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Mating behavior of the long-legged cricket *Eidmanacris meridionalis* Desutter-Grandcolas, 1995 (Orthoptera: Phalangopsidae)

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ABSTRACT

Pair-formation, courtship, copulatory, and post-copulatory behaviors of *Eidmanacris meridionalis* Desutter-Grandcolas, 1995, were described under laboratory conditions and compared with congeneric species and other Phalangopsidae crickets whose mating behavior has been previously studied. Field observations for the species are also reported. Mating behaviors were observed in *E. meridionalis* couples: they first remained motionless, and then began walking through the arena screening the substrate. Mating behavior started with antennal contact, followed by males positioning themselves in front of females, that, when receptive, mounted on the males back and started feeding on metanotum secretions of the males. Copulation (female-above-male position) started with the engaging of copulatory structures and stopped with couple detachment. The end-to-end position was observed once, right after couple detachment. Males always remained with the spermatophore, which was eaten after removal or, alternatively, left in the substrate. The main differences in mating behavior of *Eidmanacris* species regard the mating position and the duration of the reproductive stages, suggesting that other reproductive repertoires can be observed in the genus since 27 species have not yet been studied in regards their reproductive behavior. We can also assume that the morphological, genetic, and chemical diversity found among the species of Phalangopsidae reflects in the behaviors of pair-formation, courtship, copulation, and post-copulation, leading to a diversity of copulation positions, duration of the stages, methods of attracting partners and parental investment. The description of Phalangopsidae mating patterns can provide important information for future evolutionary and phylogenetic studies, apart from useful for distinguishing cryptic species.

Introduction

Crickets (Orthoptera: Grylloidea) are a diverse group of insects, with *ca*. 6,000 species distributed worldwide, except for the poles (Cigliano et al., 2023). Despite their potential for testing hypotheses regarding sexual selection, when we consider the diversity of this group, particularly Neotropical crickets, their reproductive and agonistic behaviors have been the object of few studies (Ręk, 2012; Gray and Cade, 2000; Bunting and Hedrick, 2018). The lack of such studies is even more striking if Phalangopsidae, the third most diverse cricket family, is considered (Cigliano et al., 2023).

The reproductive behavior of only 13 out of the 1093 known species of Phalangopsidae have been studied so far (Alexander and Otte, 1967; Dambach and Lichtenstein, 1978; Boake and Capranica, 1982; Boake, 1984a, 1984b; Heinzel and Dambach, 1987; de Mello and dos Reis, 1994; Nischk and Otte, 2000; Gnaspini and Pelegatti-Franco, 2002; Prado, 2006; de Mello, 2007; Zefa et al., 2008; Souza-Dias et al., 2015; Lunichkin et al., 2016; Fianco et al., 2018; Acosta et al., 2020). Although the number of species that had their reproductive behavior studied remains quite low, behavioral patterns involving pairing, courtship, copulation, and post-copulation are quite diverse, suggesting that behavioral plasticity might be much more complex. Thus, new behavioral patterns are expected to be discovered while new species are studied, especially in the highly diverse Neotropical region.

With 29 known species described so far, *Eidmanacris* Chopard, 1956 is the most diverse genus of Luzarinae (Phalangopsidae) crickets (Cigliano et al., 2023), and inhabits the Atlantic Forest, Cerrado and Chiquitano Dry Forest (de Campos et al., 2021). Most species within the genus are large, with marbled coloration, and short, coriaceous tegmina which only cover the metanotoum structures (de Campos et al., 2017).

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Thus, these crickets do not stridulate, using other strategies to attract co-specific females (Prado, 2006).

Metanotal structures produce secretions that are transferred to females during copulation as a nuptial gift (Alexander and Otte, 1967; Brown, 1997; Bussière et al., 2005; Lewis and South, 2012). It is noteworthy that such structures are absent in *E. fusca* Desutter-Grandcolas, 1995 (the species unidentified in de de Mello, 2007), which has a phallic sexual plug that prevents the female from mating with other males, leading both males and females to develop complex mating strategies (de Mello, 2007).

Here we describe the mating behavior of *Eidmanacris meridionalis*, highlighting pair-formation, courtship, copulatory, and post-copulatory behaviors. We also compared these behaviors with another *Eidmanacris* species and some Phalangopsidae species that have been studied to date, and then providing a summary of the mating behaviors exhibited by these species.

Methods

Species model

Eidmanacris meridionalis is straminicolous crickets, living inside small natural cavities during the day, and being active in the litter at night (de Campos et al., 2021). This species is characterized by its dark brown coloration with black and ocher spots, whitish brown antennae with white stripes, and male tegmina with a thickened apex. The female (Figure 1A) is larger than the male (Figure 1B) and presents a very short tegmina. For an extensive review of the *Eidmanacris* genus, see Desutter-Grandcolas (1995) and de Campos et al. (2017).

Sampling and rearing

Nymphs and adults of *E. meridionalis* were collected in the Parque Nacional do Iguaçu (Iguaçu National Park), at the Macuco Safari (lat: 25.650367ºS; lon: 54.439544ºW) and the Poço Preto (25.627344ºS; 54.461779ºW) trails, Foz do Iguaçu, Paraná State, Brazil. Active nocturnal samplings were performed between January 2018 and April 2019. After sampling, the individuals were sent to Laboratório de Orthoptera, Universidade Estadual do Oeste do Paraná (UNIOESTE) and kept in a climate-controlled room, with a temperature of 25±2°C, humidity varying between 60% and 75%, and 12-hour light/dark photoperiod. Adults (males and females) were stored in boxes having sand as substrate, with abundant food and water, and provided with egg cartons as shelter, so that they could mate and reproduce. Nymphs were individualized and reared until they became adults. From January 2018 to March 2020, over 800 individuals were kept under laboratory conditions.

For the experiments, 120 males and 120 females were isolated in 500 ml plastic vials (10 cm height and 15 cm diameter), each of them having part of its lid replaced by a fence mesh screen to ensure ventilation. Filter papers and egg cartons were provided respectively as substrate and shelter in these vials. We then offered water (a moistened cotton) and food (fish food flakes, banana, and vegetables) in open dishes (0.5 cm height and 2 cm diameter) *ad libitum*. The experiments were carried out only using virgin adult males and females, acclimated for at least 15 days to the laboratory, and each individual was studied only once, contributing with a single set of observations.

For the observation and description of pair-formation, courtship, copulatory, and post-copulatory behaviors, 55 separate couples of *E. meridionalis* were attracted, and then, we placed each couple to mate in a cleaner glass arena (20 cm long X 15 cm wide X 15 cm high) covered with filter paper as substrate. Males and females were placed on opposite sides of the arena under disposable plastic cups for one minute aiming at their habituation. After this period, the cups were removed, and the behaviors were observed and recorded with a digital camera. We interrupted the encounter five minutes after its beginning if no courtship was observed. If courtship occurred, we interrupted the encounter if copulation was not observed in 15 min. Observations continued for 10 min after copulations to check post-copulatory behaviors.

Pair-formation, courtship, copulation, and post-copulation of *E. meridionalis* have been timed, reporting mean values, standard deviations, and ranges for all recorded behaviors. We then created an ethogram, which describes mating behavior sequences. We removed some copulatory papillae from mated females and remated some of them to observe whether mated females exhibit papillae obstructed by spermatophores, described as female monopolization by de de Mello (2007).

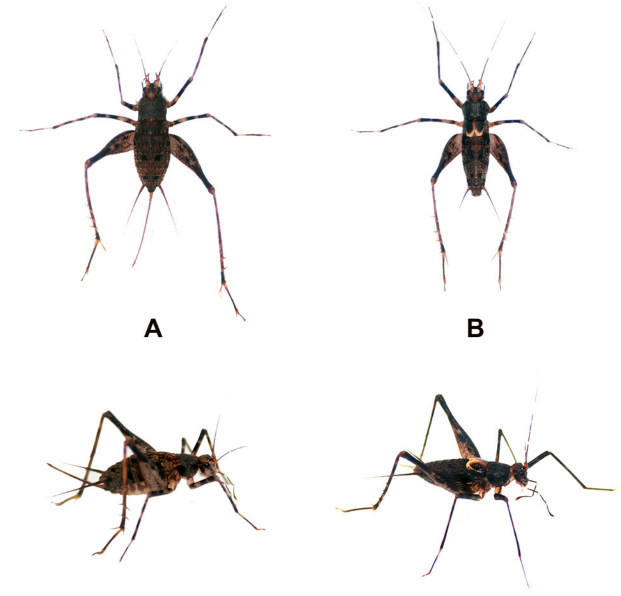

Figure 1. Dorsal and lateral view of *Eidmanacris meridionalis* Desutter-Grandcolas, 1995. A) Female. B) Male. Photo: LC Macarini.

Finally, some behaviors of males, females, and couples observed during field expeditions were reported (between January 2018 and April 2019). We did not time these behaviors because the field conditions were unfeasible and/or because even the subtlest movements made by the researchers caused a sharp response of individuals (the behavior was interrupted, and they escape).

Results

Fifteen out of the 55 recorded encounters resulted in complete copulation (pair-formation, courtship, mating, and post-copulation behaviors). When copulation failed (n = 40), females rejected the males (n = 9), or the encounters were interrupted because there was no courtship (n = 15) or copulation (n = 16).

After removing the plastic cups, the male and female remained motionless for 32.13 s ± 50.60 (4 - 199, n = 15) and then, began walking through the arena touching the substrate with the antennae until the pair was encountered. While male and female walked alone, they randomly passed their antennae, hind-tibiae, and hind-tarsi through mouthparts (Figure 2a) and continued inspecting the substrate with their antennae. The first female/male antennal contact occurred either with any body part of each other (n = 8), when then, the couple quickly took the face-to-face position, or the first antennal contact already occurred when they were adopting the face-to-face position (Figure 2b; n = 7). The first female/male antennal contact occurred 87 s ± 66.72 (35 - 254, n = 15) after the plastic cups were removed.

After taking the face-to-face position, male and female vibrated their antennae both dorsoventrally and laterally, at an approximate angle of ca. 45° (hereinafter related to the horizontal crickets' body axis), a behavior that have lasted for 8.7 s ± 4.60 (3 - 17, n = 15). After recognizing antennal contact, males positioned themselves in front of the females, raising their tegmina at ca. 90°, and exposing the metanotum (Figure 2c). When receptive, the females touched the male's abdomen, metanotum, and tegmina with their maxillary palps (Figure 2d, n = 15), and started to mount on the male's back. In five encounters, the females did not immediately accept the males, and started walking through the arena. The males then followed the females, positioning themselves again in front of the females, while keeping their tegmina raised and exposing the metanotum, until the females touched the metanotum surface with their antennae, and climbed on the male's back. The time elapsed from the moment the male positioned himself in front of the female to the moment the female mounted on the male's back lasted 99.33 s ± 145.37 (6 - 560, n = 15).

After touching the male metanotum with its maxillary palpi, the female started feeding on the secretions released by the males' metanotum (Figure 2e). While feeding, the females bit the male tegmina, and five females bit the male hind femora as well. After 77.93 s ± 27.51 (33 - 145, n = 15) from when females started feeding, the males exposed the spermatophore, which began to crystallize, gradually becoming translucent and rigid (Figure 2f). After exposing the spermatophores, the females continued to feed on the secretions from the male metanotum. During this period, the males remained motionless for an average duration of 206.86 s ± 116.41 (38 - 417, n = 15), except when bitten by the females. In response to females' bites, the males would move their abdomen and tegmina laterally, as well as slightly adjust their forelegs. After that, the males began to stretch their abdomen, almost doubling their size, remaining 5 s ± 3 (2 - 8, n = 33) with their abdomen stretched and motionless (Figure 2g).

Copulation started when males performed rapid dorsoventral movements of their entire abdomen, moving downwards both the genitalia and the female subgenital plate, and engaging their phallic complex to the female copulatory papilla. Once attached, males performed rapid anteroposterior movements, followed by dorsoventral movements of the pseudepiphallic parameters in an in-and-out sequence, while females continued to feed on metanotum secretions (Figure 2h).

While copulating, four females left the mating position and began walking randomly around the arena, even though they were connected to the males, who followed the females, preventing them from detaching (*i.e.*, the females dragged the male for a few seconds, detaching right after). One female moved abruptly, trying to detach herself from the male; as the decoupling failed, the pair assumed the end-to-end position, then detaching quickly. Copulation lasted 518.33 s ± 228.10 (142 - 850, n = 15), considering the interval between couple attachment and detachment.

Post-copulation behavior started after the couple detached. The male remained with the spermatophore in all encounters, removing it by rubbing the terminal part of their abdomen against the substrate. Five males ate the spermatophore (Figure 2i) while the others left it in the substrate. After removing the spermatophore, the males walked randomly through the arena, screening the substrate with their antennae. The females also walked randomly (n = 8), screening the substrate with their antennae. Even detached, the females remained on the males' back, in the copulation position, in seven pairing, feeding on metanotum secretions. In all encounters, there were subsequent copulation attempts, which initiated with antennal contact and recognition. The sequence observed in five rematings was the same as described above, including the overall elapsed time of each event. For this reason, we interrupted the observations of rematings and did not include them in our analysis.

In the field, males often positioned themselves in cleaner places, near sites with litter or shrubs (n = 40). At these sites, the males changed the direction of their bodies intermittently, always raising their tegmina two or three times, and passing their antennae over their mouthparts. In general, larger males were always surrounded by at least four to seven females (n = 12), while smaller males attracted no more than three females (n = 8). Larger females always seemed to mate (n = 12), while the smaller ones screened the substrate and showed grooming behavior (n = 30). It was not possible to observe a complete copulation or mating of males with females around, because our movements always caused either the interruption of the cricket behavior or their escape.

We found no visual evidence of female monopolization (sexual plug) because the copulatory papillae morphology of virgin and non-virgin females was always visually similar (n = 8). Additionally, copulation was always successful when non-virgin females were placed to copulate more than once. These two factors are indicative of the absence of a sexual plug in *E. meridionalis* which has been reported only for *E. fusca* (de Mello, 2007).

As the reproductive behavior in Phalangopsidae has been analyzed using different methodologies by different authors using different methodologies, we propose that further studies analyze and describe at least the following stages: pair-formation, courtship, copulation, and post-copulation. In view of these stages, we summarized the behavior of the 13 species of Phalangopsidae that had some stage of reproductive behavior analyzed so far (Table 1).

Discussion

Male crickets are known for their songs, using acoustic signals to attract females to mate. However, males of non-stridulating species may use substrate vibrations (de Mello and dos Reis, 1994), specific pheromones (Kortet and Hedrick, 2005), or cuticular hydrocarbons (Thomas and Simmons, 2011) to attract females for mating. Males of *E. meridionalis* did not exhibit body vibrations, as recorded for *Adelosgryllus rubricephalus* (Zefa et al., 2008) and *E. corumbatai* (Prado, 2006), or substrate drumming as in *Vanzoliniella sambophila*

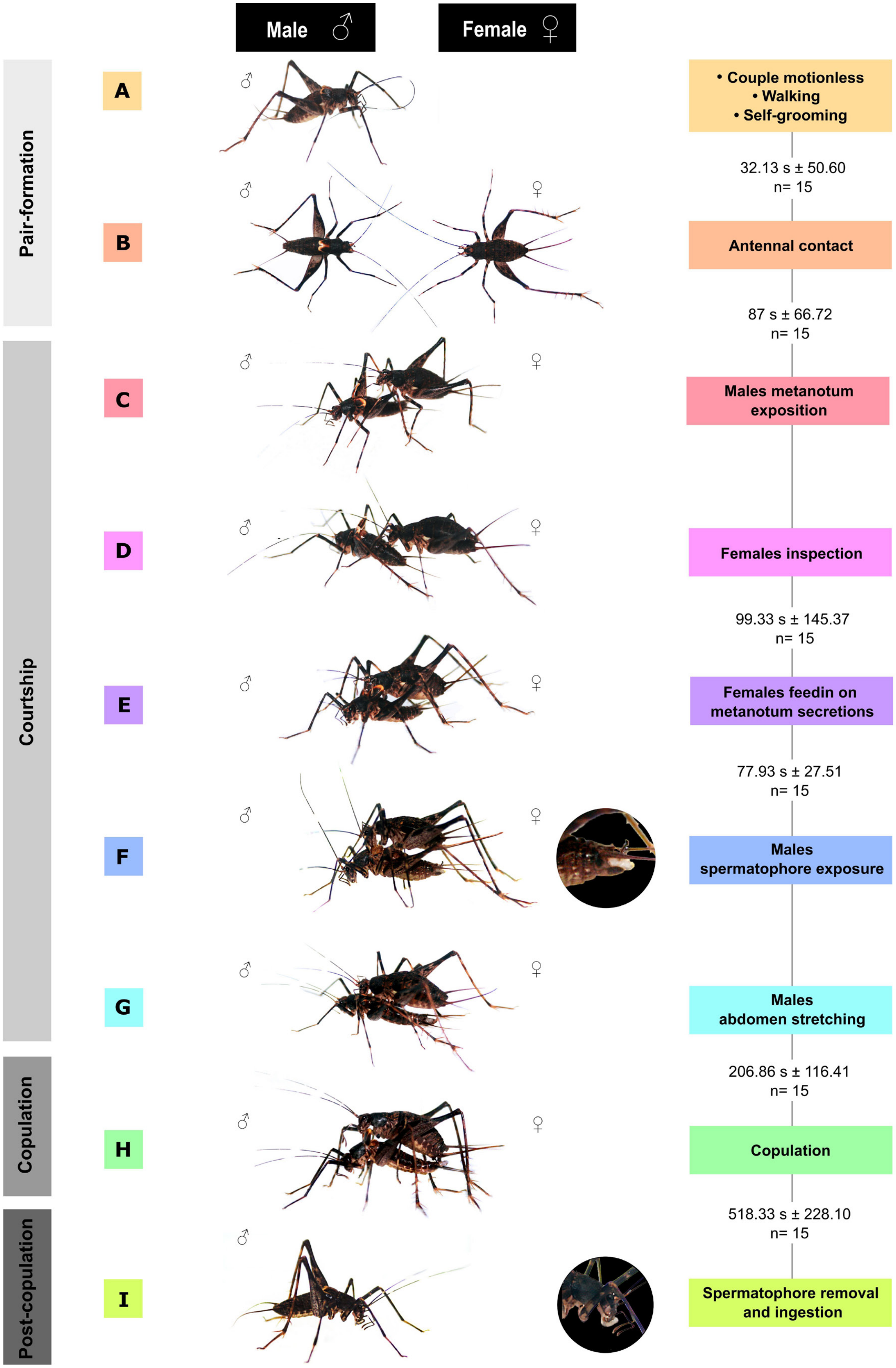

Figure 2. *Eidmanacris meridionalis* mating behavior. A) males and females screening the substrate and self- grooming; B) antennal contact between males and females; C) males in front of the females, with their tegmina raised showing the metanotum; D) receptive females touching the abdomen, metanotum and tegmina of males with their palps, than mounting on the male's back; E) females feeding on the males metanotum secretions; F) exposition of the spermatophore by males; G) males stretching its abdomen, almost doubling its size; H) copulation; I) males remain with the spermatophore, which once removed, can be eaten or leave on the substrate.

Table 1
Summary of the mating behavior of Phalangopsidae species whose reproductive behavior has been studied by several authors so far, involving pairing, courtship, copulation and post-copulatory actions. The described actions represent the transcription of the behaviors presented by the authors.

	Pair-formation	Courtship	Copulation	Post-copulation	Source
Nemoricantor maya (Hubbell, 1938)	Not described.	The couple adopts a facing position while the male chirps quite regularly, with the tegmina held in an almost vertical position, occasionally moving his body up and down. The male exposes the spermatophore, lowers his tegmina, turns around, and raises his tegmina again towards an upright position, chirping if the female does not mount immediately after his turn. By touching her palps or tarsi on the male's back, the female encourages the male to extend and lift the terminal portion of his abdomen, extruding his genitalia under the female, which, at the same instant, advances on him.	The male attaches his genitalia in the female genitalia performing several upward thrusts of his abdomen before becoming motionless. Male holds his wings a bit forward from vertical, and the female's head is held motionless behind the wings, as well as the male's and the female's antennae are held in an almost vertical position. Copulation lasted almost seven minutes.	The female suddenly leaves the mating position, and the male retains the spermatophore, removing it by dragging the end of his abdomen on the substrate, while the female remains stationary nearby. While eating the spermatophore, the male begins to stridulate and, after ingesting the spermatophore, the male reestablishes antennal contact with the female and continues to stridulate. A new spermatophore can be produced within five minutes from the end of mating. However, no remating was observed during the observations period, *ca.* 24 min.	Alexander and Otte (1967), Boake (1984a)
Phaeophilacris spectrum (Saussure, 1878)	The couple touches the antennae, and the male starts flapping his wings several times, and in an unusual way, while the females behave passively even when touched by the male. Antennae contact, called "antennae play", can occur after the male examines the female, and this behavior precedes courtship.	The male raises the tegmina up to more than 90º, inclines his body, and moves his tegmina towards the female, positioning himself in front of the female. The male then lowers the abdomen to the base and slightly spreads the wings. The female touches the male several times, while the male pushes himself further and further back, placing himself under the female with the tegmina vertically oriented.	Copulation begins with the coupling of the genitalia and introduction of the spermatophore duct into the female's genital papilla. Then the male strokes, rhythmically and at short intervals, the female's abdominal flanks. Copulation ends with the couple's decoupling. Copulation can last up to 75 min.	After decoupling, the male removes the spermatophore by dragging his abdomen on the substrate and eats it.	Dambach and Lichtenstein (1978)
Vanzoliniella sambophila de Mello & Cezar dos Reis, 1994	The males touch their antennae to any part of the female's body, stay still for a few minutes, and then begin again to touch the female's body with their antennae.	With the head turned towards the female, the male raises his tegmina about 45º and begins to stridulate. This behavior can last for hours if the female is not receptive. Along with the emission of acoustic signals, the male performs two or three drumming sequences of drumming on the substrate. If receptive, the female touches her antennae on the male's body and touches her forelegs on the male's back. When touched by the female, the male rotates 180º, directs his terminalia to the female positioning his tegmina over his head, exposing the metanotum and tergal glands. The female palpates her back and begins to feed on the secretions released in the metanotum.	The female everts the copulatory papilla, while the male couples his genitals to the female's, initiating copulation. During copulation, the male maintains his tegmina positioned over his head while the female feeds on the secretions released in the metanotum. Copulation does not occur if there are no leaves in the arena, which allows forelegs drumming by the male. Copulation can last up to 57 min.	Not described.	de Mello and dos Reis (1994)
Luzarida recondita (Nischk & Otte, 2000)	Not described.	The male begins to produce acoustic signals (trills), pointing his abdomen towards the female. With his tegmina raised, the male exposes the metanotum and then produces a new sequence of trills. The female then mounts onto the male from behind and began to feed on the secretions released in the metanotum.	The male couples his genitals to the female's genitals, copulation begins, and the couple remains in this position for 20 min. After this time, the female stops feeding on the secretions released in the metanotum and tries to detach herself from the male. Otherwise, the couple remains connected by the genitalia, but no longer in a copulation position. The pair remains in this position for 20 min and then the male separates from the female. The copulation lasts about 40 min.	Not described.	Nischk and Otte (2000)

Table 1
Continued...

	Pair-formation	Courtship	Copulation	Post-copulation	Source
Strinatia brevipennis Chopard, 1970	Not described.	Female feeds over the male.	The male's terminalia is directed towards the female's terminalia. The male produces the spermatophore, places it in contact with the female terminalia, then transferring the sperm. Copulation lasts about 1 hour.	The male rubs his abdomen against the substrate, removes the spermatophore and eats it.	Gnaspini and Pelegatti-Franco (2002)
Endecous (*Endecous*) *itatibensis* Rehn, 1918	Not described.	The male raises his tegmina vertically and begins to stridulate. Then he stops stridulating, turns his abdomen to female and starts stridulating again. The female mount over the male's back and begins to feed on the secretions released in the metanotum, while the male remains with the tegmina vertically oriented.	The authors mention that the mating behavior resembles the behavior observed in *Strinatia brevipennis*.	The authors mention that the post-copulation behaviors are like such observed in *Strinatia brevipennis*.	Gnaspini and Pelegatti-Franco (2002)
Eidmanacris corumbatai García-Novo, 1998	The pair-formation behaviors were described based on the combination of two males and several females, as there was no copulation in the other pair combinations. When placed together, males and females remained immobile for about 2 hours before antennal contact.	After sexual recognition, the males began waving their whip-like antennae. Initially, the females did not respond to the males and continued walking around the container, feeding and grooming themselves. The waving of the antennae was sometimes interrupted for a few seconds and, in addition to this movement, the males also shook their bodies and drummed the bottom of the container with one of their forelegs.	About 2 h after courtship began, the dominant male was approached by a female who made antennal contact. The female then stopped antennal movement and became indifferent to the male's behavior. The male turned 180º, directing his genitalia to the immobile female, which only showed interest in climbing on the male's back when the male raised her tegmina to 180º and exposed the metanotum. The female touched the male's back with her antennae and tried to climb on the male, who moved away a few millimeters (inciting behavior). Soon after, the female climbed onto the male and began to feed on the secretions released in the metanotum. During this period, the male exposed the spermatophore and inserted it into the female's genitalia. After 5 minutes, the female stopped feeding and dismounted from the male, even if remained connected by their genitals (end-to-end) for about 60 minutes. During this time, the male would shake his body rapidly.	Not described.	Prado (2006)
Aracamby de Mello, 1992	Not described.	As the female's integument dried and hardened, an adult male began a brief courtship (seconds).	As the female did not respond to courtship, the male turned to her, slid his terminalia under her body and quickly attached his genitalia to hers. In the three observed cases, the females, with the body wall still very soft, tried to move and free themselves, but the copulation continued until the males released them.	It is only reported that two of the females began to lay eggs within a few weeks from forced copulation and produced offspring.	de Mello (2007)
Adelosgryllus rubricephalus Mesa & Zefa, 2004	When placed together, the male was always more active than the female. The male walks a lot around the arena, palpating and antennating substrate, reaching the female and antennating her body.	After antennal recognition, the male initiates different types of intermittent behaviors: medio-lateral vibration of the antennae, anteroposterior spasms, and stridulation, always turning its abdomen towards the female. During the courtship, the receptive female approaches and touches the male's abdomen, cerci, or forelegs with her hindlegs or palps. The male then exposes the spermatophore, always after the female's contact. After the extrusion of the spermatophore, the male continues vibrating his antennae, shaking his body and stridulating intermittently, while the female intensifies her drumming.	After courtship behavior, male walks back underneath female, (female-above position), the couple attaches, and the male transfer the spermatophore. In the copulating position, male maintain his tegmina inclined forward, and female's head is held behind male forewings. Both male's and female's antennae are held motionless forward, and eventually the male lifts his abdomen tip thrusting against the female's abdomen. After female steps off male, both perform a brief end-to-end position. Copulation last ca. 6.7 min.	There is no guarding behavior, and the male retains the spermatophore, bends his body to picks it up and eats it immediately. A few minutes later, male starts courtship behavior again.	Zefa et al. (2008)

Table 1
Continued...

	Pair-formation	Courtship	Copulation	Post-copulation	Source
Pizacris zefai (Mews & Sperber, 2010)	Not described.	Not described.	This species copulates in the female-above position with the male having the tegmina raised. During mating, the female touches the male's back, head and pronotum with the maxillary palps and the ventral surface of the male's tegmina with the labial palps, while the female's copulatory papilla is everted and attached to the male's genitalia. The female then touches the ventral surface of the male's elevated tegmina with her mandible.	Not described.	Souza-Dias et al (2015)
Phaeophilacris (*Speluncacris*) *bredoides* Kaltenbach, 1986	Reproductive behavior started after an indifferent phase of 30-60 s duration, during which the male showed no detectable response towards the female. The male starts looking for the female and stops within 50–80 mm of her, with his head towards the female, and the pair arranged at an angle of 30–90°. If the angle is < 70°, the male adjusts his head so that the female is positioned between the male's antennae. The male turns and follows the female whenever she moves, targeting the female positioned between his antennae. If the female tries to escape, the male chases after her.	The male touches the female with his antennae, performing balance movements, and then the male performs characteristic wing movements towards the female. If the female does not respond to these stimuli with antennal contact, the male moves around the female, makes fanning movements, and shifts "from one leg to the other", with his head invariably facing the female. In response to this "courtship", the female turns to the male, if not already in that position. Male and female are positioned head-to-head, aligned and the distance between them decreases to 10-20 mm, and antennal contact occurs between them. During this phase, the male sometimes performs wing movements. In the following pre-copulatory phase, the male initiates regular synchronous lateral movements of the cerci. These movements continued indicating readiness for copulation until the end of reproductive behavior. Sometimes the pre-copulatory phase was observed before mutual alignment. This phase, like the previous one, may include wing movement. In response to "courtship", the female assumes the copulation position. For the couple to assume the copulation position, the male turns to bring the tip of the abdomen closer to the female's head, correcting its position in relation to the female, feeling her with the antennae. After this turn, the male's antennae are directed backwards, touching the female. After the turn, the male assumes the copulation position, moving backwards trying to stay exactly under the female, swinging his body and forcing the female to mount his back. At the same time, the male raises his tegmina by 90-120° in relation to the body. The female's abdomen is positioned between the male's cerci, aligning her genitalia with the male's genitalia.	The copulation phase begins with the coupling of the couple's genitals. The male then jerks upward with the tip of the abdomen until mating occurs, and several seconds later the spermatophore is released and sperm transfer begins. During mating and spermatophore transfer, the male stimulates the female's abdomen with lateral movements of his siccas. Copulation lasts 65 min.	At the end of copulation, the female detaches from the male with an upward movement. During the entire sequence of reproductive behavior, the female is relatively passive, while the male is more active, performing wing beats, rocking, antennal touches, and stimulation from the female's sieges. These movements seem to prevent the receptive mature female from finishing mating.	Lunichkin et al. (2016)

Table 1
Continued...

	Pair-formation	Courtship	Copulation	Post-copulation	Source
Endecous (*Endecous*) *chape* Souza-Dias & de Mello, 2017	Both the male and female walked through the arena touching the substrate with antennae and maxillary palpi. Males scavenged the substrate more actively than females, displaying grooming behavior while scavenging the substrate. The first contact between male and female occurs through mutual antennation on any part of the other's body.	After antennal contact, the males initiated courtship by placing themselves next to the female and touching her tergites, ovipositor, or cerci with their antennae or forelegs. At the same time, the male elevated its tegmina about 80° and stridulated intermittently. The female touched the male cerci or tergites with her antennae, sometimes kicking the male's antennae and body with her hindleg, while the male continued to stridulate intermittently. During this time, the male slowly neared the female and performed a series of sudden but mild anteroposterior vibrations with his body, touching the female's abdomen, cerci, and hind femora with his hind tarsus. The male also moved its cerci up and down, and slightly lifted his abdomen. During the courtship stridulation, the male can partially evert its genitalia, and slowly positioned themselves to show its backs to the female, exposing the spermatophore. Alternatively, the male can expose the spermatophore even when in the mating position. Copulation lasted ca. 11 min.	The male walked backwards with the abdomen touching the substrate, elevating its tegmina about 130°, positioning itself under the female and assuming the mating position (female-above). During mating positioning, the female moved her subgenital plate downward and the male engaged its phallic complex with the female's genitalia. During copulation, the male performed ascending and lateral movements of the cerci. Mating ended when the female separated from the male, taking no specific position.	After the couple separated, the male retained the spermatophore, removed it using its hind tibial spines The spermatophore was then eaten. Post-copulation songs can be emitted by the male right after the couple separation. The male can also begin another courtship, stridulating and producing another spermatophore.	Fianco et al. (2019)
Endecous (*Notendecous*) *onthophagus* (Berg, 1891)	After the couple was released in the arena, they both moved around, antennating the substrate until they adopted a direct visual orientation. Antennal contact on any part of their bodies started when they found each other. The male then started courtship after antennation.	The courtship is characterized by two stages: (1) pre-spermatophore extrusion: females walked slowly while the males followed her, antennating her body, and stridulating intermittently; the females lightly kicked the male with its hind legs whenever the male had approached too close to her; a few moments before spermatophore extrusion, they remained motionless and close to each other until the male completely extruded the spermatophore; the authors named this behavior as "male-follows-female". (2) post-spermatophore extrusion: at this stage, it was the female that followed the male, maintaining antennation while the male walked very slowly, and sporadically stridulating; when the female got closer to the male, she groped his abdomen, hind legs, and cerci using her antennae, palpi and forelegs; the female tried to take the spermatophore from the male, who responded by quickly moving away or by lightly kicking the female; the behavior "female-follows-male" was observed in nine of the 13 encounters.	The male moved itself backwards positioning underneath the female to take the "female-above" position, while the female, in turn, raised her body. In the copulation position, the males kept the tegmina inclined forward, over his head, and lifted his abdomen tip trying to attach the pseudepiphallus to the female's subgenital plate. During copulation, the female kept her hind legs between the hind legs of the male, and both positioned their antennae forward, longitudinally, and only the female moved them slowly, while male moved his cerci sporadically. Copulation lasted ca. four minutes.	The copulation ended either with the female pushing down the male's abdomen with her hind legs and then stepping off the male in a side movement, or when the female left the copulation position by suspending her body and stepping off the male with a side movement, without using the hind legs to push down the male's abdomen. The male remained with the spermatophore attached to its genitalia after the copulation. The male removed the spermatophore using the spines of the tibia III or by scraping the terminalia on the substrate, whey the spermatophore is or is not eaten by the male. The male kicked the female when she approached during spermatophore removal.	Acosta et al. (2020)

Table 1
Continued...

	Pair-formation	Courtship	Copulation	Post-copulation	Source
Eidmanacris meridionalis Desutter-Grandcolas, 1995	The couple remained motionless for a while (32.13 s ± 50.60 s), and then began walking scouring the substrate with the antennae and performing self-grooming until the pair met.	The first antennal contact occurs in any body part, the couple then assuming the face-to-face position; the first antennal contact, however, could occur directly in this position. Male and female vibrated its antennae both dorsoventrally and laterally, at an approximately angle of 45. Male positioned themselves in front of the females, raising its tegmina at 90°, exposing the metanotum. The female touches the male abdomen, metanotum and tegmina with its maxillary palps and started to mount on the male back. When the female has not immediately accepted them, the male followed the female, positioning themselves again in front of the females, keeping his tegmina raised. The time the females took for positioning and mounting on the male's back was 99.33 s ± 145.37 s. Females started to feed on the metanotum secretions, and while biting the males' tegmina and hind femora (77.93 s ± 27.51 s). Males exposed the spermatophore, which began to crystallize, gradually becoming translucent and rigid, while the male remained motionless, unless he was bitten by the female, so he slightly moves the abdomen, tegmina and/or forelegs (206.86 s ± 116.41 s). The male then began to stretch its abdomen while remaining motionless (5 s ± 3 s).	Male performed rapid dorsoventral movements of the abdomen, and, using its genitalia, pull the female subgenital plate downwards, to engaging its phallic sclerite to the female copulatory papillae. When such structures were attached, male performed rapid anteroposterior and dorsoventral movements, in an in-and-out sequence, while female continued to feed on the secretions released in the metanotum. Female can leave the mating position, even when they were connected to the male. Copulation ended when the detachment of the couple has occurred.	This phase starts after the couple detaches. In all encounters, the male remained with the spermatophore, removing it by rubbing the terminal part of his abdomen against the substrate. Some males ate the spermatophore and others merely left it on the substrate. The male then walked randomly through the arena, screening the substrate with its antennae. The female performs the same behavior, but could remain on the males' back, feeding on the secretions released in the metanotum. Males could eventually try to start subsequent copulation attempts, which have initiated with antennal contact.	This paper.

(de Mello and dos Reis, 1994). This may indicate that females must be primarily attracted by pheromones released by males. However, the arena in which the experiments were carried out might have been too small and so the identification/attraction of partners might have been visual, with males and females moving until they met and recognized themselves through antennation. Our field observations, however, suggest that male pheromones could be able to attract long distant females, because males lifted their tegmina intermittently and changed their body direction sometimes. Additionally, pheromones can be dispersed over long distances, and although they are condition-dependent, they can reflect the key components of an individual's somatic state, which could explain why larger males attracted more females than smaller ones (Chemnitz et al., 2015). Raising tegmina could also be a similar mechanism for attracting long distant females, a behavior that was already described for *Phaeophilacris* in Africa: when males raise their tegmina, they also blow their pheromones (Heidelbach et al., 1991; Heidelbach & Dambach, 1997). Alternatively, the intermittent raising of tegmina observed in the field could be a visual signal/ sexual visual display for females, since the tegmina show yellow light spots, especially at short distances. Still, females at the end of the reproductive cycle could even respond to the call of males, which includes courtship, territorial behaviors, and morphological cues, however when observing it, can decide or not to mate with it (Fianco et al., 2018; Prado, 2006).

Grooming behavior occurs before antennal contact, increasing the olfactory activity of the antennae (Böröczky et al., 2013), and impregnating it with contact pheromones, allowing for sexual recognition (Alexander, 1962; Otte and Cade, 1976) and pair formation. Antennal contact also provides clues on partner fitness (Simmons, 1990; Balakrishnan and Pollack, 1997; Tregenza and Wedell, 1997; Sakura and Aonuma, 2013) and age (Rodríguez-Muñoz et al., 2019), representing an important driver for starting reproductive behaviors in *E. meridionalis*.

Courtship in Phalangopsidae is quite variable, ranging from male stridulation to behaviors such as tegmina movements towards the female, substrate drumming, waving of antennae, and exposure of the spermatophore and the metanotum structures (see Table 1). The different courtships reported in only a few Phalangopsidae species studied so far reflect the diversity of the group and the need for more behavioral studies in order to understand the evolutionary history of mating behaviors in this group, and to test hypotheses regarding sexual selection.

Different copulatory positions have also been reported in Grylloidea (Alexander and Otte, 1967), yet the female-above-male position is predominant in Phalangopsidae, considering the mating behaviors recorded so far (Table 1). To date, the end-to-end position has been described only for *E. corumbatai* (Prado, 2006), and although a quick observation of the end-to-end position had been made once in *E. meridionalis*, it was followed by the interruption of mating. In this sense, we suggest that this position is not a pattern in *E. meridionalis*, but only a failure when decoupling.

The end-to-end position prevents the female from continuing to feed on the secretions released by male metanotum during sperm transfer. The consumption of these secretions is essential for the occurrence of copulation and can increase fecundity and number of laid eggs (Brown, 1999; Eberhard, 1996), as well as the life span of mated females (Brown, 1997). This may be the reason why *E. corumbatai* females spend approximately five minutes just feeding on these secretions before taking the end-to-end position (Prado, 2006). Females of *E. meridionalis*, on the other hand, consume such secretions during courtship and mating (about 13 min), and after mating (about 2 min), ingesting large amounts of nutrients, even with reduced mating time (about 13 min) compared to *E. corumbatai* (*ca.* 60 min) (Prado, 2006). Therefore, at least three hypotheses are possible: i) both species release similar amounts of secretions in their metanotum, *E. corumbatai* males releasing higher amounts of secretions during a shorter period of time, while *E. meridionalis* males keep females entertained by releasing small portions (this explains female stimulation of males by biting them); ii) the parental investment in *E. meridionalis* is higher than in *E. corumbatai*, and energy costs are compensated by higher survival rates than by number of offspring (Carrière and Roff, 1995; Brown, 1997); or iii) due to subsequent mating and the absence of sexual plug, males of *E. meridionalis* offer their metanotum secretions for a longer time (including during post-copulation) as a way to keep the female entertained, thus avoiding, or at least diminishing, mating with other males and decreasing sperm competition (Parker, 1970; Simmons, 1987; Dougherty et al., 2016). In this latter case, males have higher reproductive success because passing more time with the females can ensure that their sperm will fertilize female eggs (Gwynne, 1988), and, consequently, the female will oviposit such eggs instead of mating with other males.

There are substantial differences in mating behavior between *E. corumbatai*, as studied by Prado (2006), and *E. meridionalis*. Firstly, the behavior of *E. corumbatai* was described based on the combination of two males with several females, since there was no copulation in mating attempts with few individuals or one couple. In *E. meridionalis,* on the other hand, observations were performed between couples, and the experiment was interrupted when courtship behavior has not occurred. This difference is also consistent with laboratory observations: males of *E. corumbatai* were always alone in their arenas, with several females nearby. Secondly, after being placed together in the arena, *E. corumbatai* individuals remained immobile for about two hours, with no grooming behavior or antennal movement being reported. The *E. meridionalis* couples remained motionless for about half a minute, then displaying grooming behavior and dorsoventral and lateral movements of the antennae in order to search the partner. Third, after sexual recognition, *E. corumbatai* males began to wave their antennae in a whipping movement, together with body vibrations and drumming on the bottom of the container with one of the forelegs, even with unresponsive females. The *E. meridionalis* couples, on the other hand, took the face-to-face position shortly after antennal contact, with females ignoring males or not. Fourth, the dominant *E. corumbatai* male was approached by females, and this could not happen with *E. meridionalis*, as the experiment was carried out only with couples. In both species, exposing the metanotum attracted the interest of the female. Finally, *E. corumbatai* females fed on metanotum secretions for approximately five minutes, while males exposed the spermatophore and inserted its duct into the females' papilla. After that, the couple assumed the end-to-end position to mate. *E. meridionalis* females fed on metanotum structures since before the exposure of the spermatophore, keeping feeding even after copulation, and the copulation occurred in the female-above-male position.

Although our data relies on the comparison of only a few genera, and, particularly, two *Eidmanacris* species, considerable variations in the reproductive behavior of Phalangopsidae has been reported. Such variations emphasize that other reproductive repertoires might be observed, either in *Eidmanacris* species (27 of which yet to have their reproductive behavior studied) or in Phalangopsidae in general. In the case of Phalangopsidae, behavioral diversity can be substantially higher since even if only 13 species out of 1094 had their reproductive behavior analyzed, several differences, especially regarding the phases and times of them, were already reported. Finally, studies of reproductive behavior can provide important information for future evolutionary and phylogenetic studies, being even useful in distinguishing cryptic species.

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Conflicts of interest

The authors have no conflicts of interest to declare.

Author contribution statement

LMC, SM and MF design the experiment and carried out the work. LMC, SM, MF, PGBSD, EZ discussed the results, provided critical feedback and helped the research, analysis and manuscript. NS supervised the findings of this work.

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