



Where courtship leans left: Insights into the mating behavior of *Latheticus oryzae* (Coleoptera: Tenebrionidae)

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Abstract. *Latheticus oryzae* Waterhouse (Coleoptera: Tenebrionidae) is a cosmopolitan secondary pest of stored products, yet it remains an understudied species. In this study we examined the courtship and mating sequence of *L. oryzae*, as well as the behavioral lateralization, exploring its influence on copulation success. Males of *L. oryzae* exhibited a left-biased tendency across various phases of mating (i.e., approach of the female, mounting, departure). The side of approach and departure significantly affected copulation success rates, in contrast to the mounting side. Left-biased *L. oryzae* males achieved higher mating success and demonstrated significantly shorter mate detection and copulation attempt durations compared to males of the other directions (back, front, and right). From a control perspective, the strong directional tendency of *L. oryzae* at the mating behavior may offer novel opportunities for pest management strategies that exploit lateralization-based disruptions. Overall, these findings establish the first comprehensive description of the mating procedure of *L. oryzae* and highlight the functional significance of behavioral asymmetries in the copulation success of stored-product pests.

INTRODUCTION

Insect infestations in stored grains and food products pose a challenge to global food security (Rosentrater, 2022). Post-harvest losses attributed to stored-product pests can be both qualitative and quantitative, arising not only from direct consumption of commodities but also from contamination (e.g., increased relative humidity, micro-organisms, fungal spores, and bacteria), heating, and deterioration caused by dense insect populations (Hill, 2003; Rosentrater, 2022). To the stored-product insects belongs the secondary pest *Latheticus oryzae* Waterhouse (Tenebrionidae), the long-headed flour beetle. It is a cosmopolitan species, infesting various products, such as tea, various types of flour, sorghum, and maize (Hagstrum et al., 2013; Tripathi, 2018). Females lay approximately 400 eggs singly on the grains which hatched in 7–12 days. The larval and pupal periods are 15–80 and 5–10 days, respectively. Under the optimum conditions, 35°C and 85% relative humidity (R.H.), *L. oryzae* completes the life cycle in 25 days (Deshwal et al., 2020). As with other species of Tenebrionidae, the infestation of *L. oryzae* individuals is

accompanied by an unpleasant odor, caused by the benzoquinones of their abdomen (Hill, 2003).

Fast reproducing species like *Tribolium confusum* Jacquelin du Val (Tenebrionidae) are likely to outcompete *L. oryzae* under typical storage conditions. However, *L. oryzae* may become dominant in heating grain due to its tolerance to high temperatures (Rees, 2004). Despite the extensive bibliography on stored-product pests, *L. oryzae* is a greatly understudied species. Most of the studies are focused on biology, development, or genetics of this species (Khalifa & Badawy, 1955; Sokoloff, 1959; Nowosielski-Slepowron & Aryeetey, 1980; Xu et al., 2025). There are also limited studies on the control of *L. oryzae* (Chouhan & Yadav, 1984; Ghaly et al., 2025; Kavallieratos et al., 2026).

The capacity of the brain to perform mental activities that use the left and right hemisphere simultaneously but in different ways can be improved by brain lateralization, or the differences in functions and/or structures between the two sides of the brain (Rogers et al., 2004). Brain lateralization is already thoroughly studied for vertebrates (Valortigara & Rogers, 2005; MacNeilage et al., 2009; Rogers et al., 2013; Güntürkün et al., 2020; Miletto Petrazzini et

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al., 2020; Costalunga et al., 2022; Chitadze et al., 2024). However, in recent years, several studies have centered on the lateral behavior of mating and courtship of various coleopterans (Benelli et al., 2017; Boukouvala et al., 2023, 2025; Calla-Quispe et al., 2023; Kavallieratos et al., 2023; Gidari et al., 2024).

The mating process, as a way to population growth, is vital for insect expansion, their establishment in new locations, and their co-existence with other insect species (Kavallieratos et al., 2017). However, the mating behavior of *L. oryzae* remains uninvestigated. Thus, the current study aims to add basic knowledge, for the first time, on the mating behavior of this pest, investigating the lateralization and the related behavioral asymmetries that are associated with higher mating success.

MATERIAL AND METHODS

Latheticus oryzae individuals

Virgin female and male *L. oryzae* adults were obtained from the mass-rearing facilities of the Laboratory of Agricultural Zoology and Entomology (Agricultural University of Athens, Greece). All individuals were maintained at complete darkness, 30°C, and 65% R.H. The rearing medium was wheat flour with 5% brewer's yeast. Sex determination was carried out at the adult stage based on Halstead (1963) and Badawi (1972). After sex recognition, female and male *L. oryzae* adults were kept separately in plastic cups (30 mL) containing the aforementioned rearing medium until the start of observations. Preliminary observations revealed that adult males and females can mate 4 days after emergence. Thus, adults >3 days old were used in behavioral observations.

Behavioral experiments

Behavioral assays were conducted in a circular arena consisting of a glass Petri dish (50 mm diameter × 10 mm height), the inner wall of which was lined with a strip of Whatman No. 1 filter paper. This barrier minimized external visual stimuli and reduced potential observer-induced disturbances that could bias courtship performance (Boukouvala et al., 2021). Prior to testing, individual males and females were transferred to separate Petri dishes (50 mm diameter) and acclimated for 3 h under natural laboratory light. Previous ethological studies on stored-product Coleoptera indicate that this acclimation period is sufficient for behavioral stabilization under laboratory conditions (Boukouvala et al., 2021, 2022).

The mating sequence of *L. oryzae* was examined by introducing a single male-female pair into the arena (Boukouvala et al., 2023). Observations were performed continuously for up to 60 min or until completion of the sexual interaction, following standard methodologies for tenebrionid mating studies (Benelli et al., 2017; Boukouvala et al., 2019, 2020). For each successful interaction, the following behavioral components were recorded with a stopwatch: (i) Mate detection: latency from the introduction of the pair to the moment the male located the female. (ii) Palpating: duration of tactile assessment following first approach, during which the male contacted the female with forelegs and/or mouthparts. (iii) Copulation attempts: time elapsed from mounting to the first successful genital alignment attempt; together with palpating, these behaviors constituted the precopulatory phase. (iv) Copula: duration from aedeagal insertion into the female genital chamber to genital disengagement. (v) Post-copulatory retention: time the male remained mounted on the female following aedeagal withdrawal.

Behavioral lateralization was quantified by recording the relative position of the male with respect to the female during three key phases: (1) initial approach, (2) mounting, and (3) dismounting. Male orientation was categorized into four mutually exclusive directions: left, right, front, and back (Boukouvala et al., 2021, 2022, 2023).

Overall, 104 pairs were observed, of which 88 pairs were utilized for the analysis (Fig. 1a) and 16 pairs were rejected because no sexual interaction occurred, pairs remained motionless, or females were near the walls of the arena (Fig. 1b), affecting the direction of approach of males (Benelli et al., 2017).

Statistical analysis

All statistical analyses were performed using JMP 16.2 (SAS Institute Inc, 2021). Data for behavioral durations and lateralization measures did not meet the assumptions of normality and homoscedasticity, as assessed through Shapiro-Wilk and Levene's tests; therefore, non-parametric procedures were applied (Boukouvala et al., 2020, 2022).

Differences in the male's orientation (approach, mounting, and departure direction) in relation to the duration of specific mating components (mate detection, precopulatory behaviors, and copula) were evaluated using the Steel-Dwass multiple comparison test at $P = 0.05$. This test was chosen because it provides a conservative, distribution-free method for all-pairs comparisons under unequal sample sizes. Copulation success across lateralization categories (left, right, front, back) was analyzed using contingency tables, followed by non-parametric pairwise comparisons where appropriate. All results are reported as means ± standard error (SE) unless otherwise stated.

RESULTS

Most males approached females from their left side (44.4%), followed by males that approached from the right (31.7%), back (13.7%), and front (10.2%). The majority of those left-biased males (39.8% out of 44.4%) mounted their mates from their left side, resulting in 35.2% successful copulations. The left-biased males, regardless the mounting side, achieved 39.8% out of 44.4% successful copulations. The 33.0% out of the 35.2% of the left-mounted males, departed from the left side after the copulation. In contrast to the left-biased males, most of the males that approached their mates from the other three directions (right, back, and front) did not mount from the left side. The 22.7% of the 31.7% of the right-biased males and the 5.7% of the 13.7% of males that approached from the back side, mounted from the right side. Concerning males that approached females from their front side, they mounted equally (3.4% out of 10.2%) from the front or left side. Except from the left-biased males, a percentage of males from the other directions (5.6% out of 31.7% for right, 2.3% out of 10.2% for front, and 1.1% out of 13.7% for back), after palpating, were moved away from the females without mounting (Fig. 2).

The lateralization of approaching ($\chi^2 = 19.0$, $df = 3$, $p = 0.003$) and departure ($\chi^2 = 9.6$, $df = 11$, $p < 0.001$) the females significantly affected the mating success of *L. oryzae*, while lateralization of mounting did not ($\chi^2 = 3.3$, $df = 2$, $p = 0.196$). In addition, regardless of the approaching, mounting, and departure side, *L. oryzae* males demonstrated a left-biased trend, resulting in higher copulation

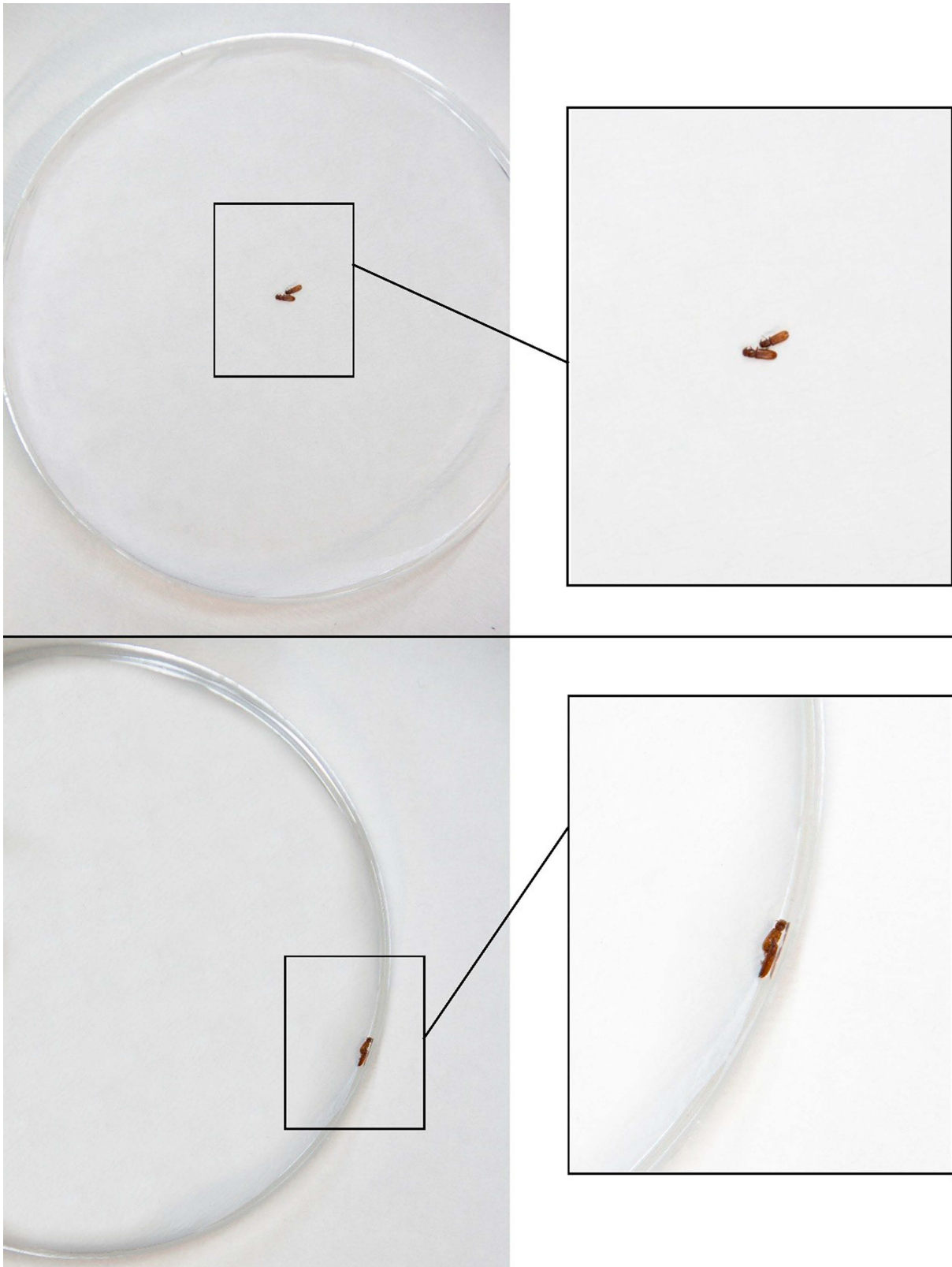


Fig. 1. (a) Pair of *Latheticus oryzae* that was incorporated in the analysis. (b) Pair of *Latheticus oryzae* near the walls of the arena, which was rejected from the analysis.

success compared to the right-biased, front-side, or back-side males. High mating success was observed in males that performed left-biased approaches ($\chi^2 = 26.7$, $df = 1$,

$p < 0.001$), mountings ($\chi^2 = 29.6$, $df = 1$, $p < 0.001$), and departures ($\chi^2 = 27.5$, $df = 1$, $p < 0.001$) (Fig. 3).

Concerning the duration of each phase, significant differences among sides (left, right, back, and front), were

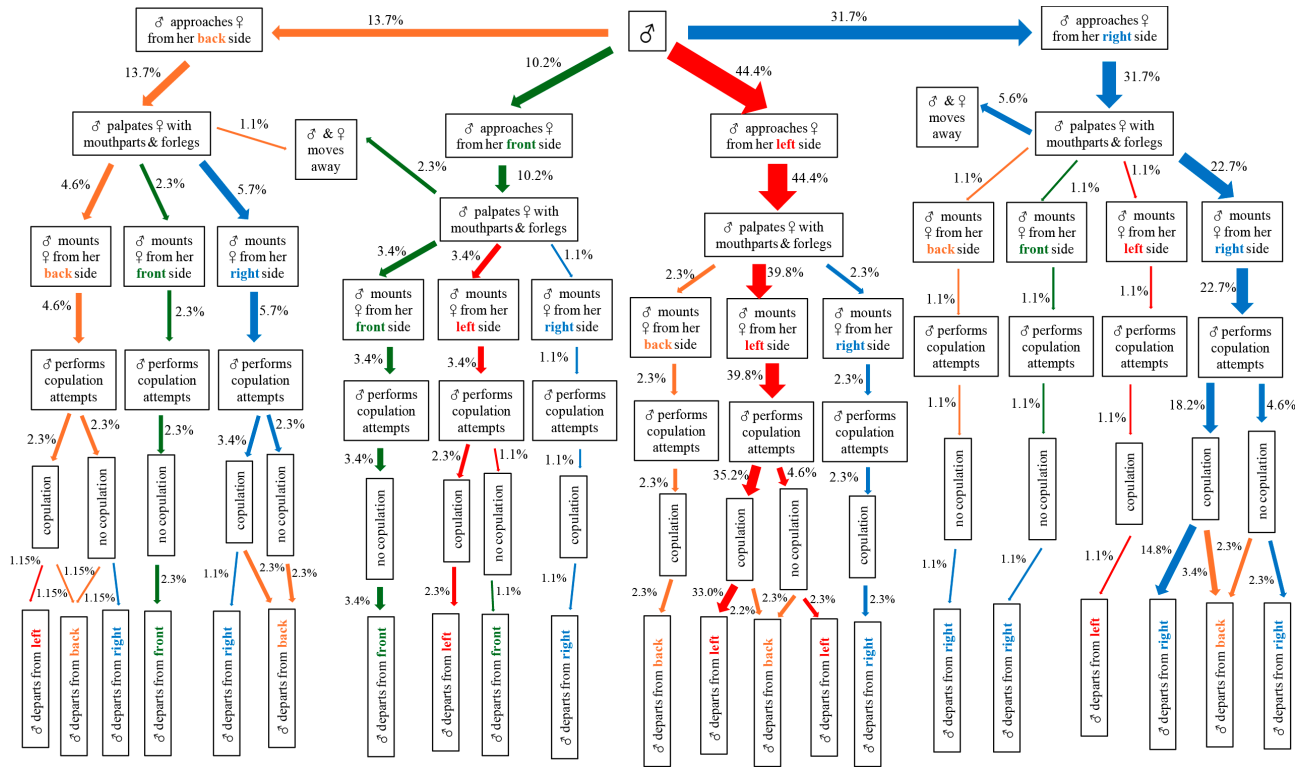


Fig. 2. Flowchart presenting the courtship and mating behavior of *Latheticus oryzae* male adults. The colors of the arrows – orange for back side approaches, green for front side approaches, red for left side approaches, and blue for right side approaches – indicate the various lateralized characteristics displayed by the males during each behavioral phase. The percentage of insects exhibiting each behavior is shown by the width of each arrow (n = 88 pairs).

detected in the duration within mate detection, copulation attempt, and copula regardless of the approaching, mount-

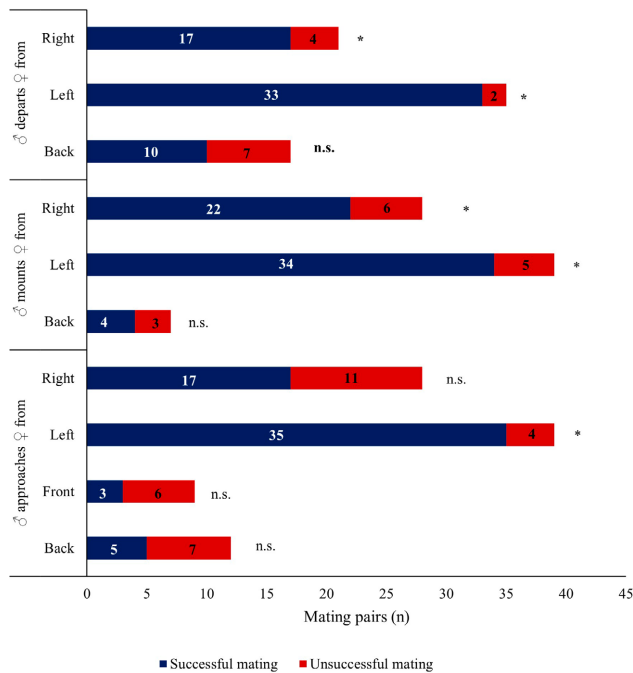


Fig. 3. Successful mating of males of *Latheticus oryzae*, performing or not, lateralized approaches, mountings, and departures. An asterisk (generalized linear model, binomial distribution, $p < 0.01$) denotes significant differences, whereas the acronym n.s. denotes non-significant differences.

ing, and departure side of males. The mean duration of the mate recognition was significantly shorter in left-biased males (108.3, 112.8, and 120.7 s, for approaching side, the mounting side, and the departure side, respectively) than the right-biased (171.5, 154.9, and 162.7 s, for approaching side, the mounting side, and the departure side, respectively), front- (189.1, 225.7, and 202.8 s, for approaching side, the mounting side, and the departure side, respectively) and back-side (245.3, 224.4, and 155.5 s, for approaching side, the mounting side, and the departure side, respectively) males ($\chi^2 = 27.5$, $df = 3$, and $p < 0.001$ for the approaching side, $\chi^2 = 18.4$, $df = 3$, and $p = 0.001$ for the mounting side, and $\chi^2 = 10.1$, $df = 3$, and $p = 0.018$ for the departure side). However, no significant differences were observed in the duration within the palpating phase and within the remaining phase (i.e., after the successful copulation, the male remained on the female), regardless of the approaching, mounting, and departure side of males (Fig. 4).

DISCUSSION

The current study is the first research effort that sheds light on the courtship and mating behavior of *L. oryzae*, highlighting the impact of lateralization and related behavioral asymmetries on successful copulation. The male recognizes the female, then approaches her and begins to palpate with his mouthparts and front legs. It then attempts to climb onto the body of the female and, once on top, tries to insert its genitalia into the female. After completing copulation and after removing the genitalia from the female, the

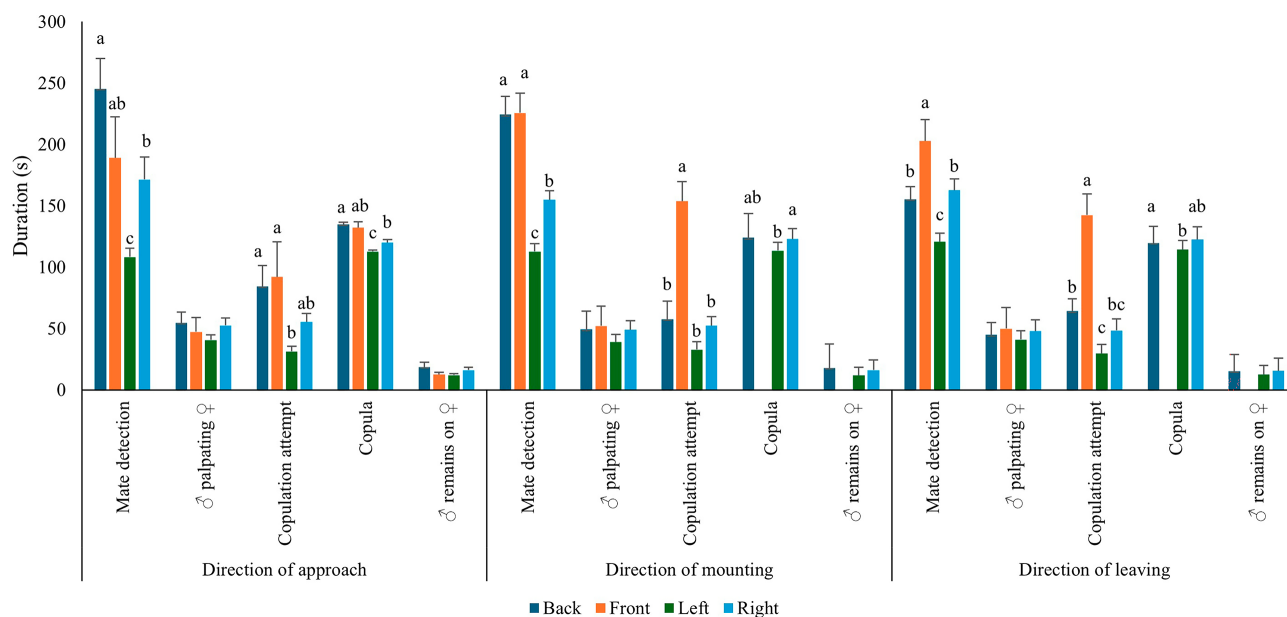


Fig. 4. Mean duration of different mating phases of *Latheticus oryzae* males performing or not, lateralized approaches, mountings, and departures. Within each phase, different letters indicate significant differences. There were no significant differences where no letters exist (Steel-Dwass test, $p < 0.05$).

male remains on top of the female for a while, palpating her thorax with his mouthparts, and then leaves.

Male *L. oryzae* consistently exhibited a left-biased tendency when approaching, mounting, and departing their mates, with this asymmetry being associated with higher mating success. The left-biased tendency has been reported in various studies related to other stored-products tenebrionids, such as *Tribolium castaneum* (Herbst), *T. confusum*, and *Tenebrio molitor* L. (Benelli et al., 2017; Boukouvala et al., 2019, 2021). At an ordinal level, species from other coleopteran families studied for their lateralization in courtship and mating behavior, appear to follow a similar lateral trend. *Cryptolestes ferrugineus* (Stephens) (Laemophloeidae), *Sitophilus zeamais* Motschulsky (Curculionidae), and *Sitophilus oryzae* (L.) (Curculionidae) also revealed a left-biased tendency during their courtship and mating process (Romano et al., 2016; Boukouvala et al., 2022, 2025).

Observing the duration of the courtship phases and the copulation success rate, certain left-biased advantages were revealed. Regardless of the approaching, mounting, or departure side, left-biased males of *L. oryzae* detected their mates significantly faster compared to the males using other directions. Additionally, in many cases, the duration of the copulation attempts was significantly lower for the left-biased males, compared to the other males. When Wang et al. (2021) studied the effects of the delayed mating on the reproduction of *Henosepilachna vigintioctopunctata* (F.) (Coccinellidae), they demonstrated that fecundity, hatch rate, pre-oviposition, and oviposition period percentages were negatively related to mating delay. Given that any difficulty or delay in the mate detection and duration of the copulation leads to decreased copulation rates and hinders population growth (Hopper & Roush, 1993; Hardy et al., 2005; Wang et al., 2021), these left-biased advantages may suggest the strengthening of the mating success

and species' population expansion. A similar trend was also observed for other species of Tenebrionidae (Benelli et al., 2017; Boukouvala et al., 2019, 2021), indicating that lateralized courtship may represent an evolutionary strategy (Rogers & Vallortigara, 2015; Siniscalchi, 2017) that takes place within this family. Moreover, the strong directional consistency observed – left-biased males not only approached females from the left side but also mounted and departed from side – demonstrates the possible presence of a robust lateralized behavioral pattern in *L. oryzae*. Such coordination suggests that mating behavior forms an efficient, interconnected sequence of the different mating traits that reduces the complexity of the necessary pattern of movements, consistent with the advantages of lateralization described in neuroethology (Rogers et al., 2004; Vallortigara & Rogers, 2005; Rogers et al., 2013).

In the stored-products environment, *L. oryzae* frequently coexists with other pests such as *T. confusum*, *Rhyzopertha dominica* (F.) (Bostrychidae), *T. castaneum*, or *C. ferrugineus* (Polnik, 1956; Castañé & Riudavets, 2015), all of them exhibiting lateralized mating behavior (Benelli et al., 2017; Boukouvala et al., 2019, 2020, 2022). Despite this common pattern, their total duration of mating sequence varies considerably. Left-biased *L. oryzae* males complete a whole mating sequence in approximately 300 s, a considerably shorter duration than the ~550-s sequence reported for left-biased *T. confusum* males (Benelli et al., 2017). When it comes to *C. ferrugineus*, the durational difference increases rapidly. Given that only the copulation phase of *C. ferrugineus* left-biased males lasts approximately 1668.0 s (Boukouvala et al., 2022), their total mating sequence (including mate recognition, precopula, and copula) greatly exceeds that of *L. oryzae*. However, when compared to *R. dominica*, the pattern is reversed; *R. dominica* males require about 111 s to complete a whole mating

sequence (Boukouvala et al., 2020), making their mating procedure notably faster than that of *L. oryzae*. Similarly, the duration of a whole mating sequence for left-biased *T. castaneum* males is ~150 s (Boukouvala et al., 2019). These findings suggest that in mixed infestations involving the aforementioned species, *L. oryzae* may achieve higher mating frequency and faster population growth compared to *T. confusum* or *C. ferrugineus*, but lower than *R. dominica* or *T. castaneum*. However, more experiments are needed to verify this hypothesis.

From a management perspective, the results of the present study may offer useful tools. For instance, on surfaces inclined in a specific direction (front, back, or right) than the preferred one (left) in conjunction with the use of attractants (e.g., food) (Rees, 2004), may reduce the mating success and eventually the population growth. However, till now, this is a hypothetical technique. It would be interesting to test these lateralization-based techniques in storages, taking advantage of all the available lateralized behaviors of the various relevant coleopteran species.

Overall, this study provides the first comprehensive description of the mating sequence and lateralized behavior of *L. oryzae*, revealing a functionally advantageous left-biased pattern, achieving fast mate detection, short copulation attempts, and high copulation success. These findings enhance the understanding of the reproductive procedure of *L. oryzae* and highlight the broader role of behavioral asymmetries in mating efficiency among stored-product pests. Importantly, the clear lateralized tendencies documented here may open new horizons for the supplement of the management strategies that exploit directional cues to disrupt the mating process. Continued exploration of lateralization across stored-product pests will be crucial for interpreting these behavioral insights into practical control applications within grain storage environments.

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CONFLICTS OF INTEREST. The authors declare that they have no conflict of interest.

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