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Multiple spermatophore transfer during prolonged mating in the apterous Neotropical cricket Unacla meridionalis (Desutter-Grandcolas, 1994) (Orthoptera: Grylloidea: Phalangopsidae)

Leanna Camila Macarini

leannamacarini@gmail.com

Universidade Federal do Parana https://orcid.org/0000-0002-9963-4999

Jessica Ricci de Lima

Universidade Estadual do Paraná: Universidade Estadual do Parana

Marcos Fianco

Universidade Federal do Parana

Edison Zefa

Universidade Federal de Pelotas

João Pedro Maruzka Roncaglio

Universidade Estadual do Oeste do Parana

Vitória Garcia de Camargo

Universidade Estadual do Oeste do Parana

Neucir Szinwelski

Universidade Estadual do Oeste do Parana

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Abstract

Phalangopsidae comprises over 1,113 species of crickets, but reproductive behavior has been documented for only a few species. Here, we describe the mating behavior of *Unacla meridionalis* (Desutter-Grandcolas, 1994), an apterous, nocturnal cricket endemic to the Brazilian Atlantic Forest. We analyzed 15 mating trials conducted under controlled laboratory conditions, including courtship, copulation, and post-copulation behaviors. Along courtship stage, male perform dorsoventral body vibrations, antennation, while female palpation of the male's abdominal tergites; spermatophores are transferred during subsequent copulations; after the mating pair separated, females consumed the spermatophores in 87% of the encounters, contrasting with the male spermatophore consumption typical of other phalangopsid species, and suggesting that the spermatophore may represent a post-nuptial gift. The total mating event lasted approximately 2 hours, representing a considerably long duration. These findings expand our understanding of the diversity of reproductive strategies within Phalangopsidae and underscore the evolutionary significance of extended mating and paternal investment in apterous crickets.

Introduction

Reproductive behavior in insects is particularly diverse and complex, involving a suite of courtship, copulation, and post-copulation interactions shaped by sexual selection (Andersson 1994; Adams and Tariq 2024). In these contexts, females typically choose mates due to their higher energetic investment in offspring, using male signals to assess genetic quality and ensure reproductive success (Kelly 2018).

Acoustic communication in crickets (Orthoptera: Grylloidea) is one of the most studied aspects of mating behavior, with males typically producing calling and courtship songs through tegminal stridulation to attract and stimulate females (Alexander 1962; Mowles 2014). However, other forms of communication, such as substrate-borne vibrational signaling (Stritih-Peljhan and Virant-Doberlet 2021) and chemical signaling (Stritih and Žunič Kosi 2017) can be used by crickets, especially in apterous species that lack the tegminal apparatus required for sound production (Desutter-Grandcolas 1995; Stritih-Peljhan and Virant-Doberlet 2021).

Phalangopsidae comprises 1.133 valid species (Cigliano et al. 2026), encompassing apterous, micropterous, and macropterous crickets with diverse ecological habits (Desutter-Grandcolas 1992). Despite this remarkable species richness, reproductive behavior has been described for only about 1% of the species (Macarini et al. 2023), leaving a substantial gap in our understanding of behavioral diversity. Among the few behavioral descriptions available, notable variation has been documented in courtship signals, copulatory mechanics, and post-copulatory investment, suggesting that Phalangopsidae harbors a yet-unexplored diversity of mating strategies (Desutter-Grandcolas 1995; Zefa et al. 2008; Fianco et al. 2018; Macarini et al. 2023).

Unacla meridionalis (Desutter-Grandcolas, 1994) is a nocturnal, completely apterous cricket endemic to the Atlantic Forest of southern and southeastern Brazil (Desutter-Grandcolas 1994; Mews et al. 2008).

As a wingless species with no described glandular structures, its mating communication is expected to rely on alternative sensory modalities such as vibrational signals, chemoreception, and tactile cues, making it a particularly interesting model for understanding reproductive behavior in the absence of acoustic signaling.

Here, we provide a comprehensive description of the complete mating repertoire of the cricket *U. meridionalis*, including courtship, copulation, and post-copulation stages. Our findings contribute to narrowing the knowledge gap on the reproductive biology of phalangopsid crickets and provide new evidence for the evolution of extended mating and nuptial investment strategies in apterous crickets.

Material and Methods

Target Species

Unacla (Campos and Souza-Dias 2025) crickets exhibit a distinctive morphology compared to other Phalangopsidae. Their dorsoventrally flattened body is likely an adaptation for occupying sheltered microhabitats, such as spaces beneath bark and narrow tree crevices, during the day (Desutter-Grandcolas 1994). *Unacla meridionalis* is a nocturnal cricket, completely wingless with no documented associated metanotal glandular structures. The males have a glossy dark brown body with complex, large genitalia with ventral projections; females are slightly larger than males, exhibit the same body coloration, and possess a long ovipositor (Desutter-Grandcolas 1994) (Fig. 1).

Sampling and Laboratory rearing

Individuals of *U. meridionalis* were collected at night from logs, branches of living or dead trees, shrubs, and leaf litter in Iguaçu National Park, Foz do Iguaçu – PR (25°22'24" S – 54°2'33" W), between March and September 2016. Upon collection, the specimens were transported to the Agricultural Biotechnology Laboratory of the Universidade Estadual do Oeste do Paraná (Unioeste), Cascavel, PR, Brazil, where they were identified and kept separately in transparent plastic containers (7 cm high × 11 cm diameter – 500 mL), with openings in the lids for ventilation.

Shelters made from egg cartons and pieces of tree branches were added to each container. All individuals were maintained in a climate-controlled room with 75% relative humidity, a temperature of 23°C, and a 12-hour light-dark photoperiod. Food (commercial fish flakes) and water were provided *ad libitum*. The crickets were kept in these conditions for 7 days for acclimatization before the start of the experiments.

Reproductive behavior

For the reproductive behavior experiments, field-collected adult males and females were randomly paired. Because individuals were collected as adults directly from their natural habitat, the prior mating

status of the males and females was unknown, and they were assumed to be non-virgin.

Firstly, we performed five pilot encounters during the daytime period that resulted in no reproductive behavior. Based on these preliminary trials, all subsequent recordings were performed at night (7:00 pm – 3:00 am), when individuals were active. Thus, a total of 85 mating trials were conducted under nighttime conditions. Trials in which no courtship behavior was observed within 15 min were terminated. As a result, 15 trials culminated in complete copulations and were included in the behavioral analyses.

At the beginning of each trial, a male and a female were placed together in an experimental arena consisting of a rectangular glass container (20 cm long × 15 cm wide × 15 cm high) lined with filter paper, which was replaced after each encounter. Individuals were initially placed on opposite sides of the arena and covered with plastic cups for a two-minute acclimatization period. After simultaneous removal of the cups, interactions were recorded using a Canon camera (PowerShot SX210 IS, 14.1 MP). The video recordings were analyzed to define the courtship, copulation, and post-copulation stages, and the duration of each stage was tabulated as mean ± standard deviation.

Results

For *Unacla meridionalis*, all mating events, including courtship, copulation, and post-copulation, lasted for 1 h 59 min 8 s ± 42 min 31.6 s (n = 15).

Courtship

Males and females of *U. meridionalis*, upon release into the arena, remained immobile for approximately 10 min 52 s ± 10 min 16 s (n = 15). After this period, the couples slowly walked around the arena, antennating and palpating the substrate with their maxillary palps (1 min 18,6 s ± 1 min 31 s).

Upon detecting females in the environment, whether by inspecting the substrate where females had previously passed or by touching any part of a female's body with their antennae, males began to exhibit dorsoventral body vibrations (Fig. 2a) for 51.7 s ± 32.3 s (n = 10). Consequently, the first physical contact between the pair occurred through antennation (Fig. 2b), which lasted for 17.7 s ± 11.8 s (n = 12). In nine instances, males approached females while antennating, after the immobility period. In the remaining cases (n = 6), females approached the males. Overall, the first physical contact between the pairs occurred 13 min 20 s ± 12 min 32 s after the start of the experiment (i.e., after the plastic cups were removed), encompassing the entire immobility period as well as the time spent performing body vibrations.

In four encounters, the males did not perform body vibrations, and in three, antennal contact was not observed between the pairs, with the interaction proceeding directly to the next stage of reproductive behavior.

When couples were close together, males turned their backs to the females (n = 14), who approached the dorsal abdominal region of males, between the fifth and seventh tergites, palpating the area with their maxillary palps (Fig. 2c). The palpating behavior was observed in all encounters, lasting approximately 1 min 34.73 s ± 52.51 s (n = 15). In one of the encounters, the male did not vibrate his body, there was no antennal contact between the pair, and in this case, the female went straight to the male's abdomen.

Copulation

Following courtship, males positioned themselves beneath the females and assumed the copulatory position. They then everted their genitalia, producing and exposing the first spermatophore over 2 min 0.27 s ± 43.73 s (n = 15). Once the spermatophore was exposed, males tilted their terminalia toward the female genitalia, while females lowered their subgenital plate. To achieve genital engagement, males performed back-and-forth movements with their terminal abdominal segments to attach their phallic complex via the pseudepiphallic arms; these back-and-forth movements lasted 6 min 9.3 s ± 2 min 50.7 s. When successfully attached (Fig. 2d), the spermatophore remained attached to the female genitalia for 34 min 57s ± 19 min 29,7 s (n = 15).

In two encounters, there was only one copulation, and in the others, males exited the copulation position and removed the spermatophore, scraping the abdomen tip against the substrate (Fig. 2e) for 40.3 s ± 23 s. During this period, females remained immobile, and immediately after removing the spermatophore, males returned to the copulatory position and the removed spermatophore remained on the substrate. After the couple re-assumed the copulation position, the male produced a new spermatophore, everted his genitalia again, and copulation proceeded as described above. Following the first copulation, an average of 4 ± 2 (n = 13) additional copulations were observed.

Post-copulation

The post-copulatory phase was initiated by the female, who dismounted from the male's back to terminate the copulatory position. To remove the transferred spermatophore, the female bent her body ventrally, utilizing her mandibles and maxillary palps to pull the structure directly from her genital papilla. Concurrently, the male did not remain stationary; upon separation, he immediately moved away and engaged in localized grooming, scraping the terminal segments of his abdomen against the substrate. Following these initial actions, both individuals began to move randomly around the arena, screening the substrate with their antennae. Females consumed the spermatophores (Fig. 2f) that were on the substrate in 87% of the encounters (n = 13). However, when females failed to consume the spermatophore, it was subsequently consumed by the male. (n = 2).

Discussion

This study provides the first comprehensive description of the reproductive behavior of the apterous cricket *Unacla meridionalis*, which lacks the acoustic signaling typically central to cricket mating.

Although several behavioral components, such as antennation, body vibrations, abdominal palpation, and female-above copulation, occur in other phalangopsids (Zefa et al. 2008; Fianco et al. 2018; Macarini et al. 2023), the repeated spermatophore transfer, predominant consumption by females, and exceptionally long mating duration represent an unprecedented behavioral repertoire for this cricket family.

In crickets, contact pheromones play a central role in species recognition and in the assessment of mate quality (Kortet and Hedrick 2005), and male body vibrations may enhance the release, dispersal, or perception of these chemical cues (Tishechkin 2022) following initial contact with the female. Under this scenario, the dorsoventral vibrations observed in *U. meridionalis* males may function as short-range mechanical stimuli that complement chemical communication. Furthermore, substrate-transmitted mechanical waves are a widely used signaling modality in cricket sexual communication (Stritih-Peljhan and Virant-Doberlet 2021). Similar vibratory behaviors have been reported during reproductive interactions in other Phalangopsidae species, such as *Vanzoliniella sambophilla* (Mello and Reis 1994) and *Adelosgryllus rubricephalus* (Zefa et al. 2008).

The effectiveness of vibrational communication, however, depends on the physical properties of the transmission medium (Cocroft and Rodríguez 2005). Because *U. meridionalis* typically inhabits tree trunks and spaces beneath bark (Desutter-Grandcolas 1994), where mechanical signals may attenuate differently than in leaf litter or soil, the communicative role of dorsoventral vibrations remains uncertain and warrants further investigation. Even so, the combination of chemical and vibrational signals could facilitate reliable partner recognition in the structurally complex microhabitats occupied by *U. meridionalis*, reducing the need for elaborate acoustic or visual signaling.

Regarding the sensory system for communication, antennae are multifunctional sensory organs that act as both chemoreceptors and mechanoreceptors, enabling individuals to obtain information about their environment, other organisms, and their specificities through direct physical contact (Loudon et al. 2014; Elgar et al. 2018). This information can reveal mate quality and reproductive status (Sakura and Aonuma 2013), including cues associated with age and sexual maturity (Mello 2007; Rodríguez-Muñoz et al. 2019). The antennation observed in *U. meridionalis* is therefore likely to play a central role in partner assessment and the initiation of courtship behavior.

The pheromonal communication is primarily mediated through antennal contact, although the maxillary and labial palps also contribute to the detection and assessment of chemical cues (Hardy and Shaw 1983; Tregenza and Wedell 1997; Iwasaki and Katagiri 2008). In this way, maxillary palps also function as multimodal sensory organs in crickets, participating in both tactile and chemical perception (Klein 1981; Iwasaki and Katagiri 2008; Matsumoto et al. 2015).

In the reproductive encounters observed in *U. meridionalis*, females palpated the male abdominal tergites with their maxillary palps prior to mounting. This behavior may be related to the female's investigation for physical and chemical cues necessary to trigger mounting (Balakrishnan and Pollack 1997). Furthermore, similar behaviors have been reported in other Phalangopsidae species and have

been associated with the presence of metanotal or tergal glands that provide nuptial secretions and may reflect male reproductive investment (Fernandes et al. 2016; Macarini et al. 2023).

During mating, the spermatophore may be displayed to the female as a sexual attribute, as observed in *Adelosgryllus rubricephalus* (Zefa et al. 2008). However, in *U. meridionalis*, the spermatophore is externally exposed only during copulation, preventing it from transmitting visual information to females, who are already on top of the males when the spermatophore becomes visible. In contrast, in all previously studied Phalangopsidae species, the spermatophore has consistently been consumed by the male at the end of copulation (Alexander and Otte 1967; Prado 2006; Fianco et al. 2018; Corrêa et al. 2018; Macarini et al. 2023).

However, in *U. meridionalis*, females consumed the spermatophore in 87% of the encounters, suggesting that it may represent a post-nuptial gift, a form of paternal investment also reported in other cricket species and associated with increased female fecundity and egg quality (Simmons 1988; Shaw and Khine 2004; Prokop and Maxwell 2008). In addition, the transfer of multiple spermatophores during a single mating may increase the amount of sperm and seminal substances received by the female. In orthopterans, these seminal compounds, including prostaglandins and proteins, are known to stimulate egg maturation and oviposition (Andrés et al. 2006; Ryan and Sakaluk 2009; Simmons et al. 2013; Bonilla et al. 2015). Whether multiple spermatophore transfer in *U. meridionalis* provides similar physiological benefits remains to be investigated.

One of the most striking findings of this study is the exceptionally long total duration of *U. meridionalis* mating, as the complete mating event, lasted on average almost two hours. This duration ranks among the longest ever documented for Phalangopsidae, being comparable to *Phaeophilacris bredoides* (Orthoptera, Gryllidae), whose mating sequence can also last up to two hours (Lunichkin et al. 2016).

The extended mating in *U. meridionalis* appears to be associated with the production of multiple sequential spermatophores (mean 4 ± 2 per event), to maximize sperm transfer and, consequently, fertilization success (Simmons 1988; Worthington and Kelly 2016). This extended copulation may also function as mate guarding, reducing the likelihood of females remating with rival males during the prolonged coupling period (Sillén-Tullberg 1981; Nuyts and Michiels 1993).

Field collected of adults provided an opportunity to examine mating behavior under conditions likely reflecting natural population dynamics, although the individuals' prior mating history was unknown. In many cricket species, female mating experience influences receptivity, mate choice, and copulation duration (Tinghitella 2014; Worthington and Kelly 2016). However, *U. meridionalis* exhibited extended mating events involving multiple spermatophore transfers despite the unknown reproductive history of the females. The frequent consumption of spermatophores suggests these structures may function as post-nuptial gifts, potentially contributing to female nutritional intake and extended mating, although their physiological and fitness benefits remain to be investigated.

Declarations

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Competing interests' declaration

The authors have reported any financial interests or personal relationships that could be construed as potential competing interests.

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References

1. Adams I, Tariq M (2024) An overview of reproduction in insects. Asian J Adv Agricultural Res 24:133–147. https://doi.org/10.9734/ajaar/2024/v24i7529
2. Alexander RD (1962) Evolutionary change in cricket acoustical communication. Evol (NY) 16:443–467. https://doi.org/10.2307/2406178
3. Alexander RD, Otte D (1967) The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera. Miscellaneous Publications Museum of Zoology, University of Michigan 133:1–62
4. Andersson MB (1994) Sexual Selection. Princenton University, New Jersey
5. Andrés JA, Maroja LS, Bogdanowicz SM et al (2006) Molecular evolution of seminal proteins in field crickets. Mol Biolology Evol 23:1574–1584. https://doi.org/10.1093/molbev/msl020
6. Balakrishnan R, Pollack GS (1997) The role of antennal sensory cues in female responses to courting males in the cricket *Teleogryllus oceanicus*. J Exp Biol 200:511–522. https://doi.org/10.1242/jeb.200.3.511
7. Bonilla ML, Todd C, Erlandson M, Andres J (2015) Combining RNA-seq and proteomic profiling to identify seminal fluid proteins in the migratory grasshopper *Melanoplus sanguinipes* (F). BMC Genomics 16:1–15. https://doi.org/10.1186/s12864-015-2327-1

8. Campos LD, Souza-Dias PGB (2025) Resolving the 150-year-old homonymy of *Laranda*: A new name for the cricket genus (Orthoptera: Phalangopsidae: Paragryllinae). Zootaxa 5716:146–148. https://doi.org/10.11646/zootaxa.5716.1.9
9. Cigliano MM, Braun H, Eades DC, Otte D (2026) Family Phalangopsidae Blanchard, 1845. In: Orthoptera Species File. http://orthoptera.speciesfile.org/otus/831778/overview. Accessed 28 Apr 2026
10. Cocroft RB, Rodríguez RL (2005) The behavioral ecology of insect vibrational communication. Bioscience 55:323–334. https://doi.org/10.1641/0006-3568(2005)055[0323:TBEOIV]2.0.CO;2
11. Corrêa RC, Pereira MR, Da Costa MKM et al (2018) Two new species of crickets *Adelosgryllus* Mesa & Zefa, 2004 (Orthoptera, Grylloidea, Phalangopsidae) from the Araripe-Apodi National Forest, State of Ceará, Brazil. Zootaxa 4420:97–112. https://doi.org/10.11646/zootaxa.4420.1.5
12. Desutter-Grandcolas L (1995) Toward the knowledge of the evolutionary biology of Phalangopsid crickets (Orthoptera: Grylloidea: Phalangopsidae): Data, questions and evolutionary Scenarios. J Orthoptera Res 4:163–175. https://doi.org/10.2307/3503472
13. Desutter-Grandcolas L (1992) Les Phalangopsidae de Guyane francaise (Orthoptères, Grylloidea): systématique, éléments de phylogénie et de biologie. Bulletin du Muséum national d'histoire naturelle Section. Zool Biol et Ecologies 14:93–177. https://doi.org/10.5962/p.289869
14. Desutter-Grandcolas L (1994) Revision of the genus *Laranda* Walker (Orthoptera, Grylloidea: Phalangopsidae) with notes on its distribution and biology. Insect Syst Evol 25:321–332. https://doi.org/10.1163/187631294X00126
15. Elgar MA, Zhang D, Wang Q et al (2018) Insect antennal morphology: The evolution of diverse solutions to odorant perception. Yale J Biology Med 91:457–469
16. Fernandes ML, Pereira MR, Sperber CF, Serrão JE (2016) A novel epidermal abdominal gland in the cricket *Ectecous segregatus* Gorochov, 1996 (Orthoptera: Grylloidea: Phalangopsidae). Zoologischer Anzeiger 261:33–37. https://doi.org/10.1016/j.jcz.2016.03.003
17. Fianco M, de Souza-Dias PGB, de Farias-Martins F et al (2018) Ethology of the cricket *Endecous chape* Souza-Dias & de Mello, 2017 (Orthoptera: Grylloidea: Phalangopsidae) I: Agonistic and reproductive behavior. Journal of Orthoptera Research 27:193–201. https://doi.org/10.3897/jor.27.29687
18. Hardy TN, Shaw KC (1983) The role of chemoreception in sex recognition by male crickets: *Acheta domesticus* and *Teleogryllus oceanicus*. Physiol Entomol 8:151–166. https://doi.org/10.1111/J.1365-3032.1983.TB00344.X
19. Iwasaki M, Katagiri C (2008) Cuticular lipids and odors induce sex-specific behaviors in the male cricket *Gryllus bimaculatus*. Comp Biochem Physiol - Mol Integr Physiol 149:306–313. https://doi.org/10.1016/j.cbpa.2008.01.008
20. Kelly CD (2018) The causes and evolutionary consequences of variation in female mate choice in insects: the effects of individual state, genotypes and environments. Curr Opin Insect Sci 27:1–8. https://doi.org/10.1016/J.COIS.2018.01.010

21. Klein U (1981) Sensilla of the cricket palp - Fine structure and spatial organization. Cell Tissue Res 219:229–252. https://doi.org/10.1007/BF00210145
22. Kortet R, Hedrick A (2005) The scent of dominance: Female field crickets use odour to predict the outcome of male competition. Behav Ecol Sociobiol 59:77–83. https://doi.org/10.1007/s00265-005-0011-1
23. Loudon C, Bustamante J, Kellogg DW (2014) Cricket antennae shorten when bending (*Acheta domesticus* L). Front Physiol 5:1–9. https://doi.org/10.3389/fphys.2014.00242
24. Lunichkin AM, Zhemchuzhnikov MK, Knyazev AN (2016) Basic elements of behavior of the cricket *Phaeophilacris bredoides* Kaltenbach (Orthoptera, Gryllidae). Entomol Rev 96:537–544. https://doi.org/10.1134/S0013873816050031
25. Macarini LC, Magro S, Fianco M et al (2023) Mating behavior of the long-legged cricket *Eidmanacris meridionalis* Desutter-Grandcolas, 1995 (Orthoptera: Phalangopsidae). Revista Brasileira de Entomol 67:e20230005. https://doi.org/10.1590/1806-9665-RBENT-2023-0005
26. Matsumoto Y, Matsumoto CS, Wakuda R et al (2015) Roles of octopamine and dopamine in appetitive and aversive memory acquisition studied in olfactory conditioning of maxillary palpi extension response in crickets. Front Behav Neurosci 9:1–9. https://doi.org/10.3389/fnbeh.2015.00230
27. de Mello F AG (2007) Female monopolization and paternity assurance in South American crickets (Orthoptera, Grylloidea): Mating plugs, extra claspers and forced copulation. Papéis Avulsos de Zoologia 47:245–257. https://doi.org/10.1590/S0031-10492007002000001
28. Mello F, de AG, Reis JC (1994) dos Substrate drumming and wing stridulation performed during courtship by a new brazilian cricket (Orthoptera: Grylloidea: Phalangopsidae). Journal of Orthoptera Research 2:21–24. https://doi.org/10.2307/3503603
29. Mews CM, Lopes-Andrade C, Sperber CF (2008) A new species of *Laranda* Walker 1869 (Orthoptera: Grylloidea, phalangopsidae) from remnant patches of the Brazilian atlantic forest. Neotrop Entomol 37:420–425. https://doi.org/10.1590/S1519-566X2008000400010
30. Mowles SL (2014) The physiological cost of courtship: Field cricket song results in anaerobic metabolism. Anim Behav 89:39–43. https://doi.org/10.1016/j.anbehav.2013.12.014
31. Nuyts E, Michiels NK (1993) Integration of immediate and long term sperm precedence patterns and mating costs in an optimization model of insect copulation duration. J Theor Biol 160:271–295. https://doi.org/10.1006/JTBI.1993.1019
32. Prado R (2006) Reproductive behavior of *Eidmanacris corumbatai* Garcia (Orthoptera: Phalangopsidae). Neotrop Entomol 35:452–457. https://doi.org/10.1590/s1519-566x2006000400005
33. Prokop P, Maxwell MR (2008) Interactions between multiple forms of nuptial feeding in the wood cricket *Nemobius sylvestris* (Bosc): Dual spermatophores and male forewings. Ethology 114:1173–1182. https://doi.org/10.1111/J.1439-03102008.01562.X;PAGE:STRING:ARTICLE/CHAPTER

34. Rodríguez-Muñoz R, Hopwood P, Fisher D et al (2019) Older males attract more females but get fewer matings in a wild field cricket. Anim Behav 153:1–14. https://doi.org/10.1016/J.ANBEHAV.2019.04.011
35. Ryan KM, Sakaluk SK (2009) Dulling the senses: the role of the antennae in mate recognition, copulation and mate guarding in decorated crickets. Anim Behav 77:1345–1350. https://doi.org/10.1016/j.anbehav.2009.02.011
36. Sakura M, Aonuma H (2013) Aggressive behavior in the antennectomized male cricket *Gryllus bimaculatus*. J Exp Biol 216:2221–2228. https://doi.org/10.1242/jeb.079400
37. Shaw KL, Khine AH (2004) Courtship behavior in the hawaiian cricket *Laupala cerasina*: Males provide spermless spermatophores as nuptial gifts. Ethology 110:81–95. https://doi.org/10.1046/j.1439-0310.2003.00946.x
38. Sillén-Tullberg B (1981) Prolonged copulation: A male postcopulatory strategy in a promiscuous species, *Lygaeus equestris* (Heteroptera: Lygaeidae). Behav Ecol Sociobiol 9:283–289. https://doi.org/https://doi.org/10.1007/BF00299884
39. Simmons LW (1988) The contribution of multiple mating and spermatophore consumption to the lifetime reproductive success of female field crickets (*Gryllus bimaculatus*). Ecol Entomol 13:57–69. https://doi.org/10.1111/j.1365-2311.1988.tb00333.x
40. Simmons LW, Tan YF, Millar AH (2013) Sperm and seminal fluid proteomes of the field cricket Teleogryllus oceanicus: Identification of novel proteins transferred to females at mating. Insect Mol Biol 22:115–130. https://doi.org/10.1111/imb.12007
41. Stritih N, Žunič Kosi A (2017) Olfactory signaling of aggressive intent in male-male contests of cave crickets (*Troglophilus neglectus*; Orthoptera: Rhaphidophoridae). PLoS ONE 12:e0187512. https://doi.org/10.1371/journal.pone.0187512
42. Stritih-Peljhan N, Virant-Doberlet M (2021) Vibrational signalling, an underappreciated mode in cricket communication. Sci Nat 108:1–12. https://doi.org/10.1007/s00114-021-01749-7
43. Tinghitella RM (2014) Male and female crickets modulate their courtship behaviour depending on female experience with mate availability. Anim Behav 91:9–15. https://doi.org/10.1016/j.anbehav.2014.02.022
44. Tishechkin DY (2022) Vibrational communication in insects. Entomol Rev 102:737–768. https://doi.org/10.1134/S001387382206001X
45. Tregenza T, Wedell N (1997) Definitive evidence for cuticular pheromones in a cricket. Anim Behav 54:979–984. https://doi.org/10.1006/anbe.1997.0500
46. Worthington AM, Kelly CD (2016) Direct costs and benefits of multiple mating: Are high female mating rates due to ejaculate replenishment? Behavioural Processes 124:115–122. https://doi.org/10.1016/j.beproc.2015.12.009
47. Zefa E, Martins L, de Szinwelski P N (2008) Complex mating behavior in *Adelosgryllus rubricephalus* (Orthoptera, Phalangopsidae, Grylloidea). Iheringia Série Zoologia 98:325–328. https://doi.org/10.1590/S0073-47212008000300006

Figures

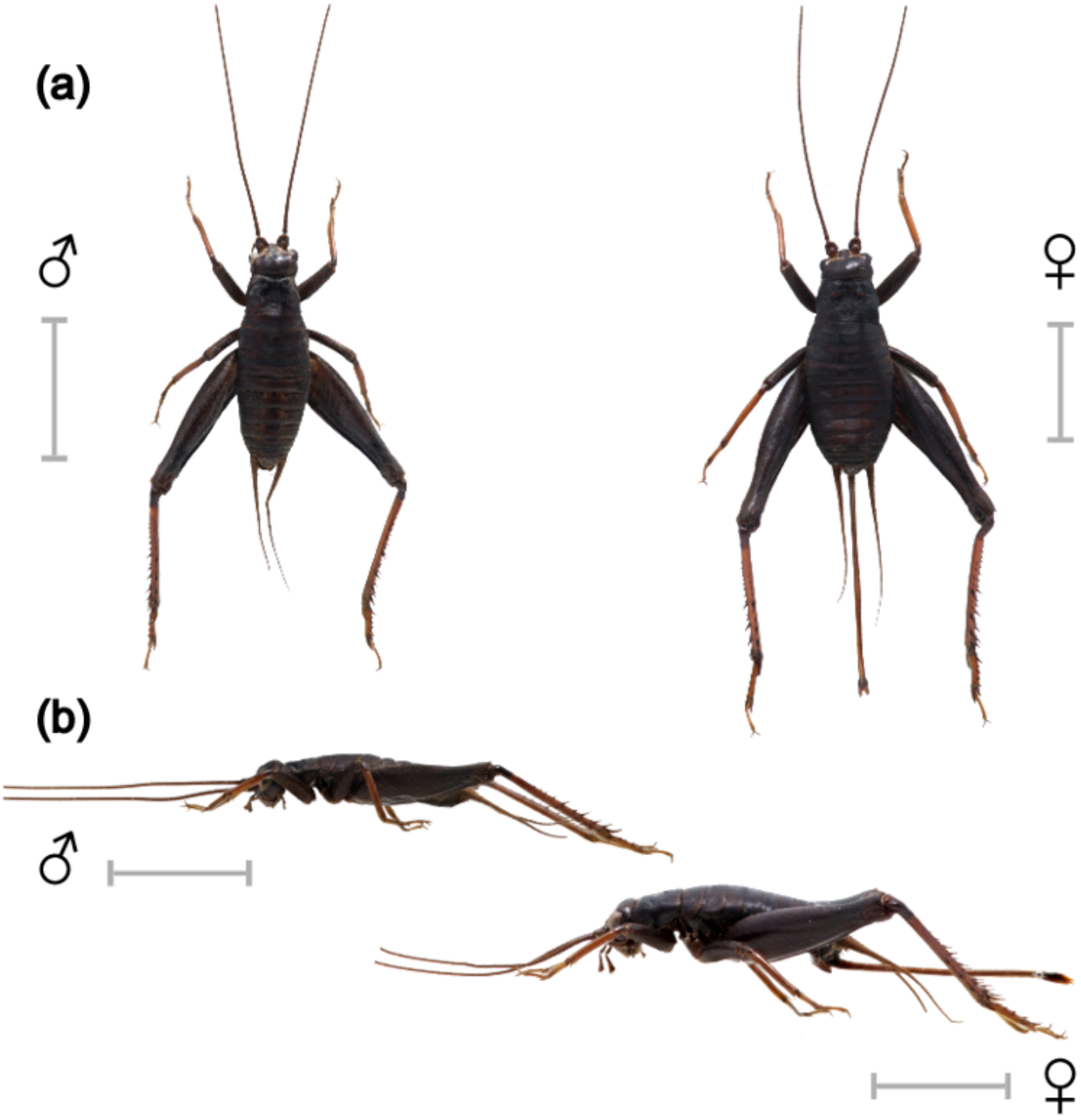


Figure 1

Male (♂) and female (♀) of *Unacla meridionalis*. (a) Dorsal and (b) lateral views, post-fixation, detailing the external morphology. Grey scale bars represent 1 cm.

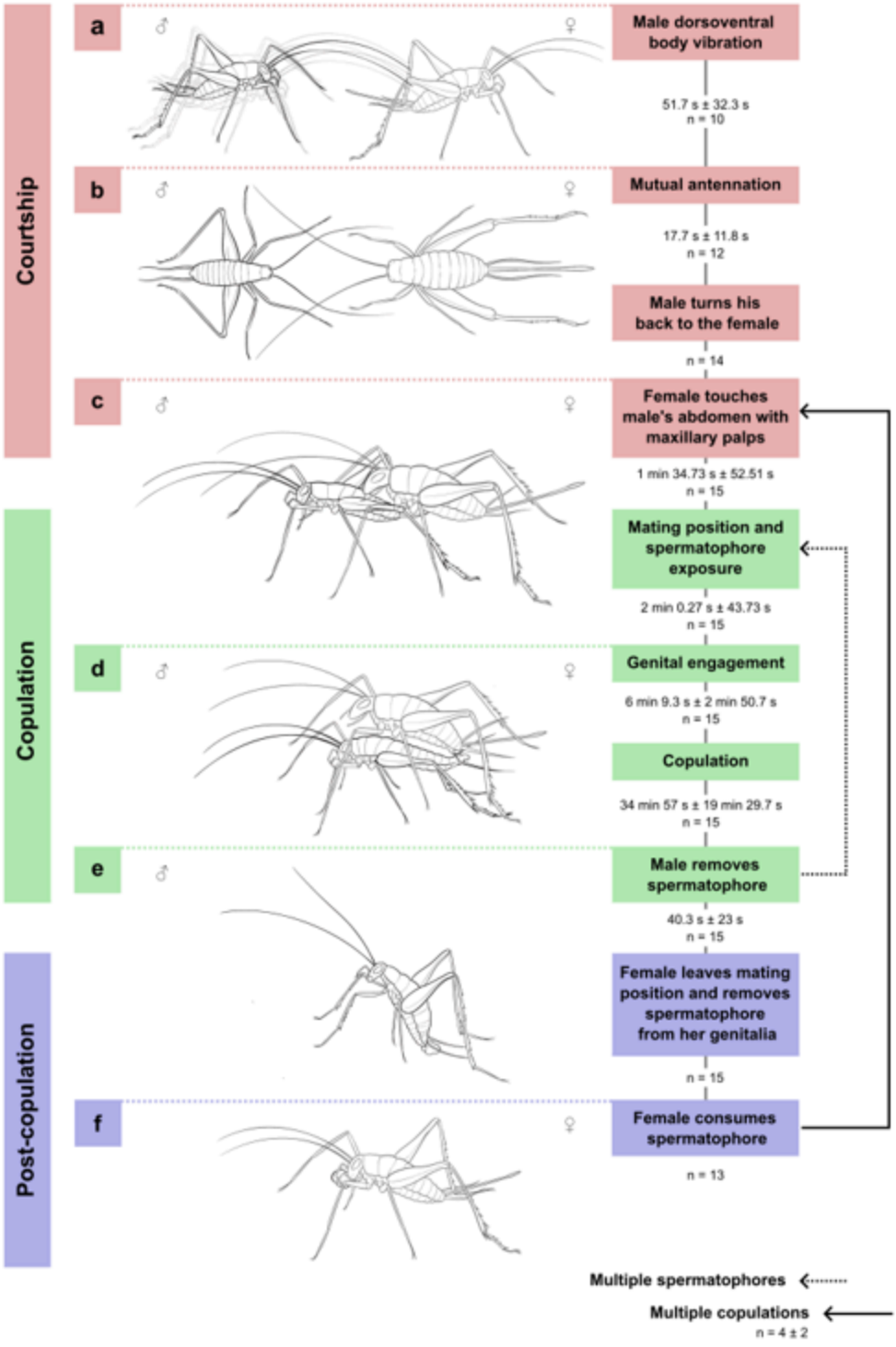


Figure 2

Ethogram of the reproductive behavior of *Unacla meridionalis* ethogram. Pre-copulation: male performing (a) dorsoventral vibration, (b) antennation, (c) female palpating male's abdomen. Copulation: (d) positioning, spermatophore production, and couple mating; post-copulation: (e) male removing the spermatophore; (f) female consuming the spermatophore.