





A tritrophic interaction at the Brazilian triple frontier: new record of parasitism on *Conocephalus saltator* (Sausurre, 1859) (Orthoptera, Tettigoniidae)

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ABSTRACT

We report for the first time a tritrophic relationship (host-parasitoid-hyperparasitoid) among *Conocephalus saltator* (Sausurre, 1859) (Orthoptera, Tettigoniidae), *Ormia* cf. *crespoi* Tavares, 1965 (Diptera, Tachinidae), and *Perilampus* sp. (Hymenoptera, Perilampidae). Specimens of *C. saltator* were collected at the Parque Nacional do Iguaçu (Foz do Iguaçu, Paraná, Brazil) and reared in the laboratory, in order to detect eventual parasitoids. We collected and reared 904 katydids, with 113 of them parasitized, producing 123 fly puparia, and 18 puparia that developed to adults of *Ormia* cf. *crespoi*. We also recorded the emergence of four hyperparasitoid wasps, *Perilampus* sp., from the fly puparia.

A parasitoid is an organism whose larval stage feeds on a single host, killing it as a result of its development (Eggleton and Belshaw, 1993; Wajnberg et al. 2008). The successful development of the parasitoid relies on overcoming complex barriers such as finding, evaluating host quality, and overcoming defensive behaviours and the immune response of the hosts (Brodeur and Boivin, 2004). Some parasitoids develop on other parasitoids, constituting multitrophic systems that may include several levels; thus, parasitoids may be referred to as primary, secondary and even tertiary – all levels above the second being considered hyperparasitoids (Gauld and Bolton, 1988; Gordh et al., 1999). In this relationship, although only the parasitism of the secondary host can occur, the hyperparasitoid only completes its development if the primary host is also present (Smith, 1912, 1958). The ecological and evolutionary relevance of parasitoids is well established (see e.g. Santos and Quicke, 2011), as they are key components of terrestrial biota (e.g. LaSalle and Gauld, 1991), trophically interact with several other organisms (e.g. Lewis et al., 2002), and are able to regulate the population size of several arthropods (Hassell, 2000), which led to their substantial use as agents of biological control (e.g. Wang et al., 2019).

A significant portion of known insect parasitoids belong to the orders Diptera and Hymenoptera (Waage and Hassell, 1982; Hassell and Waage, 1984). In Diptera, parasitoidism occurs mostly within Tachinidae, a family with about 8,500 species that are exclusively parasitoids of other arthropods, with varying degrees of host specificity (Wood and Zumbado, 2010), including the tribe Ormiini (Lehmann, 2003). This tribe of Tachininae, with 71 species (O'Hara et al., 2020), are parasitoids of Ensifera (Orthoptera) as an ancestral trait (Lehmann, 2003). Only eleven species of Ormiini have their hosts formally recorded to date (reviewed in Lehmann, 2003).

The species of Ormiini are unusual in that they are crepuscular/nocturnal. Females are attracted by singing male Ensifera, by phonotaxis, and lay a large number of planidial larvae nearby the potential host (Cade, 1975; Adamo et al., 1995). The planidium then enters the host body, in which 1-2 larvae usually complete the development (Vincent and Bertram, 2009), attaching themselves to a tracheal funnel in the host body wall and killing the host at the time of pupariation (Cade, 1975; Adamo et al., 1995). Regarding *Ormia* Robineau-Desvoidy, 1830, five out of the 27 species have known hosts, two of them associated with Conocephalinae (Tettigoniidae), two with Gryllidae, and one mainly with Gryllotalpidae, the latter a derived trait within Ormiini (Lehmann, 2003). Reports suggest that *Ormia* species can have a

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wide, but phylogenetically restricted, host range (Lehmann, 2003). Concerning the interaction between Conocephalinae and *Ormia*, *Ormia brevicornis* Townsend, 1919 has been recorded from two species of *Neoconocephalus* Karny, 1907, and *Ormia lineifrons* Sabrosky, 1953 from one species of *Neoconocephalus* and four species of *Orchelimum* Serville, 1838 (Lehmann, 2003). No information on host range or interactions between *Ormia* species and their hosts was presented after Lehmann's (2003) review, aside from data on *Ormia ochracea* (Bigot, 1889) and *Ormia depleta* (Wiedemann, 1830), which are widely studied species. Additional information on the parasitoidism of Tettigoniidae by other Tachinidae is provided by Frisch (1936), Young (1977), Arnaud (1978), Cantrell (1986), Allen (1995), Shapiro (1995), Allen and Pape (1996), Barraclough and Allen (1996), Lakes-Harlan et al. (2007), Nihei and Toma (2010), Tachi (2011), Tschorsnig (2017), Inclán et al. (2018), Toma and Olivier (2018).

Three quarters of parasitoid species are found within the Hymenoptera (Belshaw et al., 2003), mostly in the superfamilies Chalcidoidea, Cynipoidea, Ichneumonoidea, Ceraphronoidea and Trigonalioidea, besides more isolated occurrences in Proctotrupeoidea (Muesebeck, 1977; Gauld and Bolton, 1988). Chalcidoidea, a remarkably speciose lineage within Hymenoptera, encompasses Perilampidae, a small family with about 300 species sorted into 17 genera (Noyes, 2019). *Perilampus* Latreille, 1809 is the only genus of the family for which biological associations are known to date (Noyes, 2019). The species of this genus are primary parasitoids of Coleoptera, Neuroptera, and other Hymenoptera, and secondary parasitoids (hyperparasitoids) of Hymenoptera (Braconidae and Ichneumonidae) and Diptera (Sarcophagidae and Tachinidae), which are, in this case, primary parasitoids of Lepidoptera and Orthoptera (Smith, 1917; Léonide and Léonide, 1969; Heraty and Darling, 1984). There are, however, reports of planidial larvae of *Perilampus* on orthopteroid insects (Kelly, 1914; Ford, 1922; Frisch, 1936; Smith, 1944; Smith and Finlayson, 1950; Howitt, 1951; Smith, 1958; Blackith, 1967). Smith (1958), for instance, noted the presence of planidial larvae of *Perilampus* in 22 Orthoptera species within the families Acrididae, Gryllidae, and Tettigoniidae. Regarding more specifically the association with katydids, Ford (1922) reported on individuals of *Conocephalus fasciatus* (De Geer, 1773) housing planidial larvae, apparently of *Perilampus hyalinus* Say, 1829, in Canada; however, he stated that it was unlikely that *C. fasciatus* could be the actual host of *P. hyalinus* and that the wasp probably was searching for its primary host within the body of the katydid. This strategy of waiting for the target host to parasitize was described for *P. hyalinus* by Smith (1912) for a tritrophic interaction involving *Hyphantria* Harris, 1841 caterpillars.

Twelve dipteran species are assigned as primary hosts of *Perilampus*, five within Sarcophagidae and seven within Tachinidae (Noyes, 2019). Among the dipteran species that host larvae of *Perilampus*, two species were indirectly associated with katydids. Allen and Pape (1996) describe, although indirectly, *Perilampus* associated with *Blaesoxipha* Loew, 1861 (Diptera: Sarcophagidae) obtained from the katydid *Sciarasaga quadrata* Rentz, 1993 (Tettigoniidae: Austrosaginae). Frisch (1936) reared *Perilampus* from puparia of Tachinidae and Sarcophagidae parasitoids of katydids; although this author stated that he could not observe the emergence of the flies directly from the katydids and emergence of *Perilampus* as well, he postulated a possible association of *Perilampus* with *Senotainia trilineata* (Wulp, 1890) (Diptera: Sarcophagidae) reared in cells provisioned with two species of Conocephalinae: *Neoconocephalus ensiger* (Harris, 1841), and *Conocephalus (Anisoptera) attenuatus* (Scudder, 1869).

Studies on parasitoidism are strongly precluded by the Linnean (Brown and Lomolino, 1998) and Wallacean (Lomolino, 2004) shortfalls, and even by the recently proposed Haeckelian shortfall (i.e. the lack of knowledge regarding the semaphoronts of species; see Faria et al.,

2021), so that many interactions remain unknown and/or undescribed. We could also consider that our ignorance of interactions itself are part of the Eltonian shortfall, i.e., the missing information about species interactions (Hortal et al., 2015).

To our knowledge, there are no previous records that specifically describe a host-parasitoid-hyperparasitoid multitrophic interaction involving *Conocephalus* Thunberg, 1815 (Orthoptera, Tettigoniidae, Conocephalinae), *Ormia* (Diptera, Tachinidae), and *Perilampus* (Hymenoptera, Perilampidae), including observation and detection of the species directly from reared individuals. Therefore, we report here for the first time both interactions among this host-parasitoid-hyperparasitoid system.

Specimens of *Conocephalus saltator* (Sausurre, 1859) were collected between September 2019 and February 2020, at the Parque Nacional do Iguaçu, Foz do Iguaçu, Paraná, Brazil (25.6299°S, 54.4630°W). This forest remnant is the largest fragment of Atlantic Forest in southern Brazil (Ribeiro et al., 2009; Paviolo et al., 2016), comprising both Seasonal Semideciduous and Mixed Ombrophilous Forests (Cervi and Borgo, 2007).

The katydids were collected by diurnal and nocturnal searching, through aural and visual localization, and with the aid of flashlights, sweeping and beating entomological nets. After collected, individuals were transported to the laboratory, individually kept in plastic containers (10 cm height x 15 cm diameter) and reared under controlled temperature (~25°C), relative humidity (~70%), and light/dark period of 10/12h, with fish food flakes and water *ad libitum* until their death. When puparia were found, each puparium was removed and placed in a small plastic container until the emergence of the adult parasitoid.

Identification of *Ormia* cfr. *crespoi* was based on the keys and descriptions provided by Tavares (1962, 1965a, 1965b, 1965c). Even if the specimens could be safely identified using the key provided by Tavares (1965b) (couplets 1-3-4-5), some characteristics of the specimens disagree with the original description of *Ormia crespoi*: (i) three humeral bristles, (ii) four bristles at the base of R5, (iii) abdomen (terga 4 and 5) slightly darkened, and (iv) entirely yellow calyptera. We then decided to adopt a more cautious approach, using "cfr.". The hindrance of safely identifying the species within the genus is even reported by Tavares himself (Tavares 1965a), when he even highlighted the need for further studies in order to better clarify the identity of the species. All vouchers were deposited at "Coleção Entomológica Danúncia Urban - CEDU-UNILA, (Foz do Iguaçu, Brazil)".

We reared 904 individuals of *Conocephalus saltator* (Fig. 1), obtaining 123 puparia that emerged from 113 parasitized katydids. From these 123 puparia, 18 adult flies emerged, nine males and nine females of *Ormia* cfr. *crespoi* (Fig. 2), and four *Perilampus* sp. (three females, one male) (Fig. 3). We can safely assume that the perilampid hyperparasitoids emerged from puparia of the same tachinid species, by comparing those from where the adult flies and the adult wasps emerged.

Literature data suggest that the larvae of *Ormia* develop within the host for a period of seven to ten days, when they emerge, killing the host and pupariating (Cade, 1975; Walker and Wineriter, 1991; Adamo et al., 1995; Zuk et al., 1995). Because we brought to the laboratory katydids that had been parasitized in the field, at an unknown time, we cannot present robust data on the timing of larval development; however, it was possible to estimate the duration of the pupal stage. We found that the time between pupariation and the emergence of adults ranged from 15 to 21 days (N = 18), a longer timespan than what was previously presented for *Ormia ochracea* (12–15 days; N = 91) and *Ormia depleta* (11–13 days; N = 78) (Wineriter and Walker, 1990). Regarding the development time of perilampids, Vinson and Iwantsch (1980) reported that adult wasps emerge from the puparium of their hosts between 20 and 30 days. We could track the development time of three wasps, i.e., the timespan between the pupariation of the

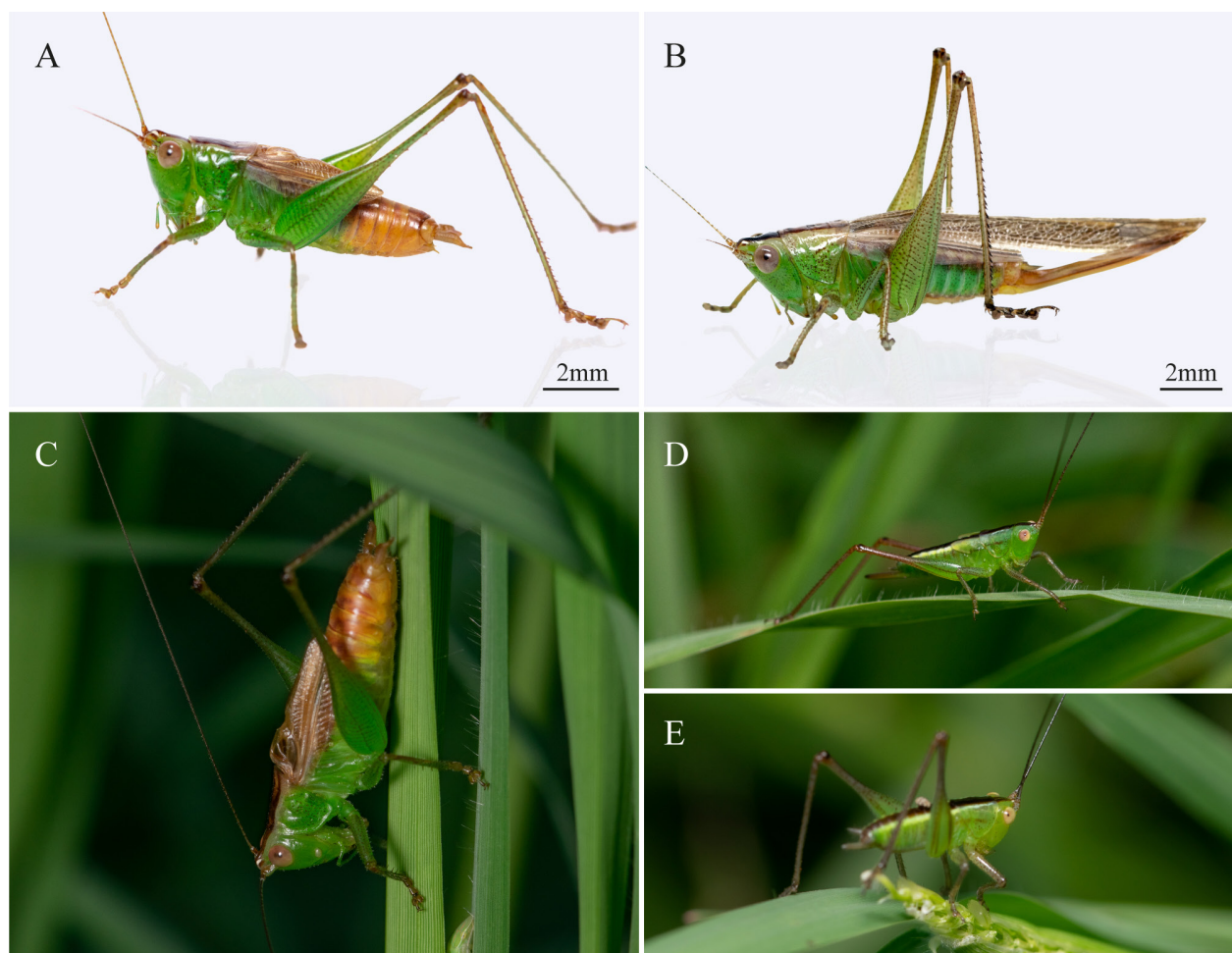


Figure 1 Individuals of *Conocephalus saltator*. A: Adult male; B: Adult female; C: Male nymph; D: Female nymph; E: Male nymph, feeding on grass seeds.

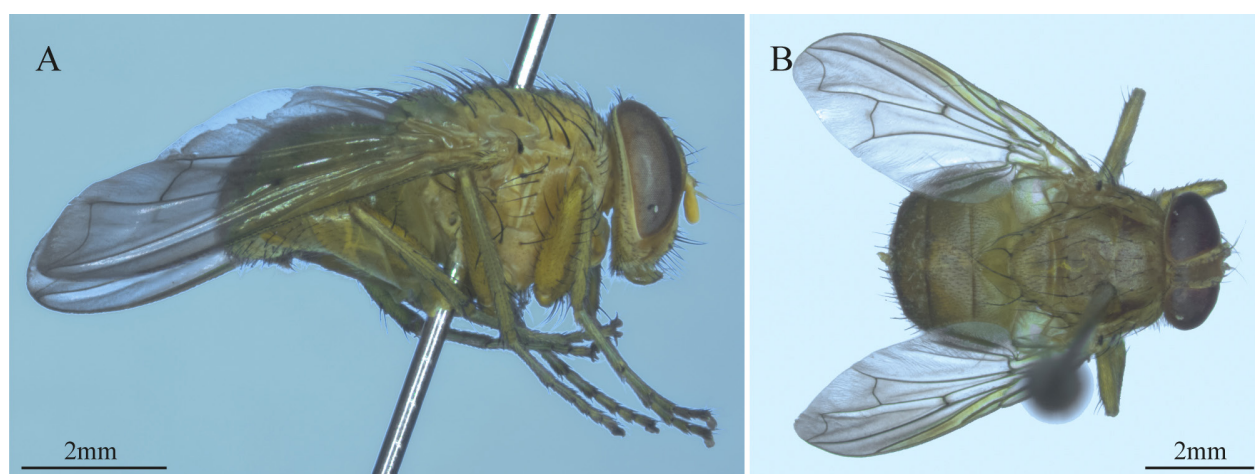


Figure 2 Individual of *Ormia* cfr. *crespoid*. A: Female, lateral view; B: Female, dorsal view.

tachinid fly and the emergence of adult wasps from those puparia, and we observed a slightly longer development time (27, 36 and 37 days).

Lehmann (2003) suggested the existence of regional preferences in host selection by species within Ormiini, as these flies are opportunistic parasitoids. This author also stated that repetitive song pattern in the species of Conocephalinae, with small differentiation between the sound produced by distinct species could favor host-switching. Thus,

it is noteworthy that we had not previously recorded any puparia of *Ormia* from sampled individuals of other katydid species (see Fianco et al., 2022). This is certainly an observation that demands additional studies.

A better understanding of host-parasite interactions and host ranges and even the increased availability of specimens of Ormiini in taxonomic collections can be a desirable by-product of projects where

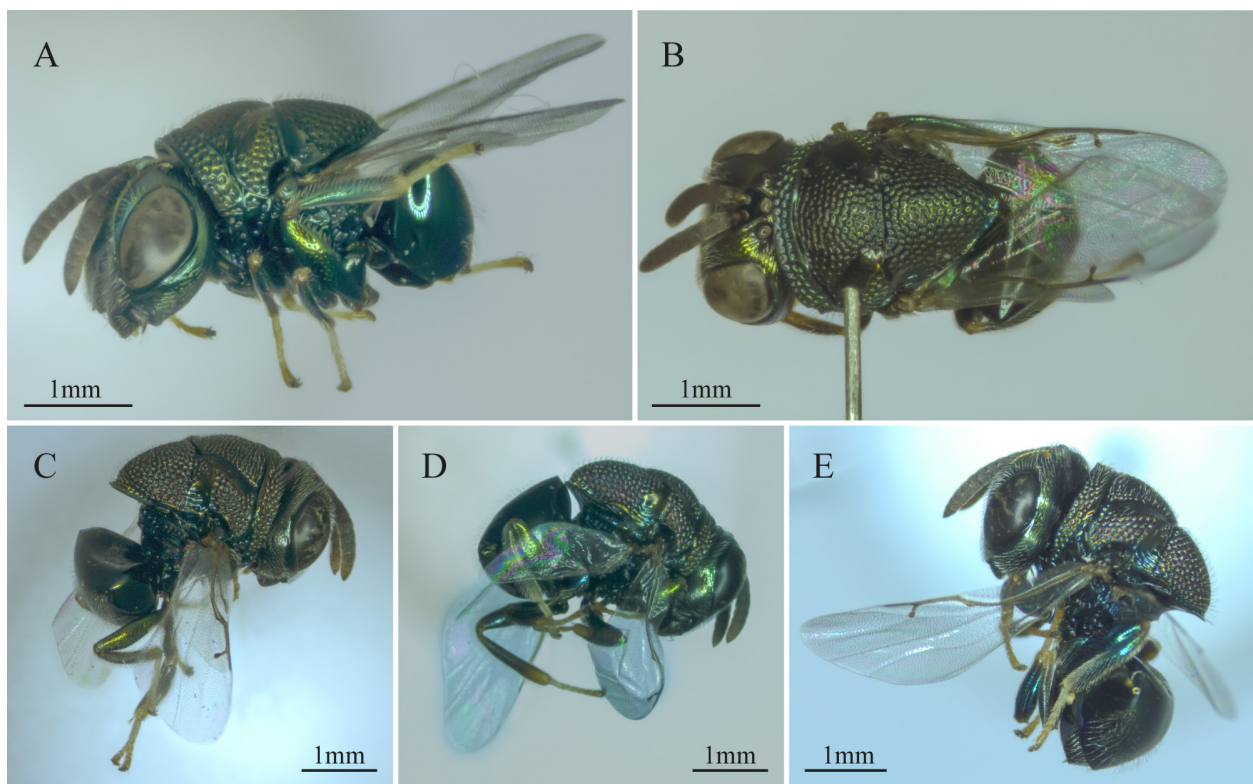


Figure 3 All reared specimens of *Perilampus* sp. A: specimen 477, lateral view; B: specimen 477, dorsal view; C: specimen 40; D: specimen 337; E: specimen 55.

orthopterans are reared aiming at recording their sounds. Lehmann (2003) stated that individuals of Ormiini are scarce in entomological collections, due to their crepuscular habits, despite being highly biased toward females, due to the use of sound traps for the samplings. Therefore, the collection of male flies becomes even more relevant.

It is worth noting that external evidence that a specimen of Ormiini is parasitized can be easily observed, especially in the case of hosts with lighter coloration, as the respiratory funnel of larvae imprints the host integument with a dark brown macula (Lehmann and Heller, 1998). After being detected, the maintenance of Diptera puparia is cheap and is not time consuming, requiring only space and periodical monitoring.

Current knowledge about these complex host-parasitoid-hyperparasitoid interactions is incipient, but the possibility that those interactions are much more widespread cannot be dismissed. We strongly believe that studies involving rearing and monitoring species of Orthoptera in laboratory will provide additional records of interactions in the future.

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Conflicts of interest

The author declares no conflicts of interest.

Author contribution statement

HP Conceptualization-Equal, Data curation-Equal, Investigation-Equal, Methodology-Equal, Writing – original draft-Equal, Writing – review & editing-Equal.

MF Conceptualization-Equal, Data curation-Equal, Investigation-Equal, Methodology-Equal, Writing – original draft-Equal, Writing – review & editing-Equal.

ADM Conceptualization-Equal, Data curation-Equal, Investigation-Equal, Methodology-Equal, Writing – original draft-Equal, Writing – review & editing-Equal.

EDGS Conceptualization-Equal, Data curation-Equal, Investigation-Equal, Methodology-Equal, Writing – original draft-Equal, Writing – review & editing-Equal.

LRRF Conceptualization-Equal, Data curation-Equal, Investigation-Equal, Methodology-Equal, Writing – original draft-Equal, Writing – review & editing-Equal.

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