lateralized behavioral displays and acoustic emissions. Environmental conditions were controlled to minimize external noise and ensure reliable behavioral and acoustic measurements.

to identifying whether the males exhibited left- or right-biased courtship behaviors.

2.11 Observation of lateralized mating behaviors

Lateralized mating behaviors were assessed through visual observation of male wing fanning, which generates ultrasonic courtship songs. Males were categorized as left-biased or right-biased based on whether they predominantly used their left or right side during courtship attempts, continuing until copula attachment and the achievement of mating success. Males that mated by turning their copula 180° to the left side of the female were named as 'left-biased displays', while those turning 180° to the right side were named as 'right-biased displays', to establish end-to-end genital contact.[34]

Males that exhibited both left- and right-biased courtship attempts simultaneously, along with wing fanning, were excluded from the analysis to prevent interference from overlapping ultrasonic signals. Only males that displayed left-biased behaviors at a time and successfully achieved genital contact were included in the analysis, ensuring that the ultrasonic features associated with left-biased displays were isolated. Similarly, males that displayed right-biased courtship behaviors and successfully achieved genital contact were analyzed separately. This approach allowed us to specifically assess the impact of left-only *versus* right-only biased displays on mating success, isolating the effects of lateralization without confounding factors.

2.12 Lateralized courtship behavior phases recorded for analysis and sample size

The following courtship behaviors were systematically recorded and analyzed in both left- and right-biased males: (i) male ultrasonic courtship songs duration (the time the male spent fluttering his wings toward the female while producing ultrasonic sounds); (ii) copulation attempt (the time the male spent attempting to mount the female and establish genital contact); and (iii) male ultrasonic sound frequency (the frequency of ultrasonic signals produced by each male during mating attempts, including both successful and unsuccessful mating to evaluate their influence on mating success).[11] Mating success (yes) and unsuccess (no) were compared within both left- and right-biased groups across these behavioral parameters to assess how variation in each metric affected reproductive outcomes. Mating success was defined as the successful completion of intromissive copulation, characterized by sustained end-to-end genital contact following the courtship display.

Pairs in which males failed to exhibit courtship behaviors or remained inactive during the 30-min observation period were excluded from the analysis and replaced with new, active males. Of the 60 mating pairs initially tested, 57 were included in the final statistical analyses based on active engagement in courtship behaviors. Among these, 33 males exhibited left-biased courtship displays and 24 showed right-biased behavioral displays during their attempts to achieve intromissive copulation.

2.13 Acoustic parameters

We focused on seven key acoustic parameters characterizing each train of sound pulses produced by male moths during their left- and right-biased courtship behaviors:

(1) Chirp duration (CD): the total length of each chirp, measured in milliseconds.

(2) Chirp interval (CI): the time interval between consecutive chirps, measured in milliseconds.

(3) Chirp rate (CR): the rate at which chirps are produced, measured in chirps per second.

(4) Pulse duration (PD): the duration of individual pulses within a chirp, measured in milliseconds.

(5) Pulse interval (PI): the time interval between individual pulses, measured in milliseconds.

(6) Pulse rate (PR): the rate at which pulses are emitted, measured in pulses per second.

(7) Number of pulses per chirp (NP): the total number of pulses within a single chirp.

From the total sample analyzed for behavioral parameters and mating success (pairs = 57; acoustic subset = 16), a representative subset of eight left-biased and eight right-biased males ($n = 16$) was selected for detailed analysis of acoustic parameters, oscillograms, and frequency spectra. This allowed a clear comparison between the two courtship types before evaluating the impact of different behaviors (Section 2.12) on mating success. Of the eight measured acoustic parameters, only PD and PI were selected for further analysis to assess their influence on reproductive outcomes. These parameters were recorded across five chirps per train, five trains per male, for both left-biased ($n = 8$) and right-biased ($n = 8$) courtship displays, to generate accurate oscillograms, spectrograms, and power spectra. Additionally, for comparison, ultrasonic courtship song data were recorded from eight males that did not achieve successful mating during the trials (from both bias groups), and their PD and PI values were analyzed to evaluate their association with mating failure. Finally, differences in PD and PI were compared between successful (yes) and unsuccessful (no) copulation outcomes within both left-biased and right-biased groups. This analysis allowed us to determine the parameter ranges associated with successful *versus* unsuccessful mating attempts in each lateralization category.

2.14 Statistical analysis

The sample size was calculated using Cohen's w formula for the chi-square test, assuming a medium effect size ($w = 0.3$), a significance level of $\alpha = 0.05$, and a power of $1 - \beta = 0.8$. The required sample size for detecting significant differences was 41 pairs.[40] The inclusion of 57 samples in the study ensured sufficient statistical power to detect meaningful differences in lateralized courtship behaviors and mating success. To avoid observer bias in data collection, one reviewer was blinded to the data and independently observed the lateralization. Inter-rater reliability was calculated using Cohen's kappa[41] and the concordance index.[42] The concordance index yielded a value of 0.95, indicating almost perfect agreement, while Cohen's kappa was 0.91, reflecting highly significant agreement between reviewers on the behavioral lateralization patterns in *O. furnacalis* mating displays.

2.14.1 Acoustic parameters analysis

Acoustic parameters, including CD (ms), CI (ms), CR (chirps s^{-1}), PD (ms), PI (ms), PR (pulses s^{-1}), and NP (n), were analyzed to compare left-biased ($n = 8$ males) and right-biased courtship ($n = 8$ males) displays in *O. furnacalis*. Signals were pre-processed using a 5 kHz filter[28] in Python (version 3.13.1) to minimize noise and isolate ultrasonic courtship signals. These parameters were extracted using automated analysis pipelines in Python (version 3.13.1), incorporating SciPy for spectrogram generation, NumPy for Fourier transforms, and Librosa for frequency mapping.[43]
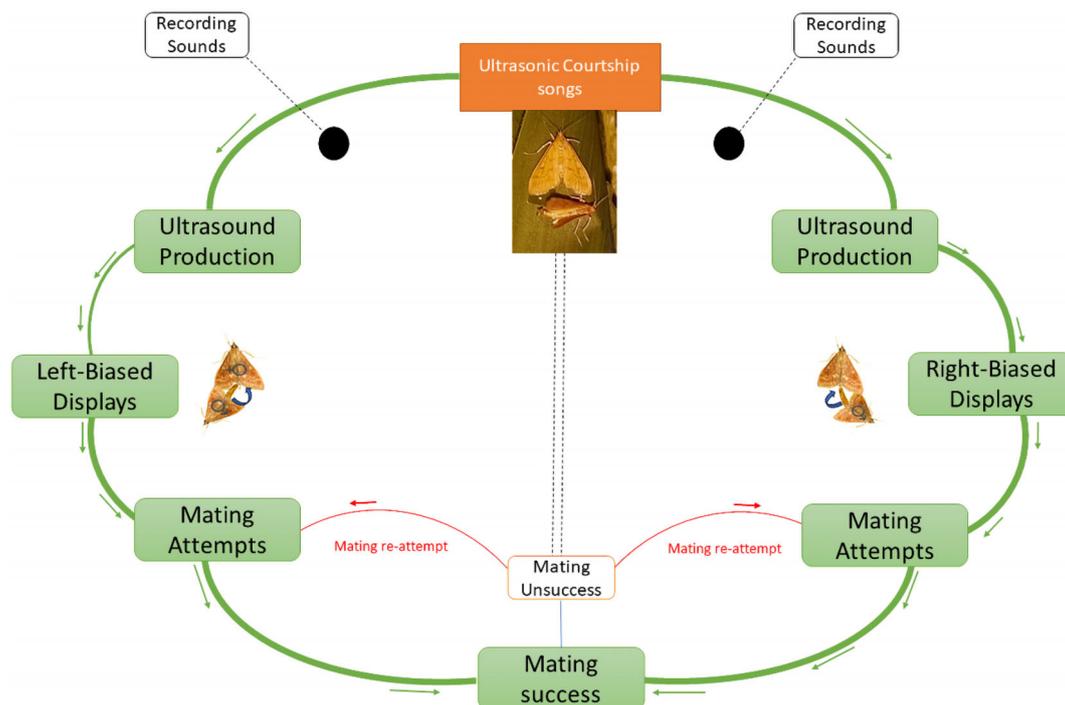
Figure 3. Sequential representation of lateralized courtship behaviors and ultrasonic song production in *Ostrinia furnacalis*. Following orientation and flight toward a pheromone-emitting female, the male lands nearby and initiates wing fanning, displaying a lateralized bias, either left- or right-sided. During this display, the male elevates its wings and produces ultrasonic courtship songs via rapid wing vibrations. Subsequently, the male bends its abdomen toward the same lateral side to attempt intromissive copulation. If the female is receptive, copulation is achieved; otherwise, rejection is signaled by the female through abdominal bending or flight escape, often followed by reattempted courtship by the male.

Descriptive statistics, including mean, standard deviation (SD), and coefficient of variation (CV), were calculated for each parameter in both groups. Data visualization was performed using Matplotlib (version 3.8) in Python (version 3.13.1). Bar plots, boxplots, and violin plots with error bars (SD) were used to compare the mean values of acoustic parameters between groups. The CV was used to assess the relative variability for each parameter.[44]

Oscillograms were generated using Matplotlib to observe the time-domain characteristics of the acoustic signals, and spectrograms and power spectra were computed using SciPy and NumPy, respectively, to analyze the frequency domain of the signals (left + right: $n = 8 + 8 = 16$ pairs). Frequency heatmaps were created using Librosa (melspectrogram), and the Seaborn (seaborn. heatmap) function was used to visualize the heatmaps, highlighting frequency patterns in the acoustic data.[45]

2.14.2 Logistic regression for mating success

A logistic regression model was applied to evaluate the combined effects of mating attempts, ultrasonic courtship duration, and ultrasonic frequency on mating success. Mating success (binary: 1 = successful mating, 0 = mating failure) was used as the dependent variable (sample size: $n = 57$ pairs). Independent predictors included mating attempts (n), ultrasonic courtship song duration (s), ultrasonic courtship song frequency (kHz), and lateralization bias (categorical: left-biased or right-biased). Interaction terms were included to assess the combined effects of behavioral parameters and lateralization. Odds ratios (ORs) and their 95% confidence intervals (CIs) were calculated to quantify the effect size of each predictor. Continuous predictors were modeled on their natural measurement scales (mating attempts per attempt,

ultrasonic courtship duration per 1-s increase, and ultrasonic frequency per 1-kHz increase). To facilitate comparison across predictors with different units, all continuous variables were also standardized (z-scores). Model fit was evaluated using Nagelkerke R^2, and predictive accuracy was assessed with a confusion matrix, with statistical significance set at $P < 0.05$. A heatmap was generated to visualize predicted mating success (yes) and failure (no) outcomes in relation to behavioral predictors and lateralization bias. To validate model performance, we performed tenfold cross-validation, randomly partitioning the data into ten subsets, with nine used for training and one for testing in each iteration. Model performance was summarized by mean accuracy and the area under the receiver operating characteristic curve (AUC = 0.91), indicating strong discriminatory ability. The confusion matrix yielded an overall accuracy of 85%, precision of 0.88, and recall of 0.83, confirming high predictive power. Residual analysis revealed no systematic patterns, supporting that model assumptions were met. Lateralization (left- *versus* right-biased displays) was treated as a fixed effect in the logistic regression model.[46]

2.14.3 Non-parametric analysis

Behavioral data, including male mating attempts (n), ultrasonic courtship song duration (s) and frequency (Hz and kHz), PI duration (ms), and PD (ms), were tested for normality using the Shapiro–Wilk test ($P < 0.05$), based on a sample size of $n = 57$ pairs. Because the data were not normally distributed, non-parametric methods were used: Kruskal–Wallis test ($P < 0.05$) was applied to compare differences across mating groups.[11,47] To account for multiple comparisons across the five behavioral
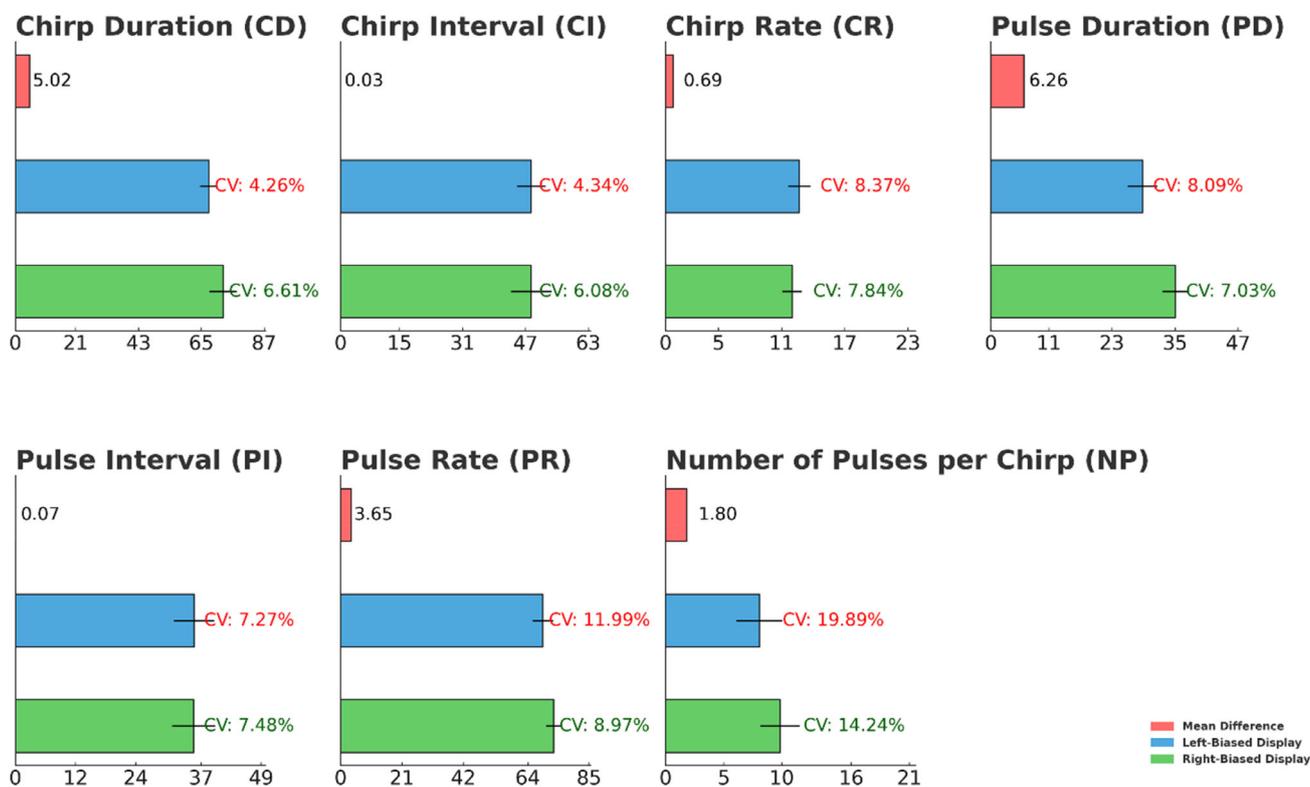
Figure 4. Ultrasonic acoustic characteristics of *Ostrinia furnacalis* males exhibiting lateralized courtship displays. Bar graphs show the mean values, standard deviations (SD), and coefficients of variation (CV) for seven acoustic parameters: chirp duration, chirp interval, chirp rate, pulse duration, pulse interval, pulse rate, and number of pulses per chirp. Data were obtained from 16 males ($n = 8$ left-biased and $n = 8$ right-biased). For each individual, five chirps per train were analyzed across five trains, yielding standardized acoustic measurements representative of each male's courtship song.

parameters, Bonferroni correction was applied, adjusting the significance threshold to $\alpha = 0.01$.

2.14.4   Analysis of lateralization differences

Laterality differences in the number of males exhibiting left and right-biased displays were analyzed using the chi-squared (χ^2) test with Yates" correction ($P < 0.05$). Contingency analysis was performed to examine the relationship between left–right lateralization of key courtship behaviors and mating success.[11]

3   RESULTS

3.1   Mating displays sequence

In the current study, male *O. furnacalis* exhibited a distinct sequence of lateralized courtship behaviors in response to female sex pheromones. Initially, males flew upwind toward the pheromones released by calling females, landing near one of them. Upon approaching, males began their courtship by exposing their genitalia while fanning their wings. This was followed by raising their wings to an upright position and rapidly vibrating them near the female. The ultrasonic courtship song is produced by the male during this phase of wing fanning, generating vibrational movements that emit ultrasonic signals. A typical courtship song consists of a series of chirps followed by pulses, and this song is recorded once the male successfully copulates. The key acoustic parameters that characterize the ultrasonic courtship song in this species include CD, CI, CR, PD, PI, PR, and NP. These parameters

are critical for mate selection as they convey important information about male fitness. During the courtship sequence, males turned their genital organs either to the left or right in preparation for intromissive copulation, reflecting their lateralized courtship behavior (Fig. 3). Following these courtship actions, males bent their abdomens to attempt copulation with the stationary females. Ultrasonic courtship song production was observed exclusively during the phase of wing vibration for intromissive copulation and was absent in other phases of the courtship, including post-copulation ($n > 57$). Notably, females did not produce ultrasonic sounds or exhibit any phonotactic responses to the male's ultrasonic courtship signals. This sequence of behaviors highlights the coordinated role of lateralized directional turning and ultrasonic courtship songs in influencing reproductive success. These observations align with the experimental focus on how lateralized behaviors contribute to differential mating outcomes in *O. furnacalis*.

3.2   Lateralized acoustic parameters

Acoustic parameters for left- and right-biased courtship displays in *O. furnacalis* revealed distinct differences in several key metrics. For CD, left-biased males exhibited a mean value of 67.63 ms (CV 4.26%), which was shorter than right-biased males with a mean of 72.65 ms (CV 6.61%). The CI showed similar values for both groups, with left-biased males averaging 48.47 ms (CV 4.34%) and right-biased males averaging 48.49 ms (CV 6.08%). In terms of CR, left-biased males had a slightly higher
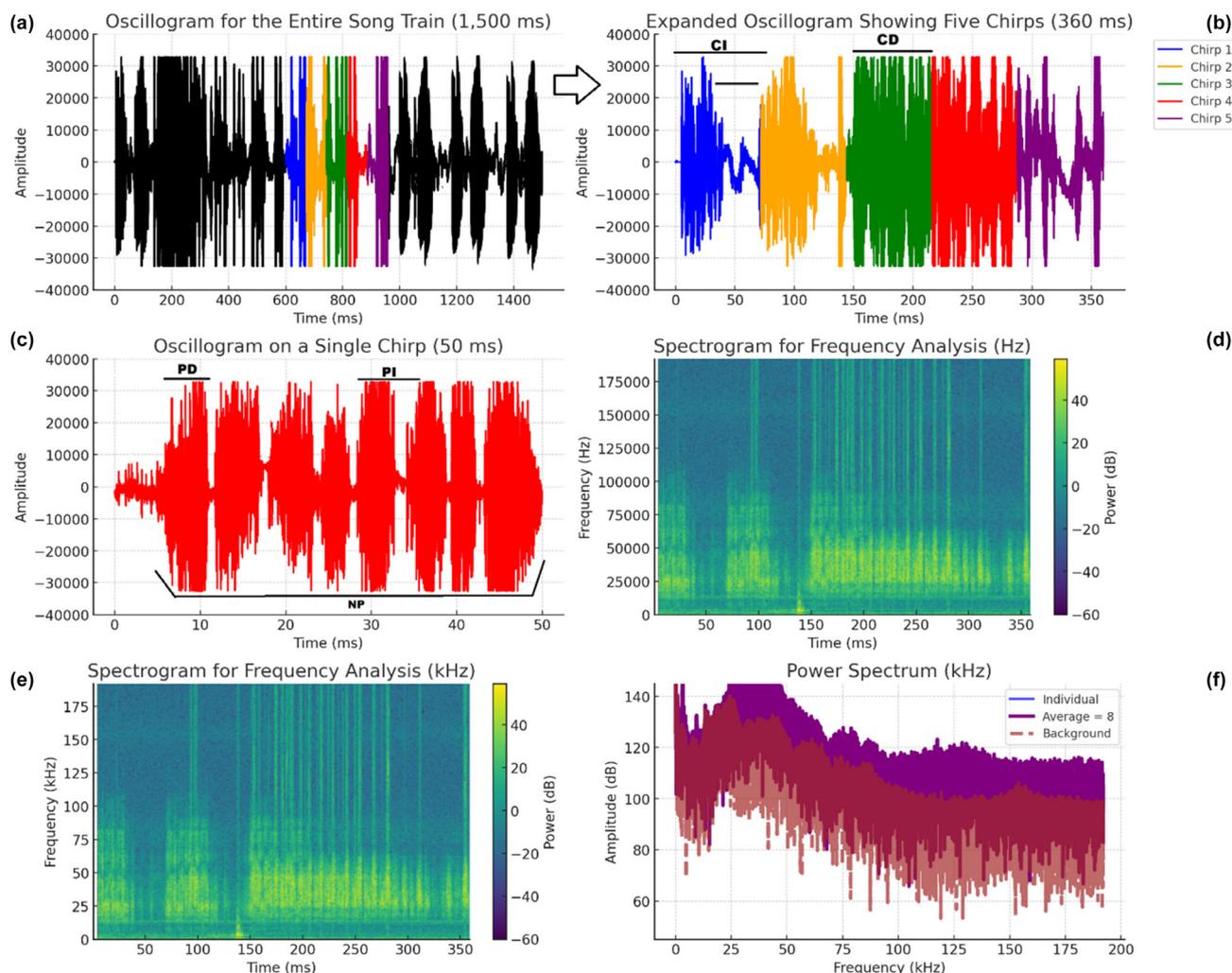
Figure 5. Song structure of a male *Ostrinia furnacalis* exhibiting left-biased courtship displays. (a) Oscillogram of the complete ultrasonic song train over a 1500-ms time window. (b) Expanded view of five chirps (pulse groups) over 360 ms. (c) Oscillogram of a single chirp captured over 50 ms. (d, e) Spectrograms displaying the frequency distribution of the chirp in Hz (d) and kHz (e). (f) Power spectra of the chirps. Solid lines represent individual recordings from eight males. The bold line indicates the average spectrum across these individuals and the dashed line shows the mean background noise spectrum. Acoustic parameters include chirp duration (CD), chirp interval (CI), pulse duration (PD), pulse interval (PI) and number of pulses per chirp (NP).

mean of 12.69 chirps s^{-1} (CV 8.37%) compared with right-biased males with a mean of 12.01 chirps s^{-1} (CV 6.97%). For PD, left-biased males had a significantly shorter mean of 28.86 ms (CV 8.09%) compared with right-biased males, who had a mean of 35.12 ms (CV 7.79%). The PI was very similar for both groups, with left-biased males averaging 35.66 ms (CV 7.27%) and right-biased males at 35.59 ms (CV 7.48%). The PR was lower for left-biased males, with a mean of 69.23 pulses s^{-1} (CV 11.99%), compared with right-biased males at 72.88 pulses s^{-1} (CV 8.97%). Finally, NP was lower for left-biased males, with a mean of 8 pulses (CV 19.89%), compared with right-biased males with a mean of 10 pulses (CV 14.24%). These findings indicate notable differences in the acoustic structures of courtship signals between left- and right-biased males, with left-biased males displaying shorter chirp durations and fewer pulses per chirp, but slightly higher chirp rates (Figs 4, 5a–c, 6a–c). The pulses produced by males exhibiting left-biased displays contained energy within a broad frequency range of approximately 35–115 kHz (Fig. 3d,e). By contrast, the pulses produced by males exhibiting right-biased displays contained energy across a broader

frequency range of approximately 10–150 kHz (Fig. 4d,e). These frequency differences highlight the distinct acoustic characteristics of left- and right-biased displays and their potential role in influencing mating success. Power spectra for both left- and right-biased displays revealed that the highest dominant frequency for left-biased display was also 55–65 kHz and the right-biased display was around 65–80 kHz with background noise levels significantly lower than the ultrasonic sounds produced during courtship. This indicates minimal interference from background noise, because its amplitude remained consistently below the main ultrasonic signals generated by males in both displays. This ensures that the recorded ultrasonic courtship signals accurately reflect the males' acoustic displays without distortion from environmental noise (Figs 5d–f, 6d–f).

3.3 Impact of male lateralized ultrasonic courtship behaviors on mating success

3.3.1 Ultrasonic courtship songs duration
Ultrasonic courtship durations showed significant variation for left-biased displays ($\chi^2 = 33.545$, df = 1, $P < 0.0001$), whereas no
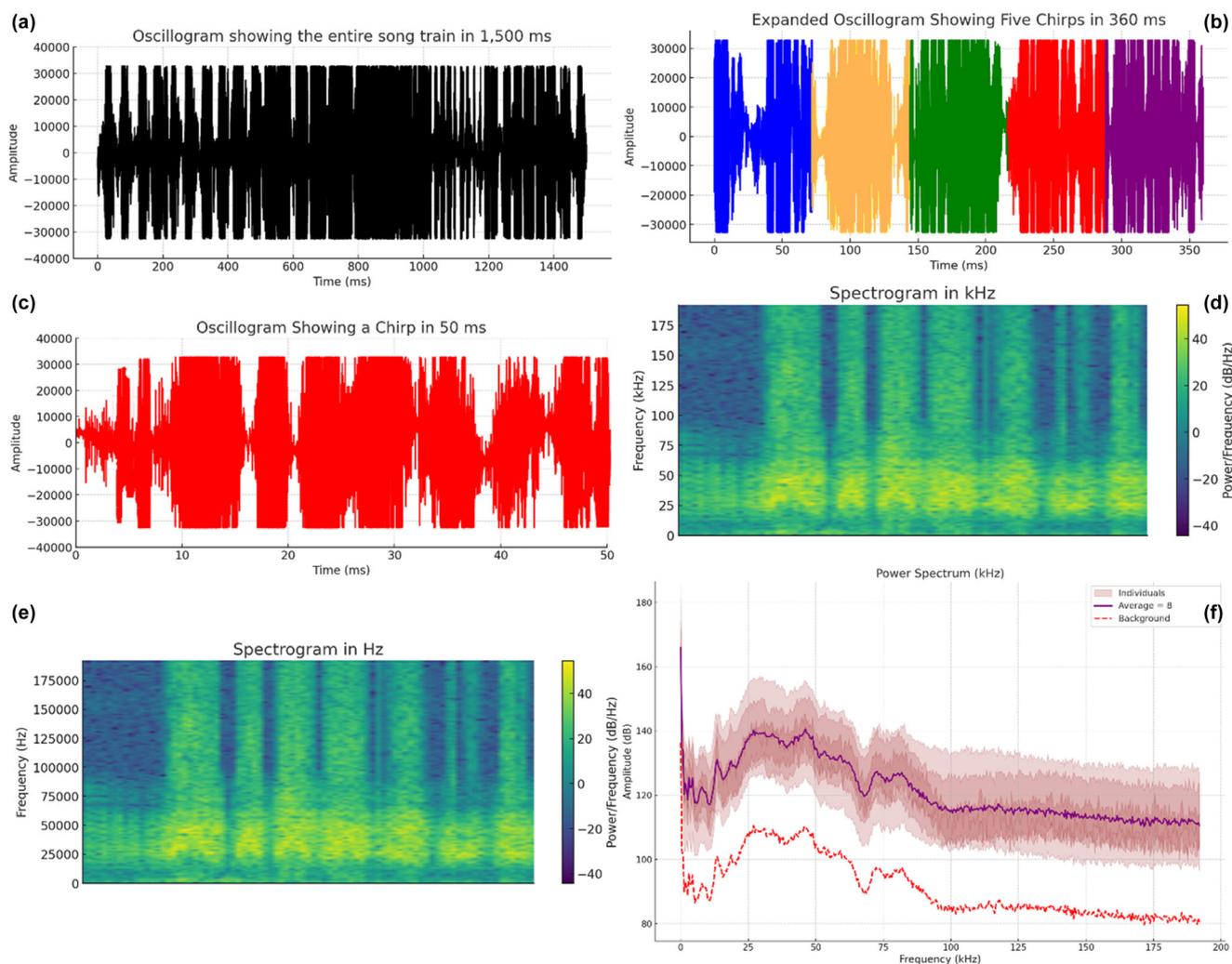
Figure 6. Song structure of a male *Ostrinia furnacalis* exhibiting right-biased courtship displays. (a) Oscillogram of the entire ultrasonic song train over a 1500-ms window. (b) Expanded view showing five chirps (pulse groups) within a 360-ms segment. (c) High-resolution oscillogram of a single chirp spanning 50 ms. (d–e) Spectrograms depicting the frequency distribution of the chirp in Hz (d) and kHz (e). (f) Power spectra of the chirps: solid lines represent individual recordings from eight males. The bold line indicates the average power spectrum and the dashed line represents the mean background noise spectrum from the same recordings. Measured acoustic parameters include chirp duration (CD), chirp interval (CI), pulse duration (PD), pulse interval (PI) and number of pulses per chirp (NP).

significant variation was detected for right-biased displays ($\chi^2 = 0.933$, df = 1, $P = 0.1824$). For left-biased displays, mating success males exhibited shorter durations (yes = 30.15 ± 5.02 s; range 20–40 s) than mating unsuccess males (no = 50.15 ± 8.12 s; range 40–65 s). By contrast, for right-biased displays, mating success males exhibited durations of 48.25 ± 6.34 s (yes; range 40–60 s) compared with mating unsuccess males (no = 62.85 ± 6.85 s; range 55–70 s). Ultrasonic courtship durations in the optimal range of 20–40 s were strongly associated with greater mating success ($\chi^2 = 25.782$, df = 1, $P < 0.001$), whereas durations exceeding this range showed no significant relationship with mating success (Figs 7 and 8).

3.3.2 Mating attempts
Mating attempts exhibited significant differences in left-biased displays ($\chi^2 = 23.228$, df = 1, $P < 0.0001$), whereas no significant differences were identified in right-biased displays ($\chi^2 = 1.4222$, df = 1, $P = 0.3855$). For left-biased displays, mating success males required fewer attempts (yes = 1.45 ± 0.65 attempts) than mating unsuccess males (no = 4.25 ± 1.21 attempts). For right-biased

displays, mating success males performed 2.25 ± 1.12 attempts (yes) compared with mating unsuccess males (no = 5.15 ± 1.56 attempts). Mating attempts limited to one or two were strongly associated with greater mating success ($\chi^2 = 20.102$, df = 1, $P < 0.001$), whereas a higher number of attempts significantly reduced their overall impact on mating success (Figs 9 and 10). Males exhibiting left-biased displays generally made one to two mating attempts across all individuals, whereas males with right-biased displays typically made four or more mating attempts. In addition, unsuccessful males in both groups showed a higher number of mating attempts. Left-biased males who were unsuccessful averaged three to five attempts, whereas right-biased males required five or more attempts before achieving mating success.

3.3.3 Ultrasonic courtship songs frequency
Ultrasonic courtship song frequencies differed significantly for left-biased displays ($\chi^2 = 8.234$, df = 1, $P = 0.003$), whereas no notable differences were identified for right-biased displays ($\chi^2 = 2.0017$, df = 1, $P = 0.0799$). For left-biased displays, mating
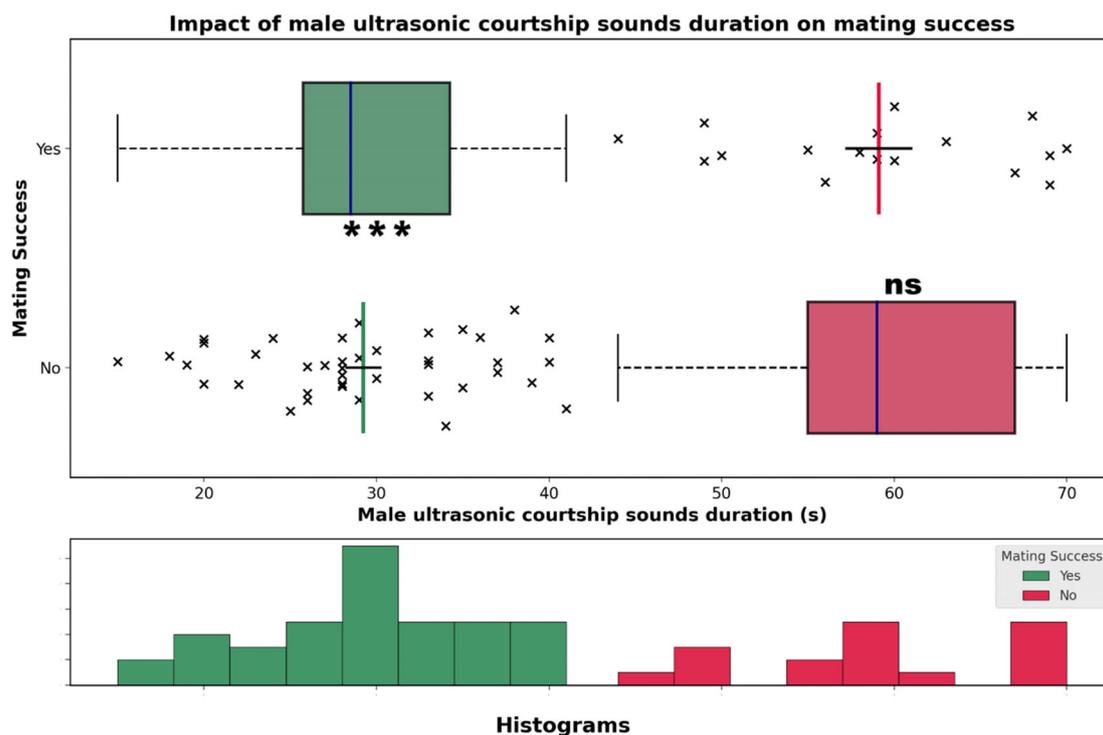
Figure 7. Effect of male ultrasonic courtship song duration on mating success in *Ostrinia furnacalis*. Boxplots illustrate the distribution of ultrasonic courtship song durations across successful (Yes) and unsuccessful (No) mating events. Green and red lines indicate the mean durations for successful and unsuccessful copulations, respectively, with individual data points overlaid. Histograms display the frequency distribution of song durations, highlighting differences between mating outcomes. Statistical comparisons were performed using the Kruskal–Wallis test with Bonferroni correction ($P < 0.05$). Significant: ***; non-signifcant: ns.

success males emitted frequencies within a narrower range (yes = 54.85 ± 3.12 kHz; range 55–65 kHz) than mating unsuccess males (no = 96.85 ± 14.21 kHz; range 80–120 kHz). For right-biased displays, mating success males emitted frequencies of 72.85 ± 5.12 kHz (yes; range 65–80 kHz) compared with mating unsuccess males (no = 90.15 ± 11.45 kHz; range 75–120 kHz).

Ultrasonic courtship song frequency had a significant impact on mating success ($\chi^2 = 15.344$, df = 1, $P = 0.002$). Frequencies within the optimal range (55–65 kHz for left-biased males) were strongly associated with greater mating success, whereas frequencies outside this range (65–120 kHz for right-biased males) were linked to reduced mating success (Figs 11 and 12).

3.3.4 Pulse interval duration

Significant differences in PIs were observed for left-biased displays ($\chi^2 = 12.442$, df = 1, $P = 0.0015$), whereas no significant differences were observed for right-biased displays ($\chi^2 = 1.123$, df = 1, $P = 0.1229$). For left-biased displays, mating success males exhibited shorter PIs (yes = 30.96 ± 5.22 ms) than mating unsuccess males (no = 62.85 ± 19.57 ms). For right-biased displays, mating success males exhibited intervals of 35.44 ± 6.99 ms (yes) compared with mating unsuccess males (no = 75.24 ± 24.56 ms). Pulse intervals within the range of 30–35 ms were significantly associated with mating success ($\chi^2 = 18.321$, df = 1, $P = 0.0005$), whereas longer intervals showed no consistent patterns or significant relationship with mating success (Figs 13 and 14).

3.3.5 Pulse duration

PD showed significant differences for left-biased displays ($\chi^2 = 22.432$, df = 1, $P < 0.0001$), whereas no significant differences were detected for right-biased displays ($\chi^2 = 2.2322$, df = 1, $P = 0.873$). For left-biased displays, mating success males exhibited shorter PDs (yes = 28.12 ± 4.23 ms) than mating unsuccess males (no = 45.15 ± 6.34 ms). For right-biased displays, mating success males exhibited durations of 35.44 ± 6.99 ms (yes) compared with mating unsuccess males (no = 55.24 ± 12.23 ms). PDs ranging between 25 and 35 ms exhibited a significant association with mating success ($\chi^2 = 19.777$, df = 1, $P = 0.001$), whereas durations outside this range showed weaker associations and no significant impact on mating success (Figs 13 and 14).

The logistic regression analysis demonstrated significant combined effects of mating attempts, ultrasonic courtship song duration, and frequency on the predicted probability of mating success. Males exhibiting left-biased courtship behaviors consistently showed higher predicted odds of successful copulation compared with those exhibiting right-biased displays. The interaction between behavioral parameters revealed that the combination of fewer mating attempts, shorter courtship durations, and optimal ultrasonic frequency ranges was strongly associated with increased mating success (Fig. 15). Specifically, mating attempts significantly predicted mating success (OR = 2.354 per additional attempt, 95% CI 1.877–3.211; $P < 0.001$), with fewer attempts associated with a greater probability of success. Ultrasonic courtship song duration also had a significant positive effect
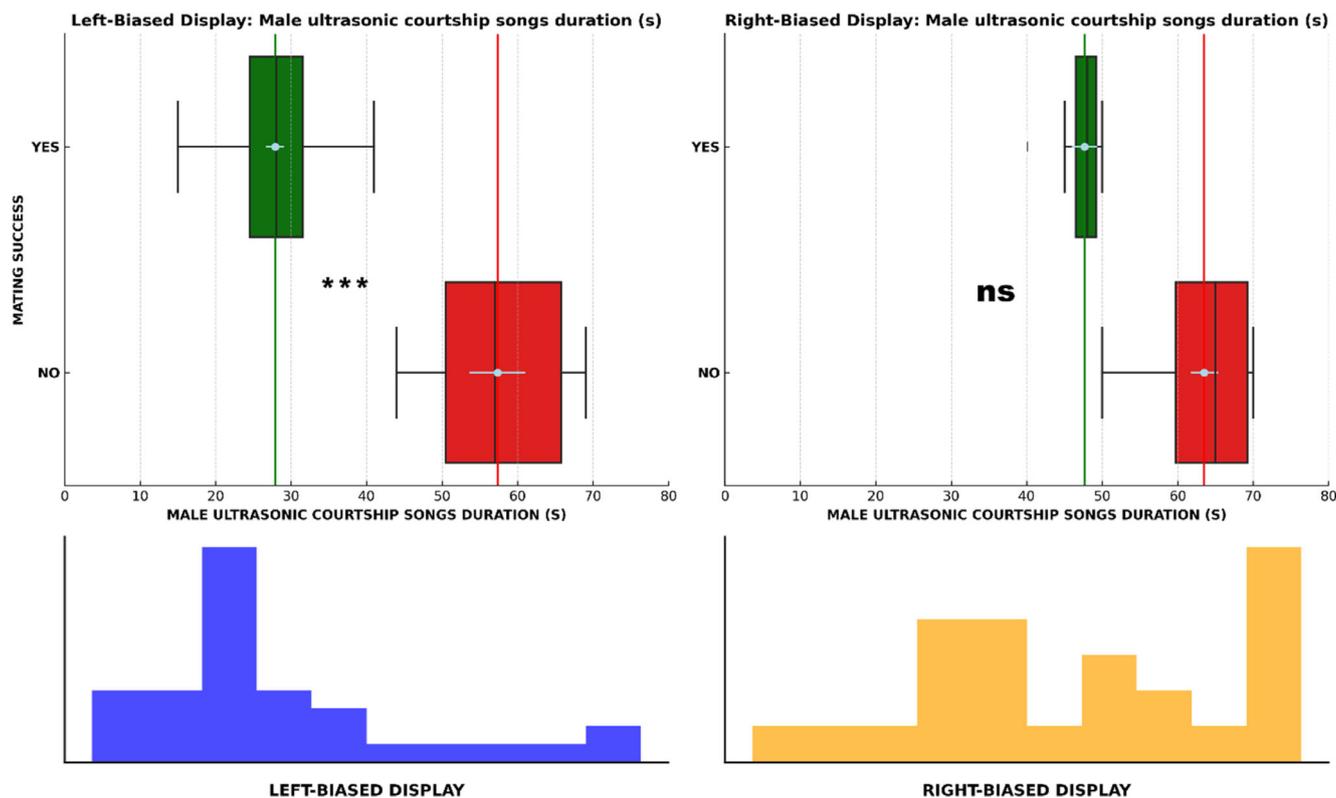
Figure 8. Lateralized differences in ultrasonic courtship song duration in *Ostrinia furnacalis* in relation to mating success. Boxplots depict the duration of ultrasonic courtship songs across successful (Yes) and unsuccessful (No) mating events, categorized by left- and right-biased courtship displays. Green and red lines represent the mean durations for successful and unsuccessful copulations, respectively, with individual data points overlaid. Histograms show the frequency distribution of song durations, emphasizing differences in acoustic patterns between lateralization types and mating outcomes. Statistical comparisons were conducted using the Kruskal–Wallis test with Bonferroni correction ($P < 0.05$). ***; ns.
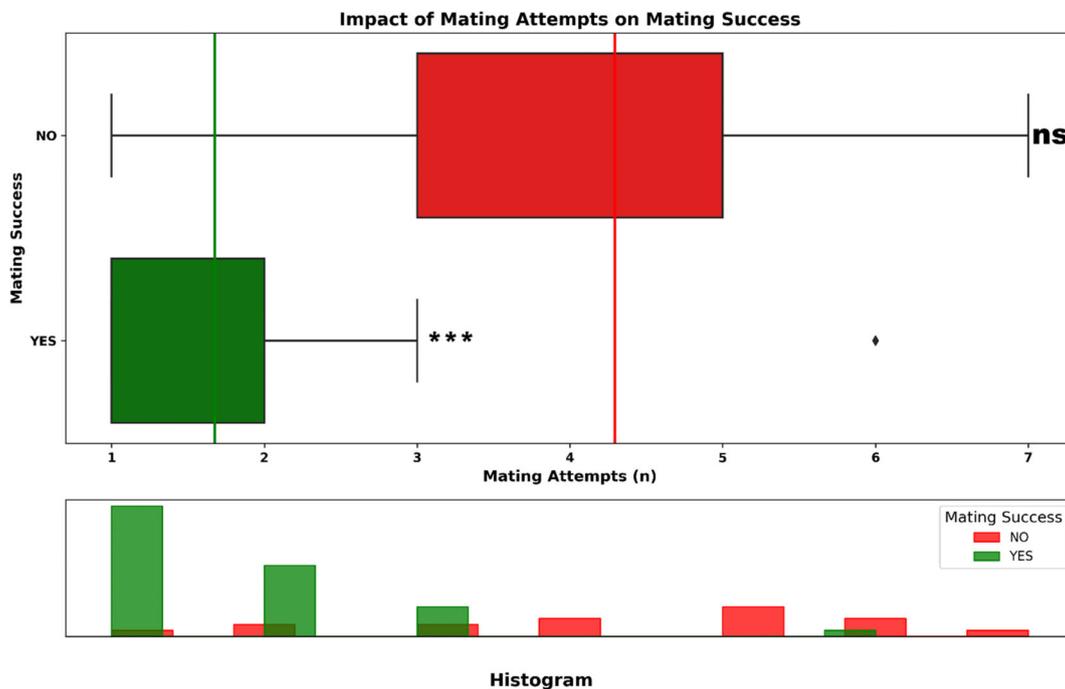

Figure 9. Impact of male mating attempts on mating success in *Ostrinia furnacalis*. Boxplots show the number of mating attempts in successful (Yes) and unsuccessful (No) mating events. Green and red lines indicate the mean values for each group, with individual data points overlaid. Histograms illustrate the distribution of mating attempts, highlighting behavioral differences associated with mating outcomes. Statistical comparisons were performed using the Kruskal–Wallis test with Bonferroni correction ($P < 0.05$). Significant: ***; non-significant: ns.
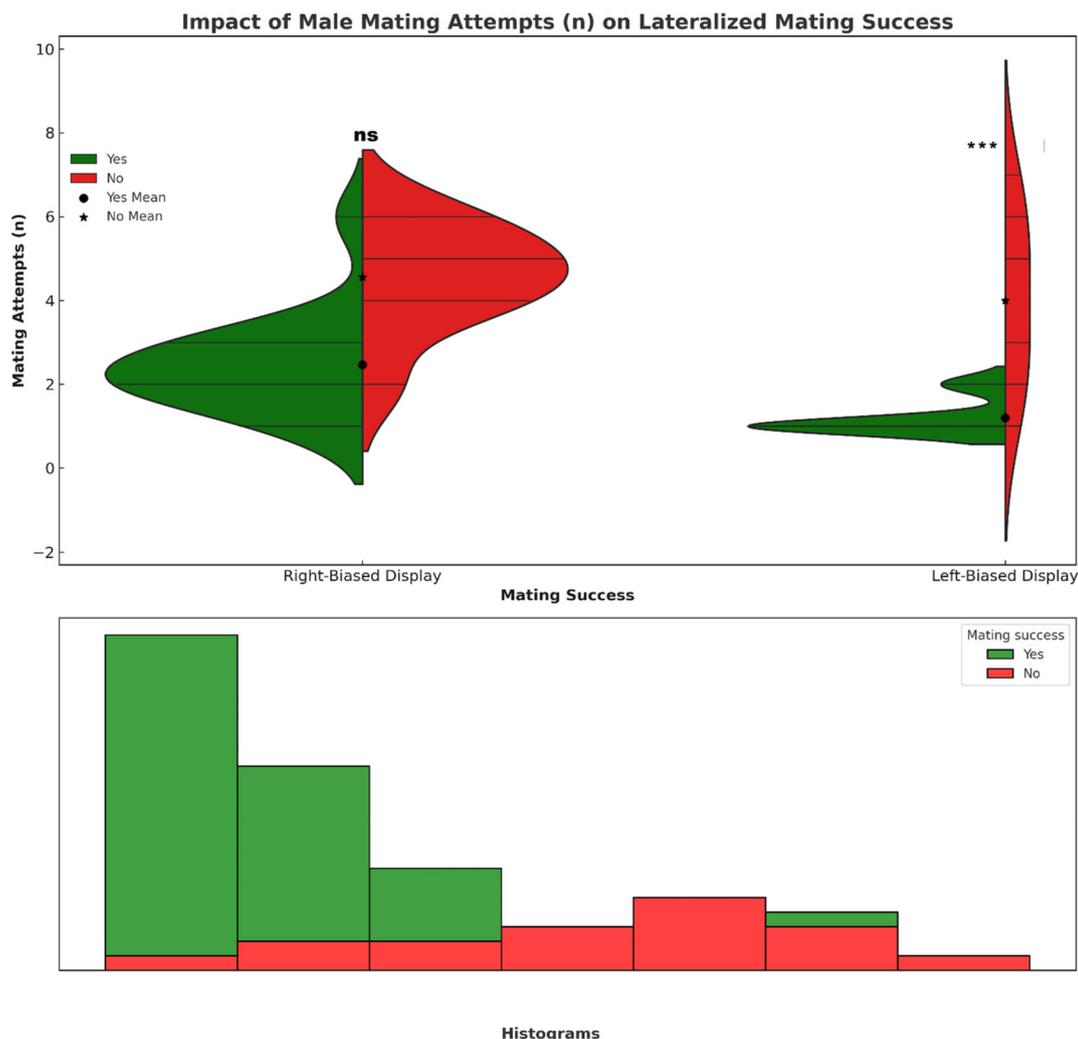
Figure 10. Lateralized differences in mating attempts between left- and right-biased males of *Ostrinia furnacalis* in relation to mating success. Boxplots show the distribution of mating attempts for successful (Yes) and unsuccessful (No) copulations, categorized by courtship lateralization (left- or right-biased). Green and red lines indicate the mean number of mating attempts for successful and unsuccessful events, respectively, with individual data points overlaid. Histograms display the frequency distribution of mating attempts between lateralization types and mating outcomes. Statistical comparisons were conducted using the Kruskal–Wallis test with Bonferroni correction ($P < 0.05$). Significant: ***; non-significant: ns.

(OR = 1.85 per 1-s increase, 95% CI 1.45–2.37; $P < 0.001$), with durations between 25 and 30 s being most favorable. Similarly, ultrasonic frequencies in the range 40–65 kHz significantly increased the likelihood of successful mating outcomes (OR = 1.622 per 1-kHz increase, 95% CI 1.299–2.044; $P < 0.001$). Interaction analysis further revealed that left-biased males exhibiting optimal behavioral combinations, namely, a single mating attempt, courtship duration of 25–30 s, and frequency of 40–65 kHz, achieved the highest predicted probabilities of mating success. Conversely, right-biased males displayed less-consistent patterns across these predictors, resulting in substantially lower predicted success rates. The logistic regression model explained 74% of the variance in mating success (Nagelkerke $R^2 = 0.74$). Model performance was further validated via tenfold cross-validation, with a classification accuracy of 85%, precision of 0.88, and recall of 0.83. The presented heatmap illustrates predicted mating success and failure outcomes as a function of these behavioral predictors and lateralization bias, highlighting their combined influence on reproductive outcomes.

3.3.6 Lateralized courtship behaviors

Overall, the success of mating was significantly higher for males exhibiting left-biased displays The success of mating was notably higher when *O. furnacalis* males approached females from the left-biased display during sexual interactions ($\chi^2 = 16.220$; df = 1; $P < 0.0001$), whereas males from the right-biased display did not significantly impact mating success ($\chi^2 = 0.0001$; df = 1; $P = 0.988$) These findings highlight the critical role of left-biased behaviors in enhancing reproductive outcomes in *O. furnacalis* (Fig. 16).

4 DISCUSSION AND CONCLUSIONS

In this study, we investigated the role of lateralized courtship behaviors in *Ostrinia furnacalis*, focusing specifically on male ultrasonic courtship songs and their relationship to mating success. Our findings revealed significant differences in the acoustic signals produced by males with left-biased and right-biased courtship behaviors, with left-biased males achieving significantly higher mating success. These results suggest that lateralized
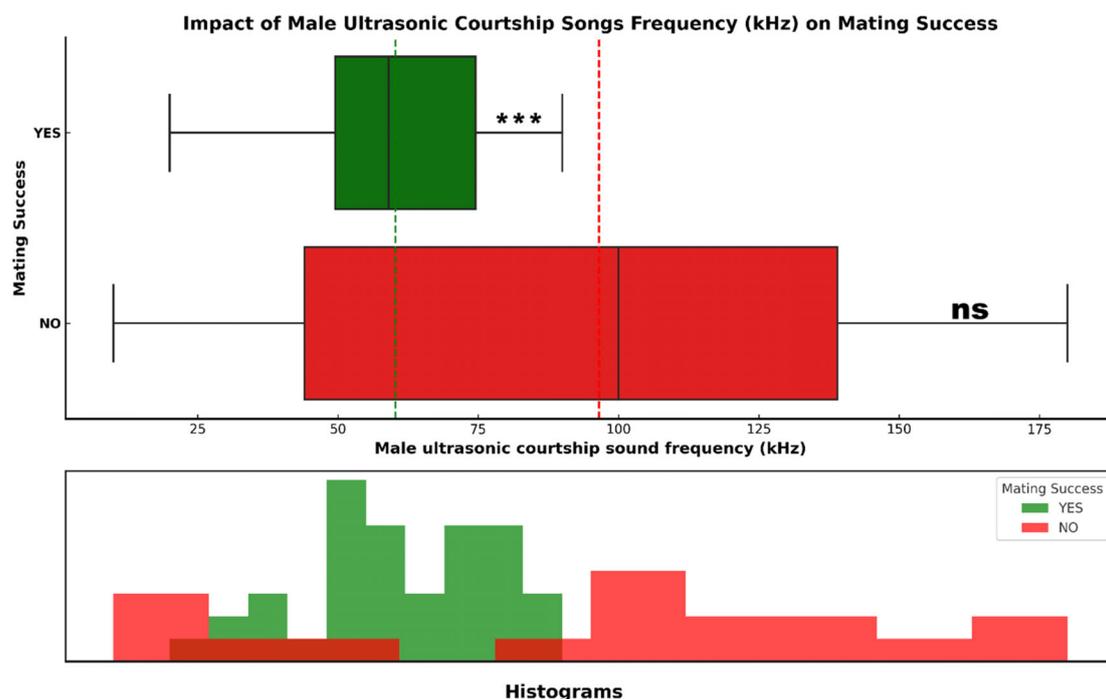
Figure 11. Association between ultrasonic courtship song frequency (kHz) and mating success in *Ostrinia furnacalis*. Boxplots show the distribution of ultrasonic frequencies in successful (Yes) and unsuccessful (No) mating events. Green and red lines indicate the mean frequency values for successful and unsuccessful copulations, respectively. Histograms below illustrate the distribution patterns of frequency values across both groups. This figure summarizes the role of acoustic frequency in influencing reproductive outcomes. Statistical comparisons were performed using the Kruskal–Wallis test with Bonferroni correction ($P < 0.05$). Significant: ***; non-signficant: ns.

courtship behaviors play an important role in sexual selection in this species, as has been observed in several other insect species.[8,11,42,48,49] In addition, we observed that consistency in mating attempts, ultrasonic courtship duration, and frequency were strongly associated with mating success, emphasizing the importance of dynamic courtship behaviors in mate selection. These findings contribute to the growing body of evidence supporting the role of lateralized behaviors in courtship and mate choice across various species.[47,50–52]

The phenomenon of lateralization, particularly in the context of courtship and mate selection, has been shown to enhance the efficiency and reliability of sexual displays.[4] For example, in birds such as zebra finches (*Taeniopygia guttata*), left-biased courtship displays have been linked to increased attractiveness and mating success.[53] Similarly, studies on *Lycosa tarantula* spiders demonstrated that lateralized visual and vibrational courtship displays contribute to successful mating outcomes.[54] In insects, lateralized behaviors during courtship have been observed in *Gryllus bimaculatus* crickets; males exhibit lateralized stridulatory courtship songs, and females may show preferences for specific patterns in these signals. However, it is important to note that the study on *G. bimaculatus* does not explicitly link lateralized acoustic signals to mating success, and further research is needed to establish this connection. Although lateralization in courtship songs has been identified in this species, the role of these behaviors in mating success requires additional exploration.[55,56] In addition, in parasitic wasps such as *Psyttalia concolor* and *Lysiphlebus testaceipes*, lateralized wing-fanning behaviors have been correlated with reproductive success.[11,32] A study of the giant water bug *Belostoma flumineum* also demonstrated significant lateralization, with individuals making more left turns than right turns, even when

naive and first introduced to a maze.[57] These findings validate the hypothesis that lateralized courtship behaviors, particularly left-biased signals, provide adaptive advantages by ensuring consistent and reliable communication. Females preferentially select these displays as indicators of male fitness, leading to higher mating success.

The left-biased signals likely represent a more consistent or reliable indicator of male fitness, which females preferentially select. By contrast, the ultrasonic sounds produced during right-biased displays were found to be inconsistent, with acoustic characteristics, durations, and frequencies deviating significantly from optimal ranges, thereby reducing the likelihood of successful mating. This is consistent with findings in other taxa, in which asymmetries in courtship behaviors, such as left-biased displays in birds, enhance mate recognition and reproductive success.[58–60] Neural asymmetries may underlie these lateralized behaviors, with asymmetric sensory and motor processing playing a role in courtship in insects.[61] Although this asymmetry may explain why left-biased displays are more effective and associated with higher reproductive success, it should be noted that direct neural data were not collected in our study, and inferences are therefore limited to behavioral and acoustic evidence. Our study confirms that ultrasonic communication is a key mechanism for mate attraction and selection in *O. furnacalis*, with ultrasonic sound duration, frequency, and temporal structure playing critical roles in female mate choice.[18,27,28] For example, in *Bactrocera oleae*, *Achroia grisella*, and *Syntomieda epilais*, females prefer males that produce species-specific ultrasonic signals with optimal pulse durations and intervals.[62–64] Similarly, a study found that ultrasonic signals are positively correlated with mating success
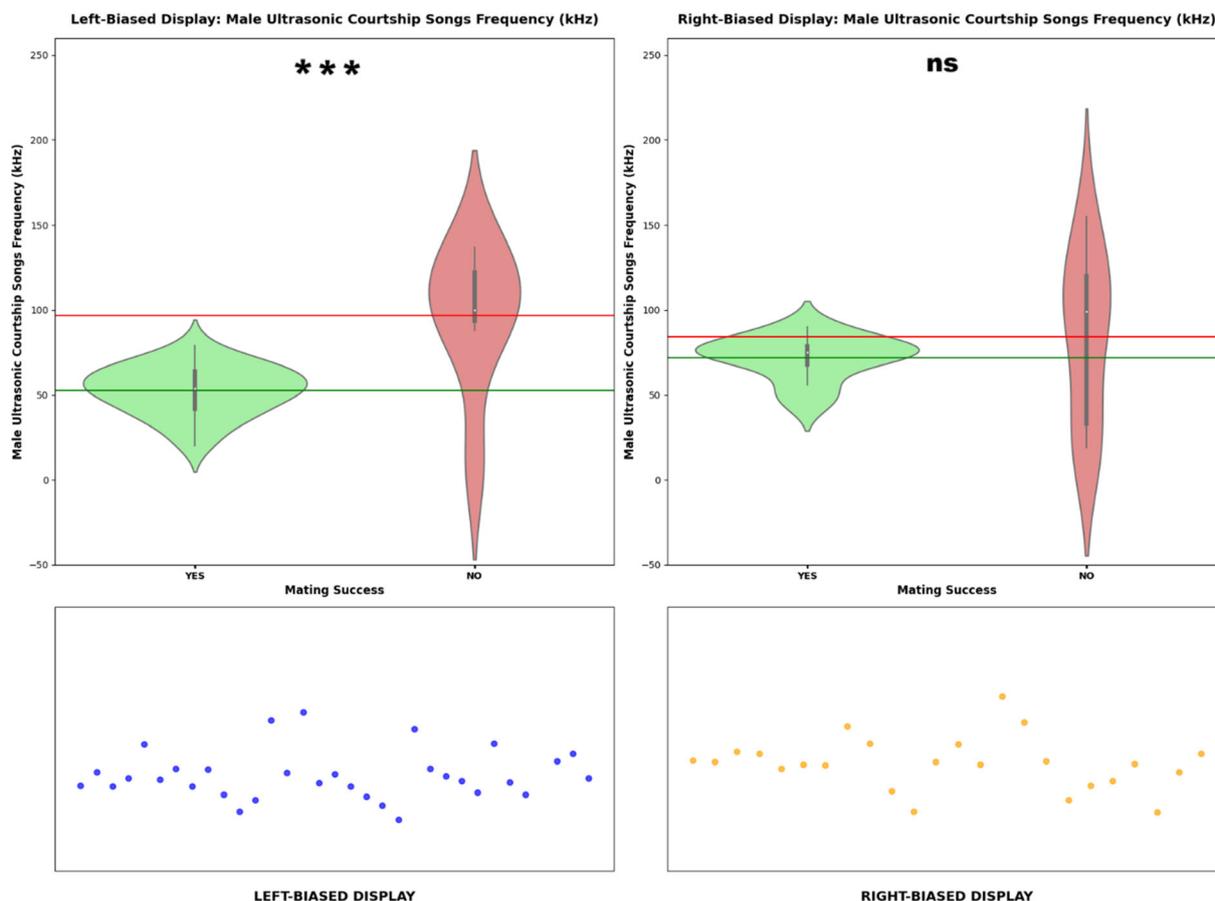
Figure 12. Lateralized differences in ultrasonic courtship song frequency (kHz) in *Ostrinia furnacalis* and their association with mating success. Boxplots show the distribution of ultrasonic frequencies in successful (Yes) and unsuccessful (No) mating events for left- and right-biased males. Green and red lines represent mean frequencies for successful and unsuccessful copulations, respectively. Corresponding histograms illustrate the frequency distribution patterns across both lateralization types and mating outcomes. Statistical differences were assessed using the Kruskal–Wallis test with Bonferroni correction ($P < 0.05$). Significant: ***; non-significant: ns.

in crickets,[65] because these signals convey information about male fitness or genetic quality.

Courtship signal duration was a critical factor in mating success, with females selecting males with left-biased signals as higher-quality mates based on frequency cues that reflect male fitness. Left-biased males with shorter and more intense ultrasonic signal durations achieved significantly higher mating success than right-biased males, whose longer, inconsistent durations were associated with lower success. These results align with findings in *Heliothis virescens*, in which shorter, more energetically efficient courtship displays were linked to higher female receptivity.[66] The shorter duration of left-biased displays may signal higher efficiency or reduced energetic costs, making these males more attractive to females. Males that engaged in more frequent wing fanning exhibited higher success rates than those with lower frequencies or inconsistent displays. Wing-fanning frequency significantly impacts mating success by acting as a vibrational stimulus that enhances female receptivity.[67–69] This behavior has been observed in other moth species, such as *Cactoblastis cactorum*, in which wing-fanning frequency correlates with mating success.[70]

Dynamic behaviors like wing-fanning frequency are more influential in female mate choice than static courtship parameters. Interestingly, the dynamic features of wing fanning and ultrasonic

signals may also serve to reduce male–male competition.[71–73] By producing consistent and intense displays, males with left-biased behaviors may outcompete their rivals, securing higher reproductive success. This aligns with studies on lateralized behaviors in other insects, in which lateralization is thought to enhance coordination and reduce interference during courtship.[74] The presence of lateralized behaviors in *O. furnacalis* highlights the evolutionary significance of lateralization in sexual selection. Lateralized courtship displays may have evolved as a means of reducing cognitive or motor conflicts, allowing males to perform complex behaviors more efficiently.[75,76] Furthermore, lateralization may enhance signal reliability, making it easier for females to assess male quality. This has been observed in other taxa, such as *Apis mellifera* honeybees,[77] where lateralized antennal displays improve the efficiency of chemical communication during mating.[78] Several confounding factors could influence future studies on mating success, including environmental variables (temperature, humidity, light cycles), geographic location, male size and age, and female receptivity and sexual experience. These factors may introduce biases in courtship behavior and mating outcomes. Future research should carefully account for these variables to ensure accurate interpretations of lateralized courtship behaviors.

In conclusion, this study presents the first empirical evidence demonstrating that lateralized courtship behaviors, particularly
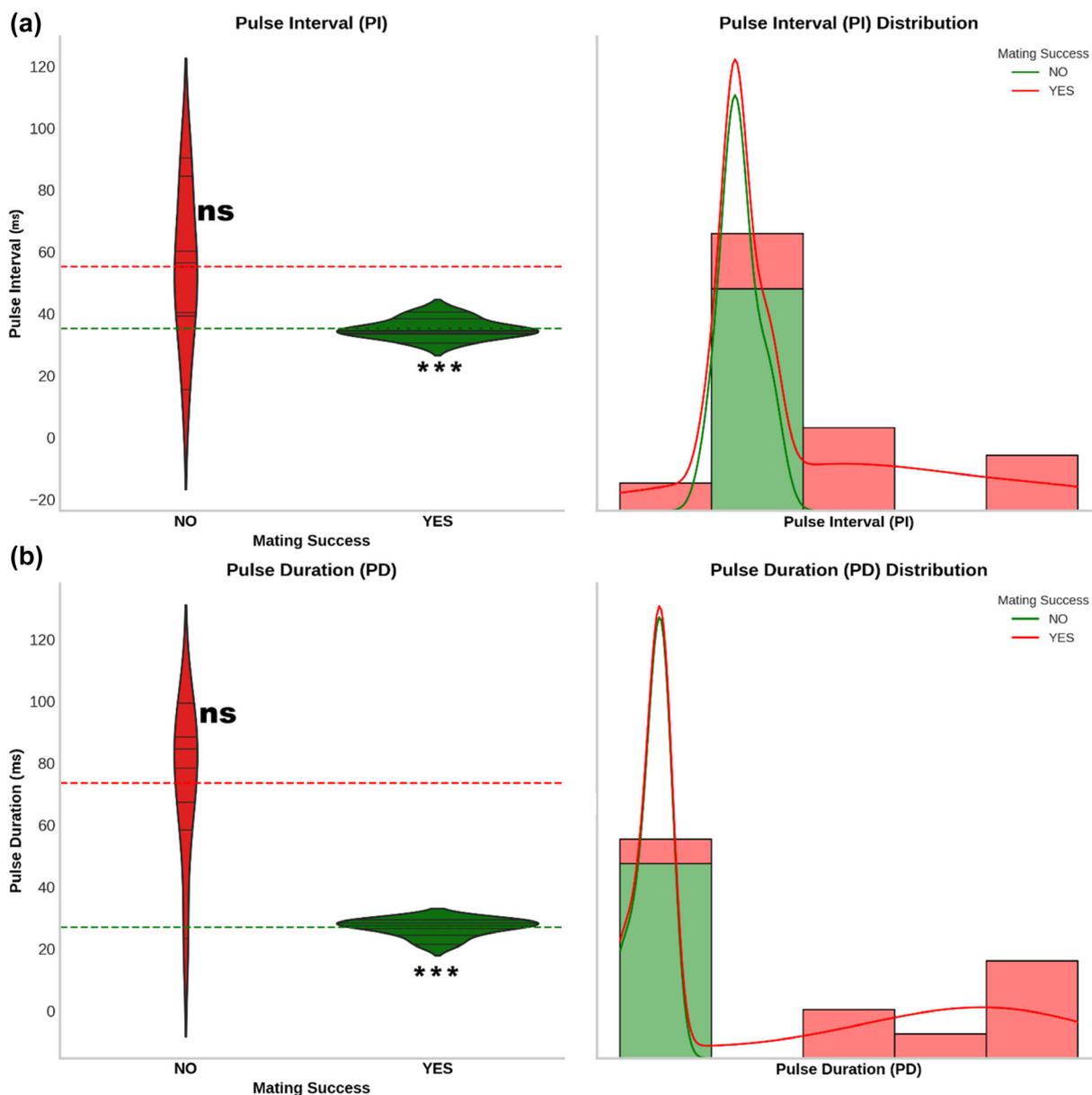
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Figure 13. Effects of pulse interval (PI) and pulse duration (PD) in male ultrasonic courtship songs on mating success in *Ostrinia furnacalis*. Boxplots display the distribution of PI and PD (ms) across successful (Yes) and unsuccessful (No) mating events. Green and red lines indicate the mean values for successful and unsuccessful copulations, respectively. Histograms present the frequency distributions of PI and PD for both groups. Statistical differences were assessed using the Kruskal–Wallis test with Bonferroni correction ($P < 0.05$). This figure summarizes how PI and PD are associated with mating outcomes in *O. furnacalis*. Significant***; non-significant: ns.

left-biased ultrasonic displays, significantly enhance mating success in *O. furnacalis*. The findings emphasize the functional role of lateralization in modulating acoustic courtship signals and improving reproductive outcomes, thereby revealing an adaptive behavioral asymmetry that may confer selective advantages in mating efficiency. The integration of motor lateralization and species-specific ultrasonic signaling mediated through wing-fanning indicates a neuroethologically significant trait that is likely governed by hemispheric specialization and brain asymmetry. The presence of such lateralized communication strategies in a major lepidopteran pest underscores the evolutionary conservation and ecological relevance of lateralization across taxa.

Importantly, our results suggest that even phytophagous pest species exploit lateralized motor behaviors and acoustic cues as part of their reproductive repertoire. This provides a novel avenue for the development of species-specific, behaviorally based pest control strategies. Future investigations should explore the neuro-anatomical, genetic, and molecular determinants of lateralization, including brain region asymmetries, neural circuitry organization, and transcriptional regulation during development. Furthermore, understanding how lateralized communication contributes to mating success in pest populations may facilitate the development of innovative control strategies, including ultrasonic mating disruption systems, behavior-modifying agents, and gene-
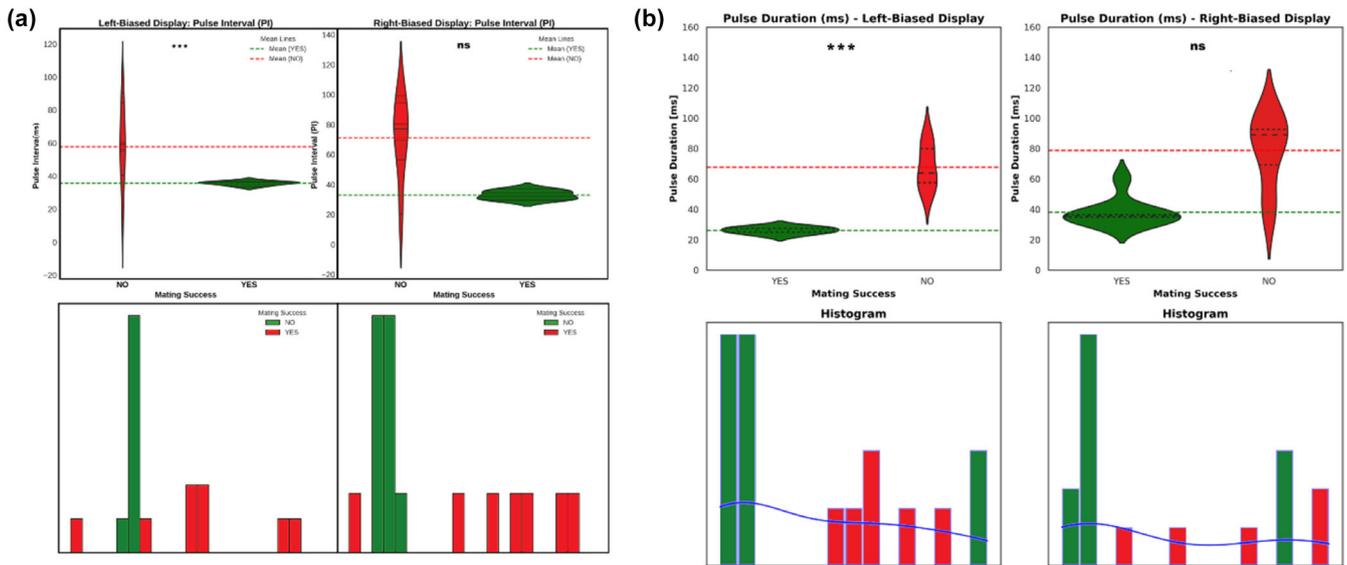
Figure 14. Male lateralized left-biased and right-biased ultrasonic courtship sounds pulse interval duration (ms) and pulse durations (ms) differences in *Ostrinia furnacalis* (Kruskal–Wallis test with Bonferroni correction, $P < 0.05$). The boxplot illustrates the distribution of ultrasonic courtship sound durations for mating success (Yes) and mating unsuccess (No) mating events, separated by left- and right-biased displays. The green and red lines represent the mean sound durations for mating success and unsuccess, respectively. The accompanying histograms depict the frequency distribution of sound durations, highlighting the differences between left- and right-biased displays with mating outcomes. Significant: ***; non-significant: ns.
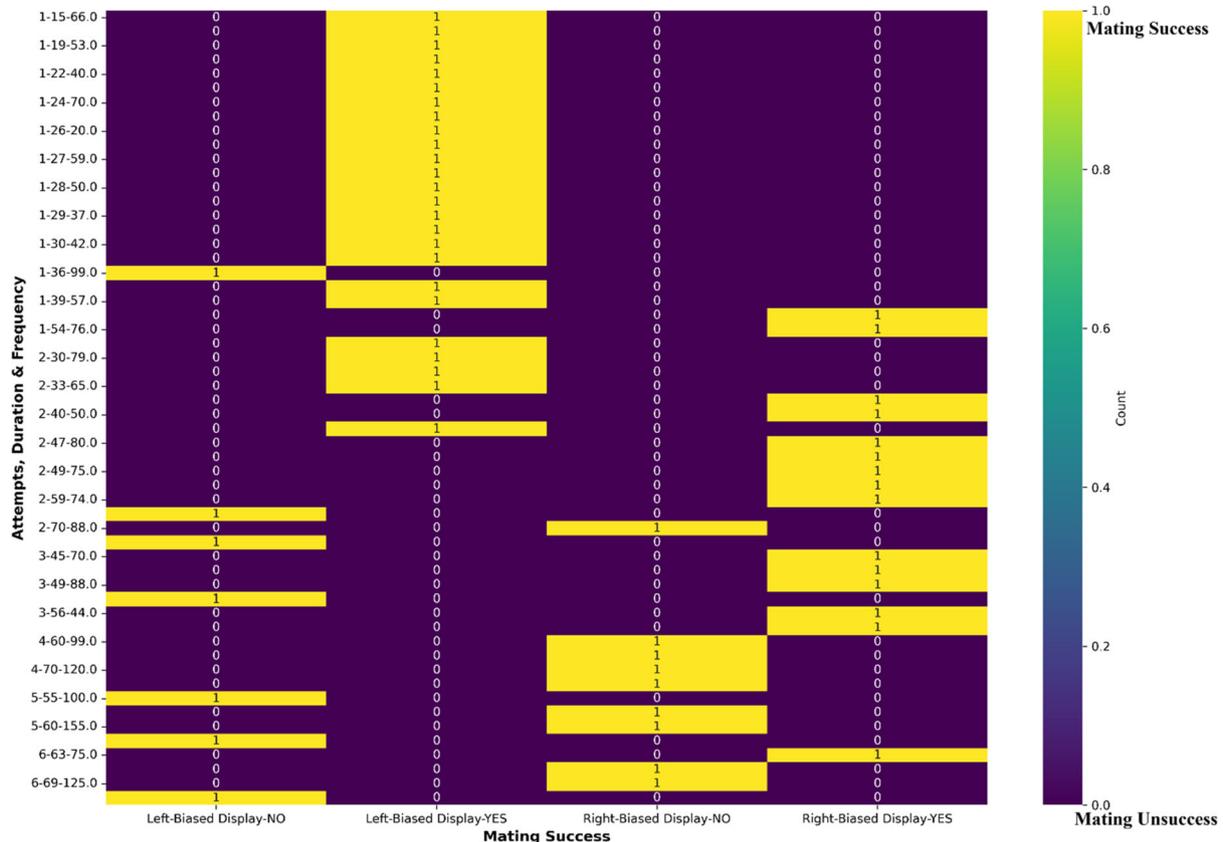

Figure 15. Predicted probabilities of mating success in *Ostrinia furnacalis* based on the combined effects of ultrasonic courtship duration, number of mating attempts, and ultrasonic frequency, as influenced by lateralized courtship behavior (left- or right-biased). The heatmap was generated using a logistic regression model with these predictors. Color gradients represent predicted mating success probabilities, ranging from purple (low probability, NO = 0) to yellow (high probability, YES = 1). This visualization highlights how specific combinations of behavioral traits, especially in left-biased males, correlate with higher reproductive success. Interaction effects among predictors are shown to demonstrate their cumulative impact on mating outcomes.
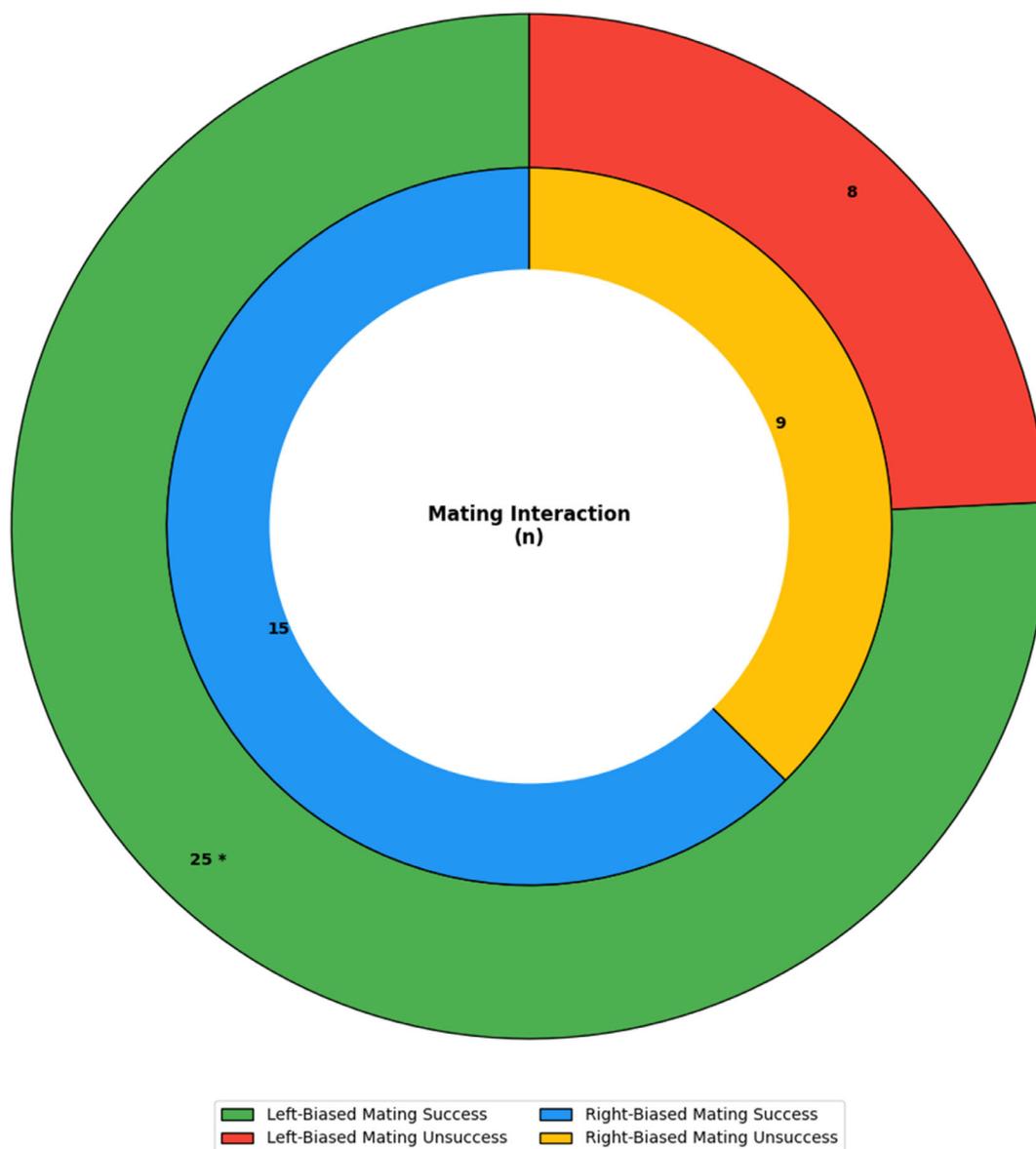
Figure 16. Distribution of mating success and failure in *Ostrinia furnacalis* males exhibiting left- or right-biased displays. The outer ring represents the total number of males exhibiting each behavioral lateralization outcome ($n = 56$), with colors indicating: Green: Left-biased mating success ($n = 25$), Red: Left-biased mating unsuccess ($n = 8$), Blue: Right-biased mating success ($n = 15$), Yellow: Right-biased mating unsuccess ($n = 9$). An asterisk (*) marks the significant difference between left-biased and right-biased displays based on the χ^2 test with Yates' correction.

silencing techniques targeting neural pathways associated with lateralized signaling. Integrating such approaches into ecological pest management programs may offer precise, non-chemical alternatives for suppressing pest reproduction and reducing crop damage in the field.

AUTHOR CONTRIBUTIONS

SA: Conceptualization, formal analysis, investigation, writing–original draft, methodology, data analysis and curation, writing–review and editing, validation, visualization, resources, data collection and investigation. AA: Writing–review and editing, software and data collection. BA and MA: Writing–review and editing. KAK and HAG: Critically revised manuscript, writing–review and editing. JA: Writing–review and editing. NEB: Writing-review and editing. MS: Writing–review, and editing. DR: Conceptualization, writing–review and editing, software and validation, supervision. QL: Supervision, writing–review and editing, validation. R-ZC: Supervision, conceptualization, methodology, funding, resources, validation, project administration, and writing–review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All the data related to the research work are presented in the manuscript. Further details are available from the authors upon reasonable request.

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