

Research Paper

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Lateralised courtship behaviour and its impact on mating success in *Ostrinia furnacalis* (Lepidoptera: Crambidae)

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Abstract

Lateralisation is a well-established phenomenon observed in an increasing number of insect species. This study aims to obtain basic details on lateralisation in courtship and mating behaviour in *Ostrinia furnacalis*, the Asian corn borer. We conducted laboratory investigations to observe lateralisation in courtship and mating behaviours in adult *O. furnacalis*. Our goal was also to detect lateralised mating behaviour variations during sexual interactions and to elucidate how these variances might influence the mating success of males. Our findings reveal two distinct lateralised traits: male approaches from the right or left side of the female and the direction of male turning displays. Specifically, males approaching females from their right side predominantly exhibited left-biased 180° turning displays, while males approaching females from the left-side primarily displayed right-biased 180° turning displays. Notably, left-biased males, executing a 180° turn for end-to-end genital contact, initiated copulation with fewer attempts and began copulation earlier than their right-biased approaches with left-biased 180° turning displays. Furthermore, mating success was higher when males subsequently approached the right side of females during sexual encounters. Left-biased 180° turning males exhibited a higher number of successful mating interactions. These observations provide the first report on lateralisation in the reproductive behaviour of *O. furnacalis* under controlled laboratory conditions and hold promise for establishing reliable benchmarks for assessing and monitoring the quality of mass-produced individuals in pest control efforts.

Introduction

Lateralisation, a phenomenon concerning the left-right asymmetrical organisation of brain functions and behaviours, has captivated the interest of neuroscientists (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 and Niven, 2020; Desaunay *et al.*, 2023). There are two levels of laterality: individual-level laterality, where an individual displays a preference towards one side, and population-level laterality, where most individuals in a population exhibit behaviour that is consistently asymmetric towards the same side (Chapelain *et al.*, 2015; Versace *et al.*, 2020). In insects, behavioural asymmetries become have been reported during several tasks and in particular during mating phases (Takanashi *et al.*, 2010). These phases involve the development of premating and mating behaviours, characterised by lateralised movements, i.e. movements to the right or left (Kavallieratos *et al.*, 2023). These directional variations play a significant role in mating success, offering distinct differences in biological fitness (Vallortigara and Rogers, 2005; Dadda *et al.*, 2009; Vallortigara and Rogers, 2020). While research on lateralised 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 *et al.*, 2017; Romano *et al.*, 2017). The lateralisation of courtship and mating behaviour has been examined in several insect species, including hymenopteran parasitoids (Romano *et al.*, 2018) (Romano *et al.*, 2020), stored-product beetles (Kavallieratos *et al.*, 2023; Othman *et al.*, 2023), mosquitoes (Benelli, 2018), and a calliphorid fly (Benelli *et al.*, 2015a). In this paper, we add to this growing body of data by investigating the lateralisation of courtship and mating behaviour in *Ostrinia furnacalis* Guenée (Lepidoptera: Crambidae). Exploring the behavioural ecology of an insect pest species holds promise for pioneering

approaches within Integrated Pest Management (IPM), offering innovative strategies for pest control and conservation (Avosani *et al.*, 2023).

The Asian corn borer, *O. furnacalis*, is a polyphagous nocturnal moth, and a pest causing significant damage to major crops in Asia and Europe (Li *et al.*, 2021; Kim *et al.*, 2022). It is known for its intricate mating rituals, where mate selection predominantly hinges on male age and vitality (Frolov *et al.*, 2022). Investigating the courtship of *O. furnacalis*, including the role of lateralisation, can yield valuable insights into effective strategies for population control and crop damage mitigation (Boukouvala *et al.*, 2022). Specifically, studying the sensory cues and behavioural elements involved in *O. furnacalis* mating behaviour can help identify potential targets for pest management, such as using pheromones or other attractants (Yao *et al.*, 2021). Variations in ultrasonic sounds and pheromones are closely related to each other in moth species and can profoundly impact mate recognition, reproductive isolation, and speciation (Takanashi *et al.*, 2010; Arminudin *et al.*, 2020). Our study involved the exploration, observation, and quantification of lateralisation in the courtship and mating behaviour of *O. furnacalis*. Our goal was to uncover patterns of population-level lateralisation during courtship and mating behaviour and to elucidate how these variances might impact the mating success of male insects. The investigations of these selected lateralised behaviours during male–female interactions aim to enhance our understanding of *O. furnacalis* behavioural ecology and the significance of lateralised traits within this species.

Materials and methods

Experimental site

The study was conducted in the Agricultural Entomology and Pest Control laboratory and Conservation Tillage Pest and Disease Monitoring Base at Jilin Agricultural University (43.815°N, 125.398°E).

Insect culture

Insects were collected from maize fields (43.815°N, 125.391°E) during early August 2023 with pheromone traps (for male adults) and aerial nets (for female adults), and transported within a plastic container (height: width: length; 23 cm × 45 cm × 70 cm) to the laboratory for mating, approximately 3 km away from the maize fields. The insects were housed in mesh cloth cages (height: width: length; 16 cm × 16 cm × 16 cm; 13 adult parent pairs per cage), at a relative humidity (RH) of 65 ± 5% and a temperature of 26 ± 2 °C. A butter paper was placed on the upper side of the mesh cloth cage for egg laying. A diet comprising 10% sugar-soaked cotton balls (10 ml water) was provided to parent adults. After an incubation period of 2–4 days, eggs were collected and placed in a plastic container (height: width: length; 23 cm × 45 cm × 70 cm), where larvae were fed with a self-made artificial diet (water, wheat germ flour, yeast powder, agar, sucrose, vitamin C (VC), sorbic acid, and nipagin; Liu *et al.*, 2023) until reaching the pupal stage.

Experimental setup for observation of courtship and mating behaviour

To prevent any premature mating interactions among the emerging adults, *O. furnacalis* pupae were individually isolated in

plastic round cups with lids (3.5 cm diameter × 3.5 cm height), which had small holes and contained cotton inside to ensure proper air circulation and humidity access. Newly emerged adult male–female pairs were introduced into the experimental containers (height: width: length; 73 cm × 53 cm × 45 cm) to study courtship and mating behaviours. We observed lateralised courtship and mating behaviours in a total of 150 male–female pairs. To improve the precision of our observations, the experiment was replicated three times, each time with an approximate cohort of 50 adult male–female pairs. It is important to note that only adult pairs displaying mating interactions were included in the analysis; any pairs not displaying such behaviour were omitted from the final dataset. The final sample size for analysis comprised 119 male–female mating pairs (adult pairs exhibited mating interaction out of 150 male–female pairs), aggregated from all three independent repetitions.

A 12-hour observation was conducted for each of the three repetitions using a REOLINK® night vision camera (model number: Reolink Duo 2 Wifi; OS Supported: Windows, Mac, iOS, Android). The same container was used consistently for all three repetitions. The process involved conducting one repetition for 12 hours, removing adults, proceeding with the next repetition for another 12 hours, and repeating the cycle for the third repetition. The camera was equipped with 1/2.7" CMOS sensors and recorded video at a resolution of 4608 × 1728 (8.0 Megapixels) with a frame rate of 20 frames/second to record the insects' behaviours. The experimental setup consisted of a large plastic container with two compartments, each maintained under controlled conditions of 65 ± 5% RH and a temperature of 26 ± 2 °C. The upper compartment (height: width: length; 63 cm × 53 cm × 45 cm) served as the habitat for the insects, while the inner compartment (height: width: length; 10 cm × 10 cm × 8 cm) housed the night vision camera. To ensure clear and unobstructed video recordings, the camera lens was positioned within the mating chamber. It was connected to an Android mobile phone with a dedicated Android application for seamless recording and data storage management. The night vision camera featured a memory card slot for directly storing recorded videos and captured pictures.

Throughout the observation period, the camera was placed approximately 1 m from the focal insects to optimise video quality and capture detailed behavioural patterns. Leveraging night vision technology, the insects' activities were monitored during the dark period when their natural mating behaviours were most frequent. Following data collection, recorded videos were stored on a memory card for subsequent analysis. These videos were examined for courtship displays, mating sequences, and the manifestation of any lateral biases (fig. 1).

After behavioural displays, observations were made regarding the male's selection of the side for approach to the female's posterior of the abdomen. Furthermore, the specific side chosen by the male for intromissive copulation at 180° turn was recorded; this manoeuvre is pivotal for facilitating the establishment of end-to-end genital linkage and initiating copulation. This evaluation sought to elucidate the potential influence of lateralised behaviours on the mating process in *O. furnacalis* (Table 1).

Statistical analysis

The impact of lateralisation on differences in the mean duration and/or number of courtship and mating behaviours acts was analysed using Origin Pro 2023b (Northampton, Massachusetts, USA) with non-parametric statistics ($P < 0.05$) because of non-

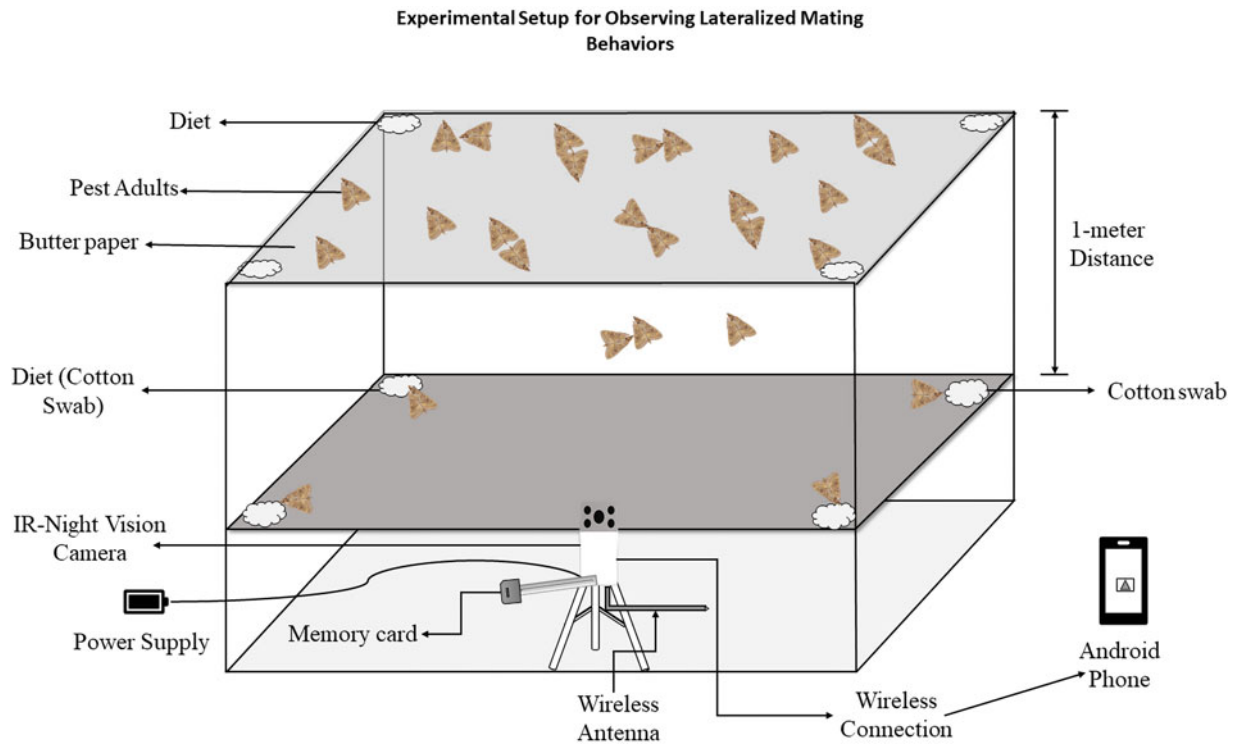


Figure 1. Experimental setup for observing courtship and mating behaviours in *O. furnacalis*.

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

Behavioural displays	Observations (Units)
Male ultrasonic courtship song	The time spent by the male on ultrasonic courtship songs until intromissive copulation (min)
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)

normal (Shapiro–Wilk test, $P < 0.05$) data distribution and non-homoscedasticity (Levene's test, $P < 0.05$). Laterality differences between the numbers of males approaching the left or right side of the female, as well as the number of males turning 180° to the left or to the right in an attempt to copula during courtship interactions, were analysed using an Chi^2 (χ^2) test with Yates' correction ($P < 0.05$) (Loriaux, 1971).

Results

Among the adults under observation, only 119 male–female pairs displayed mating behaviours and were consequently included in the analysis. When a male encounters a female, a sequence of

distinct behaviours unfolds. Initially, the male engages in a sequence of actions, including ultrasonic courtship songs through wing vibrations, exhibiting male aggression towards the female, and softly tapping the female's body with his antennae. As the male approaches the tip of the female's abdomen, he carefully touches the posterior of her abdomen with his antennae. This interaction frequently elicits a response from the female, where she raises her abdomen, indicating her receptivity. Following this, the male may respond aggressively if met with rejection or if the female attempts to evade the courtship. During this phase, the male rotates his body, forming a 180° angle relative to the female (figs 2 and 3A–B). In the later stages of courtship, the female typically becomes motionless in response to the male's persistent courtship

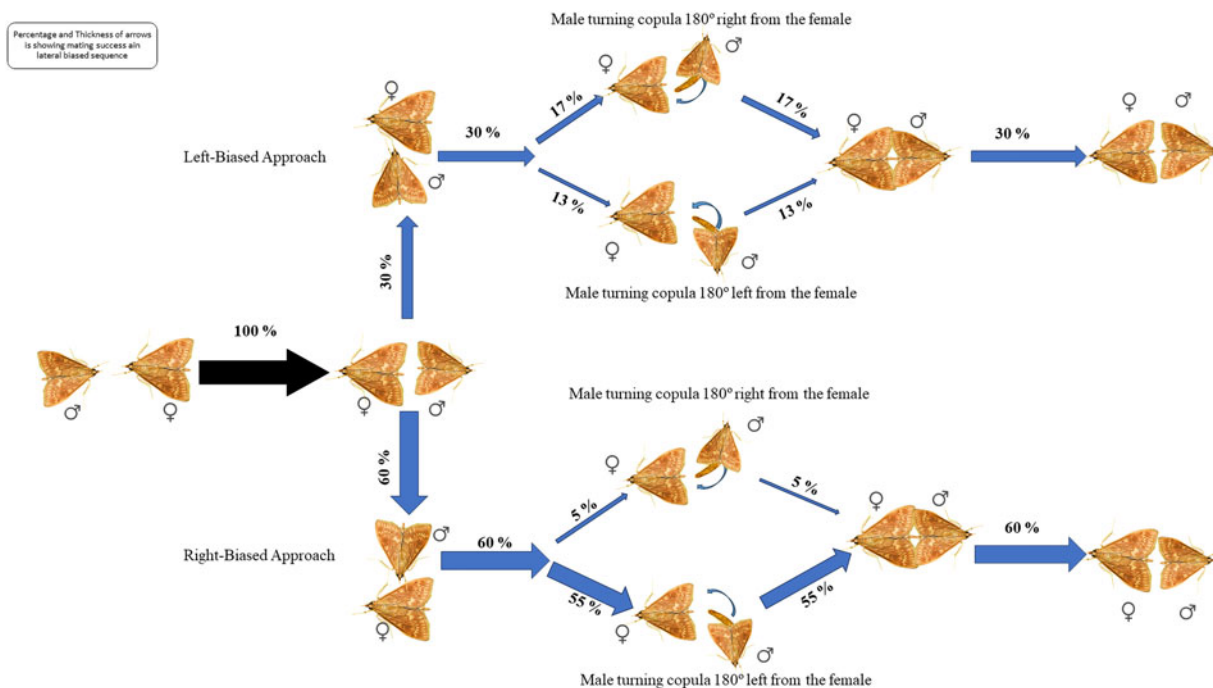


Figure 2. Ethogram depicting the courtship and mating sequence of the *O. furnacalis*. The proportion of adults displaying each behaviour is indicated by the thickness of each arrow ($n = 119$ observed mating pairs).

behaviours (Table 2). This motionlessness serves as a crucial signal, indicating her readiness to engage in end-to-end genital contact – a pivotal step in initiating copulation.

The success of mating was notably higher when *O. furnacalis* males approached females from the left side during sexual interactions ($\chi^2 = 6.700$; $df = 1$; $P < 0.0001$), while approaches from the right side did not significantly impact mating success ($\chi^2 = 0.0001$; $df = 1$; $P = 0.988$) (Table 2). Additionally, turning direction to the left while attempting copula resulted in a higher male mating success ($\chi^2 = 8.130$; $df = 1$; $P < 0.0001$) compared to males displaying a right-biased turning behaviour ($\chi^2 = 1.944$; $df = 1$; $P = 0.717$). (See Table 3.)

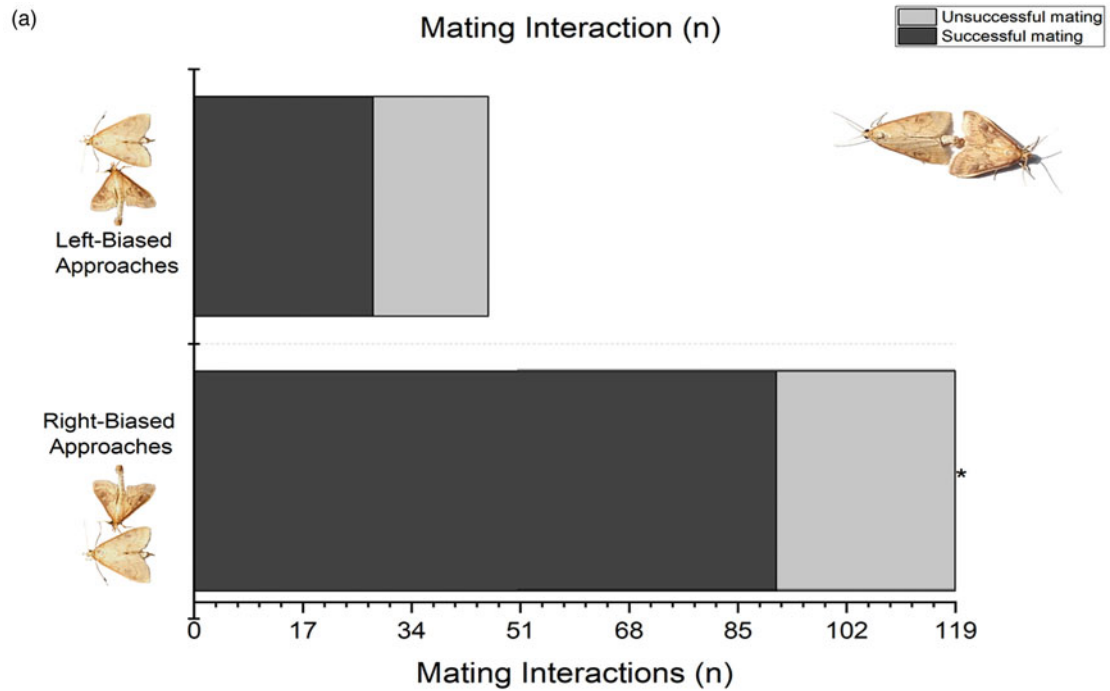
Mating success in males was significantly influenced by ultrasonic courtship songs ($\chi^2 = 15.130$; $df = 1$; $P < 0.0001$), male aggression towards female displayed during courtship ($\chi^2 = 5.590$; $df = 1$; $P = 0.011$), female courtship rejection or escape ($\chi^2 = 4.640$; $df = 1$; $P = 0.051$), as well as the number of the male copulation attempts ($\chi^2 = 6.504$; $df = 1$; $P = 0.021$). The male’s mating success, however, remained unaffected by the duration of the antennal tapping by the male on the female ($\chi^2 = 2.001$; $df = 1$; $P = 0.067$) and duration of the antennal tapping by the male on the female ($\chi^2 = 1.651$; $df = 1$; $P = 0.922$). (See Table 2.)

No significant differences between males approaching females with left- or right-biased directions were observed in the duration of the male’s ultrasonic courtship songs ($\chi^2 = 1.900$; $df = 1$; $P = 0.071$), male aggression towards female for courtship ($\chi^2 = 1.504$; $df = 1$; $P = 0.091$), the duration of the male antennal contact with the posterior of female ($\chi^2 = 0.071$; $df = 1$; $P = 0.990$), ($\chi^2 = 0.043$; $df = 1$; $P = 0.720$), and female courtship rejection or escape ($\chi^2 = 0.904$; $df = 1$; $P = 0.661$), female motionlessness in response to male courtship behaviours ($\chi^2 = 0.029$; $df = 1$; $P = 0.000$), the number of the male copulation attempts ($\chi^2 = 0.027$; $df = 1$; $P = 0.891$), as well as the duration of intromissive copulation ($\chi^2 = 0.026$; $df = 1$; $P = 0.876$). (See Table 2.)

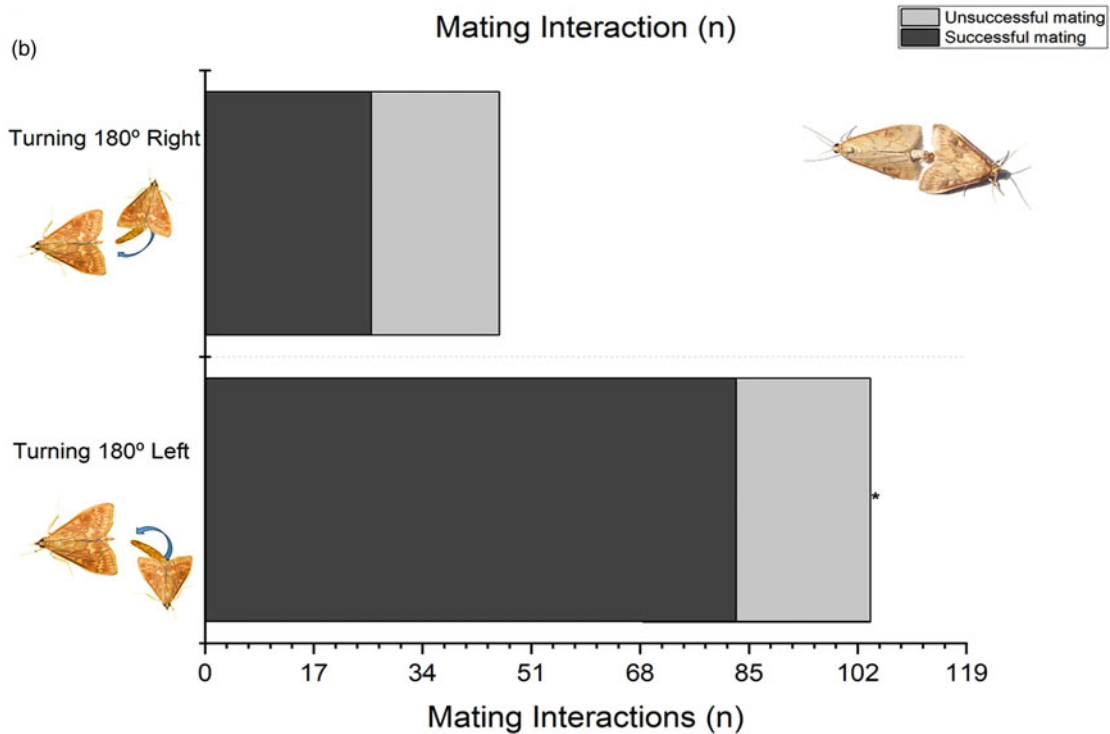
Turning direction was not associated with the duration of the male’s ultrasonic courtship songs ($\chi^2 = 0.016$; $df = 1$; $P = 0.897$), male aggression towards female during courtship ($\chi^2 = 3.969$; $df = 2$; $P = 0.137$), the duration of the male antennal contact with the posterior of female ($\chi^2 = 1.147$; $df = 2$; $P = 0.563$), male aggression towards female in response to courtship rejection or escape ($\chi^2 = 3.969$; $df = 2$; $P = 0.137$), and female motionlessness in response to male courtship behaviours ($\chi^2 = 5.128$; $df = 2$; $P = 0.077$), the number of the male copulation attempts ($\chi^2 = 3.527$; $df = 1$; $P = 0.060$), or the duration of intromissive copulation ($\chi^2 = 0.484$; $df = 1$; $P = 0.486$). (See Table 3.) However, the number of male copulation attempts was significantly affected by the side chosen by the male to turn 180° and attempt copulation ($\chi^2 = 16.017$; $df = 2$; $P < 0.0001$). Males that turned 180° from the female left side performed significantly more attempts to insert their aedeagus into the female’s genital chamber, if compared to right-biased turning males, which started copulation earlier with lower copulation attempts (Table 3).

Discussion

In the context of lateralised courtship and mating behaviours in male adults of *O. furnacalis*, various critical behaviours come into play to ensure successful mating, as reported in recent research (Sun *et al.*, 2023). Our research has discovered novel lateralisation in mating behaviours of *O. furnacalis* adult males and females, particularly in response to female calling behaviours for mating. Upon encountering a female, the male engages in a series of distinct actions. In the results section, the whole sequence of ethological units is described. Our general observations align with previous studies on other *Ostrinia* species, emphasising the consistency of these courtship and mating behaviours, specifically the role of male ultrasonic courtship songs across this group of insects (Nakano *et al.*, 2010; Nakano *et al.*, 2013; Nakano and



Asterisks indicate a significant difference between left and right-biased



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Figure 3. 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, $P < 0.05$).

Nagamine, 2019; Rizvi *et al.*, 2021; Zweerus *et al.*, 2021). Specifically, our results on the importance of laterality find resonance with numerous studies on lateralisation in mating behaviours in other insects species, including the rock ant (*Temnothorax albipennis*) (Hunt *et al.*, 2018), Khapra beetle (*Trogoderma*

granarium) (Kavallieratos *et al.*, 2023), mosquitoes (*Culex pipiens*) (Benelli, 2018), olive fruit fly (*Bactrocera oleae*) (Benelli *et al.*, 2015a; Zaynagutdinova *et al.*, 2022) and Mediterranean fruit fly (*Ceratitis capitata*) (Benelli *et al.*, 2015b). This broader alignment with the literature reinforces the generalisability of our findings to

Table 2. Courtships behavioural displays of *Ostrinia furnacalis* showing side-biased approaches towards the females

Behavioural displays	Right-biased approaches	Left-biased approaches	Tested adults (n., right + left-biased adults)
Male ultrasonic courtship song (min)	0.43 + 1.20a	1.54 + 1.18a	104 + 46 = 150
Male aggression towards female (n)	40.34 + 3.02a	37.19 + 3.28a	104 + 46 = 150
Antennal tapping by male on the female (s)	23.52 + 1.07b	20.17 + 1.98b	104 + 46 = 150
Male's antennal contact with the posterior of female (s)	21.99 + 2.09c	25.13 + 1.89c	104 + 46 = 150
Number of male copulation attempts (n)	3.90 + 1.45a	5.50 + 2.66a	104 + 46 = 150
Female courtship rejection/escape (n)	5.6 + 3.43a	6.10 + 2.89a	104 + 46 = 150
Female motionless in response to male ultrasonic courtship songs (n)	89.43 + 2.76a	27.56 + 3.17a	104 + 46 = 150
Duration of intromissive copulation (min)	70.50 + 1.01a	74.42 + 2.05a	91 + 28 = 119

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. Courtships and mating behavioural displays of *O. furnacalis* showing lateralised turning behaviour

Behavioural displays	Turning 180° right	Turning 180° left	Tested adults (n., right + left-biased adults)
Male ultrasonic courtship song (min)	0.51 + 1.20a	1.44 + 1.68a	104 + 46 = 150
Male aggression towards female (n)	33.34 + 2.02a	35.19 + 2.58a	104 + 46 = 150
Antennal tapping by male on the female (s)	21.12 + 3.07b	24.47 + 3.48b	104 + 46 = 150
Male's antennal contact with the posterior of female (s)	22.07 + 1.59c	25.73 + 2.29c	104 + 46 = 150
Number of male copulation attempts (n)	4.10 + 1.47a	5.10 + 3.42a	104 + 46 = 150
Female courtship rejection/escape (n)	6.10 + 2.96a	6.88 + 3.34a	104 + 46 = 150
Female motionless in response to male ultrasonic courtship songs (n)	79.53 + 2.82a	24.86 + 1.71a	104 + 46 = 150
Duration of intromissive copulation (min)	71.50 + 2.51a	70.42 + 3.08a	83 + 26 = 109

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

a broader context of insect behaviour and adds to the growing body of knowledge in this field.

In the present study, we have identified two specific behavioural displays in *O. furnacalis* that exhibit within-population dimorphism in laterality. It was consistently observed that a significant majority of male *O. furnacalis*, during courtship and mating, preferred to position themselves at the tip of the female's abdomen. In doing so, they occasionally engaged in antennal tapping and palpation on the left side of the female's body. Additionally, males strongly preferred clockwise and anti-clockwise rotations (right and left turns) when forming a 180-degree angle with the female's body, which is crucial for the end-to-end genital linkage. Notably, we observed that males approaching females from the right-side were primarily left-biased in their 180° turning, while those approaching from the left-side exhibited a right-biased in their turning behaviour. It is important to underline that these lateralised traits did not substantially impact the main behavioural parameters characterising courtship and mating in *O. furnacalis*. However, it is noteworthy that males executing a 180° turn from their left-side appeared to make fewer copulation attempts, suggesting a potentially better orientation and efficiency in achieving genital linkage among right-biased males. Many studies agree with our finding in

turning 180° while mating with various insects (Benelli *et al.*, 2015a; Chivers *et al.*, 2017; Kiss *et al.*, 2020; Romano *et al.*, 2022)

Significantly, our study unveiled a correlation between mating success and lateralisation. Males that approached females from the right-side and those that preferred leftward turning exhibited significantly higher mating success rates. This finding marks the first evidence of population-level lateralised mating traits in *O. furnacalis*, a species previously known primarily for motor bias in lateralisation. Our results align with a substantial body of literature highlighting the prevalence of population-level lateralised traits in social and solitary insect species (Anfora *et al.*, 2010; Sakurai and Ikeda, 2022). Recent studies have reported lateralised traits related to courtship, mating, and genital morphology (Schilthuizen, 2013) in various insects, including lesser mealworm beetle (*Alphitobius diaperinus*) (Calla-Quispe *et al.*, 2023), earwigs (*Nala nepalensis*) (Kamimura *et al.*, 2021), rusty grain beetle (*Cryptolestes ferrugineus*) (Boukouvala *et al.*, 2022), encyrtid parasitoids (*Anagyrus* sp.) (Romano *et al.*, 2018), green bottle fly (*Lucilia sericata*) (Romano *et al.*, 2021), and *Drosophila melanogaster* (Versace *et al.*, 2020; Lapraz *et al.*, 2023). Our research unveils the existence of lateralised courtship and mating behaviours in *O. furnacalis*, enriching our comprehension of this species beyond mere motor biases previously reported. This discovery

resonates with a broader trend of population-level lateralisation seen across various insect species, underscoring the pivotal role of lateralisation in insect reproductive behaviours.

Theoretical models propose that population-level lateralisation is more likely to develop in social species. The reasoning behind this hypothesis lies in the potential benefits of lateralisation in social interactions (Rogers *et al.*, 2013; Frasnelli and Vallortigara, 2018; Ocklenburg *et al.*, 2023; Tonello and Vallortigara, 2023). In social insects, individuals often need to coordinate their behaviours, such as during group movements, foraging, or communication (Johnson, 2010; Feinerman and Korman, 2017). Lateralisation, or the consistent preference for using one side of the body or brain, can facilitate efficient and synchronised interactions within the population. This may lead to improved coordination, reduced ambiguity in communication signals, and enhanced overall social cohesion (Frasnelli and Vallortigara, 2018). While the specific mechanisms and advantages may vary across species, the underlying concept is that in social environments, population-level lateralisation could confer adaptive advantages that promote effective group functioning and communication (Vallortigara, 2006). However, in many insect species (such as *O. furnacalis*), the common and intense interactions among individuals, including numerous conflicts and mating events, as well as encounters with other species like predators and host plants, may help explain the widespread occurrence of population-level lateralisation (Casanova, 2020; Manns, 2022). The theory does not necessarily suggest that social species require population-level lateralisation, but it posits that lateralisation might emerge as an Evolutionary Stable Strategy (ESS) either at the individual or population level, depending on the specific context (Rogers *et al.*, 2016; Colombo, 2023; Jacobs and Oosthuizen, 2023).

The discovery of lateralised courtship and mating behaviours across different insect orders suggests that this trait could serve as a pivotal component in the ESS governing the reproductive behaviour of these species (Vidal-Abarca Gutierrez *et al.*, 2023). While much of this research has traditionally been conducted in laboratory settings to understand the relevance of brain lateralisation as an adaptation to ecological demands (Manns, 2021), our study also focuses explicitly on population-level lateralised courtship and mating in *O. furnacalis*. This provides valuable insights, demonstrating a noteworthy parallel with several vertebrates and invertebrates that exhibit lateral biases in their natural environments, unconstrained by laboratory conditions (Ventolini *et al.*, 2005; Koberoff *et al.*, 2008). This study, revealing asymmetries in the behaviour of *O. furnacalis*, supports the hypothesis that lateralisation is a widespread phenomenon and emphasises the need for increased attention to this topic among behavioural biologists in the context of pest management and ecological studies.

In conclusion, this study provides evidence of lateralised courtship and mating behaviours at the population level in *O. furnacalis*, offering a contribution to the understanding of these behaviours. Our research advances our fundamental knowledge of the courtship and mating behaviour of *O. furnacalis*, shedding light on previously unexplored aspects of its reproductive biology. The new insights gained into the reproductive behaviour of *O. furnacalis* may also hold practical implication by identifying behavioural traits suitable for assessing the quality of mass-reared individuals in pest control programs. Comprehending population-level lateralisation enables the identification of individuals with improved coordination and communication skills. This understanding holds promise

for enhancing the effectiveness of pest management strategies by facilitating targeted releases.

Prior to this study, there were no attempts to evaluate the existence and functional importance of lateralised traits within the Crambidae. To advance our understanding, further research efforts need to extend beyond the laboratory setting and into the field to explore the existence of these lateralisation traits in *O. furnacalis* under natural conditions. The goal of these investigations is to offer a more thorough understanding of the distinct lateralisation traits displayed by this species. The quantification of mating displays in this laboratory study establishes a foundation for further research, enabling future comparative analyses with other insect species. This sets the stage for broader insights into the evolutionary and ecological implications of lateralisation among insect populations.

Availability of data and materials

Not applicable.

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Competing interests. None.

Ethical approval. Not applicable.

References

- Anfora G, Frasnelli E, Maccagnani B, Rogers LJ and Vallortigara G (2010) Behavioural and electrophysiological lateralization in a social (*Apis mellifera*) but not in a non-social (*Osmia cornuta*) species of bee. *Behavioural Brain Research* **206**, 236–239.
- Arminudin AT, Wijonarko A and Trisyono YA (2020) Ultrastructure characters and partial mtDNA-COI haplotypes of Asian corn borer, *Ostrinia furnacalis* (Guenée)(Lepidoptera: Crambidae) from Indonesia. *Biodiversitas Journal of Biological Diversity* **21**, 2914–2922.
- Avosani S, Nieri R, Mazzoni V, Anfora G, Hamouche Z, Zippari C, Vitale ML, Verrastro V, Tarasco E and D'Isita I (2023) Intruding into a conversation: how behavioral manipulation could support management of *Xylella fastidiosa* and its insect vectors. *Journal of Pest Science* **97**, 1–17.
- Benelli G (2018) Mating behavior of the West Nile virus vector *Culex pipiens*—role of behavioral asymmetries. *Acta Tropica* **179**, 88–95.
- Benelli G, Romano D, Messing RH and Canale A (2015a) Population-level lateralized aggressive and courtship displays make better fighters not lovers: evidence from a fly. *Behavioural Processes* **115**, 163–168.
- Benelli G, Donati E, Romano D, Stefanini C, Messing RH and Canale A (2015b) Lateralisation of aggressive displays in a tephritid fly. *The Science of Nature* **102**, 1–9.
- Benelli G, Romano D, Stefanini C, Kavallieratos NG, Athanassiou CG and Canale A (2017) Asymmetry of mating behaviour affects copulation success in two stored-product beetles. *Journal of Pest Science* **90**, 547–556.
- Boukouvala MC, Kavallieratos NG, Canale A and Benelli G (2022) Functional asymmetries routing the mating behavior of the rusty grain beetle, *Cryptolestes ferrugineus* (Stephens)(Coleoptera: Laemophloeidae). *Insects* **13**, 699.
- Calla-Quispe E, Irigoien E, Mansurova M, Martel C and Ibáñez AJ (2023) Lateralized movements during the mating behavior, which are associated

- with sex and sexual experience, increase the mating success in *Alphitobius diaperinus* (Coleoptera: Tenebrionidae). *Insects* **14**, 806.
- Casanova C** (2020) Abstracts of the 7th Iberian congress of primatology. *Folia Primatologica* **91**, 512–540.
- Chapelain A, Pimbert P, Aube L, Perrocheau O, Debunne G, Bellido A and Blois-Heulin C** (2015) Can population-level laterality stem from social pressures? Evidence from cheek kissing in humans. *PLoS One* **10**, e0124477.
- Chivers DP, McCormick MI, Warren DT, Allan BJ, Ramasamy RA, Arvizo BK, Glue M and Ferrari MC** (2017) Competitive superiority versus predation savvy: the two sides of behavioural lateralization. *Animal Behaviour* **130**, 9–15.
- Colombo JA** (2023) *Evolution and the Human-Animal Drive to Conflict: A Psychobiological Perspective*. Taylor & Francis, London: Routledge.
- Dadda M, Zandona E, Agrillo C and Bisazza A** (2009) The costs of hemispheric specialization in a fish. *Proceedings of the Royal Society B: Biological Sciences* **276**, 4399–4407.
- David Fernandes AS and Niven JE** (2020) Lateralization of short- and long-term visual memories in an insect. *Proceedings of the Royal Society B* **287**, 20200677.
- Desaunay P, Guillery B, Moussaoui E, Eustache F, Bowler DM and Guénolé F** (2023) Brain correlates of declarative memory atypicalities in autism: a systematic review of functional neuroimaging findings. *Molecular Autism* **14**, 1–32.
- Feinerman O and Korman A** (2017) Individual versus collective cognition in social insects. *Journal of Experimental Biology* **220**, 73–82.
- Frasnelli E and Vallortigara G** (2018) Individual-level and population-level lateralization: two sides of the same coin. *Symmetry* **10**, 739.
- Frolov A, Shchenikova A, Selitskaya O, Grushevaya I, Zhukovskaya M, Fedoseev N, Kuzmin A, Lastushkina E, Kurenschikov D and Kurenschikov V** (2022) Asian corn borer (*Ostrinia furnacalis* Gn., Lepidoptera: Crambidae): attraction to a bisexual lure and comparison of performance with synthetic sex pheromone. *Acta Phytopathologica et Entomologica Hungarica* **57**, 148–164.
- Güntürkün O, Ströckens F and Ocklenburg S** (2020) Brain lateralization: a comparative perspective. *Physiological Reviews* **100**, 1019–1063.
- Hunt ER, Dornan C, Sendova-Franks AB and Franks NR** (2018) Asymmetric ommatidia count and behavioural lateralization in the ant *Temnothorax alpepinis*. *Scientific Reports* **8**, 5825.
- Jacobs PJ and Oosthuizen MK** (2023) Laterality in the Damaraland mole-rat: insights from a Eusocial Mammal. *Animals* **13**, 627.
- Johnson BR** (2010) Task partitioning in honey bees: the roles of signals and cues in group-level coordination of action. *Behavioral Ecology* **21**, 1373–1379.
- Kamimura Y, Matsumura Y, Yang C-CS and Gorb SN** (2021) Random or handedness? Use of laterally paired penises in Nala earwigs (Insecta: Dermaptera: Labiduridae). *Biological Journal of the Linnean Society* **134**, 716–731.
- Kavallieratos NG, Boukouvala MC, Gidari DLS, Di Giuseppe G, Canale A and Benelli G** (2023) Does cross-mating affect behavioral asymmetries and mating success of khapra beetle (*Trogoderma granarium*) strains? *Entomologia Generalis* **43**, 409–419.
- Kim EY, Jung JK, Kim IH and Kim Y** (2022) Chymotrypsin is a molecular target of insect resistance of three corn varieties against the Asian corn borer, *Ostrinia furnacalis*. *PLoS One* **17**, e0266751.
- Kiss DS, Toth I, Jocsak G, Bartha T, Frenyo LV, Barany Z, Horvath TL and Zsarnovszky A** (2020) Metabolic lateralization in the hypothalamus of male rats related to reproductive and satiety states. *Reproductive Sciences* **27**, 1197–1205.
- Koboroff A, Kaplan G and Rogers LJ** (2008) Hemispheric specialization in Australian magpies (*Gymnorhina tibicen*) shown as eye preferences during response to a predator. *Brain Research Bulletin* **76**, 304–306.
- Labache L, Ge T, Yeo BT and Holmes AJ** (2023) Language network lateralization is reflected throughout the macroscale functional organization of cortex. *Nature Communications* **14**, 3405.
- Lapraz F, Boutres C, Fixary-Schuster C, De Queiroz B, Plaçais P, Cerezo D, Besse F, Pr at T and Noselli S** (2023) Asymmetric activity of NetrinB controls laterality of the *Drosophila* brain. *Nature Communications* **14**, 1052.
- Li G, Feng H, Ji T, Huang J and Tian C** (2021) What type of Bt corn is suitable for a region with diverse lepidopteran pests: a laboratory evaluation. *GM Crops & Food* **12**, 115–124.
- Liu J-L, Feng X, Abbas A, Abbas S, Hafeez F, Han X, Romano D and Chen RZ** (2023) Larval competition analysis and its effect on growth of *Ostrinia furnacalis* (Lepidoptera: Crambidae) at natural conditions in Northeast China. *Environmental Entomology* **52**, 970–982.
- Loriaux M** (1971) RR Sokal and FJ Rohlf Biometry. The principles and practice of statistics in biological research. San Francisco, WH Freeman and Company, 1969, XXI p. 776 p., 126/-.-FJ Rohlf and RR Sokal statistical tables. San Francisco, WH Freeman and Company, 1969, XI p. 253 p., \$2.75. *Recherches  conomiques de Louvain/Louvain Economic Review* **37**, 461–462.
- Manns M** (2021) Laterality for the next decade: costs and benefits of neuronal asymmetries—putting lateralization in an evolutionary context. *Laterality* **26**, 315–318.
- Manns M** (2022) Hemispheric Specialization. In Vonk, J., Shackelford, T.K. (eds), *Encyclopedia of Animal Cognition and Behavior*. Cham: Springer International Publishing, pp. 3062–3071.
- Nakano R and Nagamine K** (2019) Loudness-duration tradeoff in ultrasonic courtship songs of moths. *Frontiers in Ecology and Evolution* **7**, 244.
- Nakano R, Takanashi T, Skals N, Surlykke A and Ishikawa Y** (2010) Ultrasonic courtship songs of male Asian corn borer moths assist copulation attempts by making the females motionless. *Physiological Entomology* **35**, 76–81.
- Nakano R, Takanashi T, Surlykke A, Skals N and Ishikawa Y** (2013) Evolution of deceptive and true courtship songs in moths. *Sci. Rep* **3**, 2003.
- Ocklenburg S, El Basbasse Y, Str ockens F and M uller-Alcazar A** (2023) Hemispheric asymmetries and brain size in mammals. *Communications Biology* **6**, 521.
- Othman N, Elias NH and Zainalabidin N** (2023) Wood vinegar as an alternative insecticide in controlling rice weevil, *Sitophilus oryzae* (Coleoptera: Curculionidae). *Advances in Agricultural and Food Research Journal* **4**, a0000315.
- Rizvi SAH, George J, Reddy GV, Zeng X and Guerrero A** (2021) Latest developments in insect sex pheromone research and its application in agricultural pest management. *Insects* **12**, 484.
- Rogers LJ, Rigosi E, Frasnelli E and Vallortigara G** (2013) A right antenna for social behaviour in honeybees. *Scientific Reports* **3**, 2045.
- Rogers LJ, Frasnelli E and Versace E** (2016) Lateralized antennal control of aggression and sex differences in red mason bees, *Osmia bicornis*. *Scientific Reports* **6**, 29411.
- Romano D, Benelli G and Stefanini C** (2017) Escape and surveillance asymmetries in locusts exposed to a Guinea fowl-mimicking robot predator. *Scientific Reports* **7**, 12825.
- Romano D, Benelli G, Stefanini C, Desneux N, Ramirez-Romero R, Canale A and Lucchi A** (2018) Behavioral asymmetries in the mealybug parasitoid *Anagyrus* sp. near pseudococci: does lateralized antennal tapping predict male mating success? *Journal of Pest Science* **91**, 341–349.
- Romano D, Benelli G, Kavallieratos NG, Athanassiou CG, Canale A and Stefanini C** (2020) Beetle-robot hybrid interaction: sex, lateralization and mating experience modulate behavioural responses to robotic cues in the larger grain borer *Prostephanus truncatus* (Horn). *Biological Cybernetics* **114**, 473–483.
- Romano D, Benelli G and Stefanini C** (2021) Opposite valence social information provided by bio-robotic demonstrators shapes selection processes in the green bottle fly. *Journal of the Royal Society Interface* **18**, 20210056.
- Romano D, Benelli G and Stefanini C** (2022) Lateralization of courtship traits impacts pentatomid male mating success—evidence from field observations. *Insects* **13**, 172.
- Sakurai Y and Ikeda Y** (2022) Visual and brain lateralization during the post-hatching phase in squid under solitary and group conditions. *Animal Behaviour* **183**, 13–28.
- Schilthuisen M** (2013) Something gone awry: unsolved mysteries in the evolution of asymmetric animal genitalia. *Animal Biology* **63**, 1–20.
- Stieger B, Wesseler Y, Kaiser S, Sachser N and Richter SH** (2023) Behavioral lateralization of mice varying in serotonin transporter genotype. *Frontiers in Behavioral Neuroscience* **16**, 1095567.
- Sun H, Bu L-A, Su S-C, Guo D, Gao C-F and Wu S-F** (2023) Knockout of the odorant receptor co-receptor, orco, impairs feeding, mating and egg-laying behavior in the fall armyworm *Spodoptera frugiperda*. *Insect Biochemistry and Molecular Biology* **152**, 103889.

- Takanashi T, Nakano R, Surlykke A, Tatsuta H, Tabata J, Ishikawa Y and Skals N (2010) Variation in courtship ultrasounds of three *Ostrinia* moths with different sex pheromones. *PLoS One* **5**, e13144.
- Tonello L and Vallortigara G (2023) Evolutionary models of lateralization: steps toward stigmergy? *Frontiers in Behavioral Neuroscience* **17**, 1121335.
- Vallortigara G (2006) The evolutionary psychology of left and right: costs and benefits of lateralization. *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology* **48**, 418–427.
- Vallortigara G and Rogers L (2005) Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences* **28**, 595–596.
- Vallortigara G and Rogers LJ (2020) A function for the bicameral mind. *Cortex* **124**, 274–285.
- van Dijk ES, Bhattacharjee D, Belli E and Massen JJ (2023) Hand preference predicts behavioral responses to threats in Barbary macaques. *American Journal of Primatology* **85**, e23499.
- Ventolini N, Ferrero EA, Sponza S, Della Chiesa A, Zucca P and Vallortigara G (2005) Laterality in the wild: preferential hemifield use during predatory and sexual behaviour in the black-winged stilt. *Animal Behaviour* **69**, 1077–1084.
- Versace E, Caffini M, Werkhoven Z and de Bivort BL (2020) Individual, but not population asymmetries, are modulated by social environment and genotype in *Drosophila melanogaster*. *Scientific Reports* **10**, 4480.
- Vidal-Abarca Gutierrez MR, Nicolás-Ruiz N, Sánchez-Montoya MdM and Suárez Alonso ML (2023) Ecosystem services provided by dry river socio-ecological systems and their drivers of change. *Hydrobiologia* **850**, 2585–2607.
- Wang L, Luo Y, Lin H, Xu N, Gu Y, Bu H, Bai Y and Li Z (2023) Performance on inhibitory tasks does not relate to handedness in several small groups of Callitrichids. *Animal Cognition* **26**, 415–423.
- Yao S, Zhou S, Li X, Liu X, Zhao W, Wei J, Du M and An S (2021) Transcriptome analysis of *Ostrinia furnacalis* female pheromone gland: esters biosynthesis and requirement for mating success. *Frontiers in Endocrinology* **12**, 736906.
- Zaynagutdinova E, Kölzsch A, Müskens GJ, Vorotkov M, Sinelshikova A, Giljov A and Karenina K (2022) Visual lateralization in flight: lateral preferences in parent-offspring relative positions in geese. *Ethology* **128**, 159–167.
- Zweerus NL, van Wijk M, Schal C and Groot AT (2021) Experimental evidence for female mate choice in a noctuid moth. *Animal Behaviour* **179**, 1–13.