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Defensive behaviors of the mealybug *Nipaecoccus nipae* (Maskell, 1893) (Hemiptera: Pseudococcidae) and the green lacewing *Ceraeochrysa claveri* (Navás, 1911) (Neuroptera: Chrysopidae), with videos of dorsal packet loading and mealybug ostiole function

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Defensive behaviors of the mealybug *Nipaecoccus nipae* (Maskell, 1893) (Hemiptera: Pseudococcidae) and the green lacewing *Ceraeochrysa claveri* (Navás, 1911) (Neuroptera: Chrysopidae), with videos of dorsal packet loading and mealybug ostiole function

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Abstract. The interactions between the lacewing *Ceraeochrysa claveri* (Navás) (Neuroptera: Chrysopidae) larva and the coconut mealybug *Nipaecoccus nipae* (Maskell) (Hemiptera: Pseudococcidae) were recorded. The third-instar lacewing larva constructed a dorsal packet using mealybug wax from both male pupal cases and the bodies of adult females. Surprisingly, live nymphs were also frequently placed into the dorsal packet. Prey mealybugs were discarded and not incorporated into the packet after consumption. When disturbed, adult female mealybugs reflex bled from their dorsal ostioles, contacting the mouthparts of the lacewing. The lacewing quickly retreated to clean the mouthparts on the substrate, providing further evidence that ostiolar fluids act as a defense mechanism for mealybugs. Despite repeatedly contacting the ostiolar fluid, the lacewing pupated and eclosed successfully. Macro video footage of dorsal packet construction and ostiolar reflex bleeding is included. This is the first report of *C. claveri* preying on *N. nipae*, the first evidence of *C. claveri* using mealybug wax to construct the dorsal packet, and the first account of reflex bleeding via the dorsal ostioles to deter predators in *N. nipae*.

Key words. Ostiole, reflex bleeding, dorsal cloak, Coccoidea, Coccoomorpha, predation, biological control.

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Introduction

Many lacewing larvae in the family Chrysopidae use exogenous materials to make a dorsal packet, a form of predator defense that earns them the common name, “trash-carriers” (reviewed in Tauber et al. 2014). Materials used to construct the dorsal packet may include arthropod remains, spider silk, aphid exudates, pieces of wood, trichomes, lichen, sand, and other debris (Smith 1922; Eisner et al. 1978, 2002; Tauber et al. 2014). These dorsal packets serve as camouflage and conceal their identity to potential predators (New 1969; Eisner et al. 1978; Nakahira and Arakawa 2006; Hayashi and Nomura 2011). As frequent feeders of economically important pest groups such as scale insects, aphids, thrips, and mites, lacewings are valuable natural enemies in both the natural environment and in agricultural settings (reviewed in Tauber et al. 2000b; McEwen et al. 2001; Miller et al. 2004).

The behaviors associated with loading the dorsal packet have been described for relatively few species (Smith 1922; Eisner et al. 2002; Eisner and Silberglied 1988; Tauber et al. 1995, 2014). Furthermore, there are relatively few detailed accounts of lacewing larvae using wax in the packet and rarely is the source of the wax identified (reviewed in Tauber et al. 2014). In 1922, Smith noted that chrysopids were using the cottony secretions of unspecified aphids. The behavior of using wax from sternorrhynchan bugs was detailed in Eisner et al. (1978) where the green lacewing *Chrysopa slossonae* Banks, 1924 plucks the wax of the woolly alder aphid *Prociphilus tesselatus* (Fitch, 1851) to construct their dorsal packet. This accumulation of wax effectively disguised the lacewing larvae from the ants that tend and aggressively protect the aphids (Eisner et al. 1978). When the dorsal packet was removed, the ants recognized the lacewing larvae as intruders and attacked them (Eisner et al. 1978). In other examples, psyllid wax is utilized in the dorsal packet of *Rexa lordina* Navás 1920 (Canard and Labrique 1989) and

flatid wax is used by *Ceraeochrysa lineaticornis* (Fitch, 1855) in the dorsal packet, along with sycamore trichomes and the flatid exuviae (Wheeler and Stocks 2019).

A similar behavior was recorded for *Ceraeochrysa cincta* (Schneider, 1851) larvae using the wax of the mealybug *Leptococcus eugeniae* (Miller and Denno, 1977) in the dorsal packet (Eisner and Silberglied 1988). Lacewings plucked the long wax filaments from mature mealybugs and incorporated the remains of mealybugs they had previously eaten to construct their packets (Eisner and Silberglied 1988). Mimicking mealybugs may deceive ant associates and dissuade predators that actively avoid eating mealybugs because of their wax and defensive secretions from dorsal ostioles (Gullan and Kosztarab 1997). The same species of lacewing is also known to use the wax of a whitefly, *Metaleurodicus griseus* (Dozier, 1936) in the dorsal packet (Mason et al. 1991). In another example, the lacewing *Apochrysa matsumurae* (Okamoto, 1912) (unconfirmed identification) was photographed with a dorsal packet constructed with male pupal cocoons of the monophleboid scale insect, *Drosicha corpulenta* (Kuwana, 1902) (Tauber et al. 2014).

Dorsal ostioles, slit-like openings that allow for defensive reflex bleeding, are present in many species from multiple families of Coccoomorpha including the mealybugs (Pseudococcidae), giant mealybugs (Putoidae), root mealybugs (Rhizoecidae), and Phenacoleachiidae (Ferris 1950; McKenzie 1967; Williams 1978; Gullan and Kosztarab 1997). Most species in these families have two pairs of dorsal ostioles, typically with one anterior pair on the prothorax and one posterior pair in the submarginal area between the six and seventh abdominal segments (Ferris 1950; McKenzie 1967). In a small percentage of species, the anterior pair of ostioles are absent or both pairs may be absent (Ferris 1950; Williams 1978). Ferris and Murdock (1936) found that the ostiolar fluid was the same as the body fluid (haemocoel) and Pesson (1939) suggested that the liquid expelled contains free wax. When mealybugs bearing dorsal ostioles are disturbed, a globule of liquid is released from one or more of the ostioles which quickly hardens once exposed to air (see Williams 1978 for further discussion on ostioles).

Ostioles have long been presumed to have a defensive mechanism, but this has rarely been tested, even though ostioles could have major implications in defensive interactions with natural enemies and/or by attracting the ants that tend them (Williams 1978; Gullan and Kosztarab 1997). Šulc (1909) posited that expelled free wax could coat the mouthparts of an attacker, which subsequent studies have supported (Gillani and Copeland 1999; Tapajós et al. 2016; Carvalho et al. 2023). In interactions between the lacewing *Symphorobius fallax* Navás, 1908 and the mealybug *Pseudococcus longispinus* (Targioni Tozzetti, 1867), the fluid quickly hardened on the lacewing mouthparts and caused death by starvation in some cases (Gillani and Copeland 1999). In others, the ostiolar fluid caused small lacewing larvae to become stuck to the mealybugs and die (Gillani and Copeland 1999). Larger third-instar lacewing larvae were better able to withstand the ostiolar fluid and had higher survival rates when attacking *Pseudococcus longispinus* (Gillani and Copeland 1999). In another study, *Phenacoccus peruvianus* Granara de Willink, 2007, *Planococcus ficus* (Signoret, 1875), *Pseudococcus calceolariae* (Maskell, 1879), and *Pseudococcus viburni* (Signoret, 1875), but not *Planococcus citri* (Risso, 1813), exhibited reflex bleeding when contacted by a parasitoid wasp (Bugila et al. 2014). In contrast with those findings, ostiolar fluid from *Planococcus citri* caused high mortality in *Chrysoperla externa* (Hagen, 1861), especially in first-instar nymphs (Carvalho et al. 2023). *Ferrisia dasyliirii* (Cockerell, 1896) third-instar nymphs and adults employed the use of ostiolar fluids to repel lacewing larvae (Tapajós et al. 2016). Again, the ostiolar fluid on the mandibles killed first-instar larvae and in older lacewings, hindered feeding which caused them to eclose as malformed adults (Tapajós et al. 2016).

The lacewing *Ceraeochrysa claveri* (Navás, 1911) is distributed from Brazil to Cuba (Adams and Penny 1985) and in south Florida in the United States (Tauber et al. 2000a). Though it is easily reared in the laboratory, little is known about the biology of *Ceraeochrysa claveri* in natural settings. In a laboratory setting, they can be raised exclusively on *Diatraea saccharalis* (Fabricius, 1794) crambid moth eggs (Scudeller et al. 2013) and *Plutella xylostella* (Linnaeus, 1758) diamondback moth eggs and larvae (Almeida et al. 2009). However, they fail to develop when fed mainly red palm mite, *Raoiella indica* Hirst, 1924 (Palomares-Pérez et al. 2021). In the field, they are reported to feed on two coccoids: the tea scale, *Fiorinia theae* Green, 1900 in Florida (Munir 1981) (Diaspididae), and the pink sugarcane mealybug *Saccharicoccus sacchari* (Cockerell, 1895) (Pseudococcidae) in Guyana (Bodkin 1917). Notz (1974) also reported "*Chrysopa* prob. *claveri*" as feeding on *Selenaspidus articulatus* (Morgan, 1889) (Diaspididae), *Pinnaspis* sp. (Diaspididae), and *S. sacchari* (Pseudococcidae) in Venezuela. This species has received much interest as an effective biological control agent and extensive work has tested its

resilience to insecticides such as neem oil (Scudeler and Carvalho dos Santos 2013; Scudeler et al. 2013, 2014, 2016) and *Bacillus thuringiensis* (Bt) Berliner, 1915 (Daquila et al. 2023).

The coconut mealybug, *Nipaeococcus nipae* (Maskell, 1893), is a widespread polyphagous species recorded to feed on over 113 genera of plants across 51 families (García Morales et al. 2016). In Florida, the most common plant hosts include *Psidium guajava* L., *Persea americana* Mill., *Annona* L., *Cocos nucifera* L., *Phoenix roebelenii* O'Brien, and *Ficus* L. (FDACS-DPI Database 2023). Several natural enemies are known for this pest mealybug across its distribution range including the green lacewing *Mallada basalis* Walker, 1853 (Caasi-Lit et al. 2012), brown lacewing *Micromus igorotus* Banks, 1920 (Caasi-Lit et al. 2012), seven species of coccinellid beetles (Bennett and Simmonds 1964; Moore 1988; Kondo and Watson 2022), nine encyrtid parasitoid wasps (Moore 1988; Kondo and Watson 2022), one aphelinid parasitoid wasp (Kondo and Watson 2022), and two predatory flies (Malumphy 2014; Kondo and Watson 2022). *Nipaeococcus nipae* is also known to associate with at least four species of ants in the Philippines (Caasi-Lit et al. 2012) and does associate with ants in Florida (pers. obs.), though the specific species have not been recorded. *Nipaeococcus nipae* females have two pairs of dorsal ostioles and produce copious amounts of dense wax arranged in rows of granular masses on the dorsum and in short tufts around the margin (Maskell 1893).

In the present study, defensive behaviors and interactions between the lacewing larva *Ceraeochrysa claveri* (Neuroptera: Chrysopidae) and the coconut mealybug *Nipaeococcus nipae* (Hemiptera: Pseudococcidae) were observed. Two main observations were captured on video and discussed herein 1) the construction of the dorsal packet using mealybug wax by *Ceraeochrysa claveri* and 2) the use of ostiolar fluids (i.e., reflex bleeding) by the coconut mealybug *Nipaeococcus nipae* to repel the lacewing larva.

Materials and Methods

Annona sp. (Annonaceae) plant material infested with *Nipaeococcus nipae* mealybugs was collected from a residential property in Palm Beach County, Florida on November 30th, 2022, by S. Simmons (DPI-LIST E5491-12012022-10510) and received in the lab on December 2nd, 2022. A single third-instar *Ceraeochrysa claveri* larva was present amongst the infestation. Behavior of the lacewing larva was observed, and photographs and video were taken with a Canon EOS 6D Mark II and a 65mm Canon MP-E f/2.8 1–5× macro lens. Photographs of the cocoon and adult were later taken with the same system. The larva was kept with the plant material and mealybugs for prey until pupation in a plastic Tupperware container. Upon spinning a cocoon near the midvein of a leaf, the leaf was removed and placed in a large snap cap vial. The larva spun a cocoon on December 7th, 2022, and emerged as an adult on December 29th, 2022.

Identification of *Ceraeochrysa claveri* was made following Tauber et al. (2000a) and of *Nipaeococcus nipae* using Williams and Granara de Willink (1992). The *C. claveri* voucher specimen and its cocoon is deposited in the Florida State Collection of Arthropods (FSCA) in Gainesville, Florida, United States (FSCA 00072095). Videos were corrected with video stabilization software (<https://online-video-cutter.com/stabilize-video>) and edited with Microsoft Video Editor. Supplemental Videos S3–S4 are first given at normal speed and then part of the clip is slowed to 0.5× and repeated. To ensure perpetuity and open accessibility of the videos, they have been archived in three repositories. Videos can be found on YouTube, Open Science Framework, and Archive.org. Links are available in the supplemental file captions.

Results

The lacewing larva rapidly alternated between constructing the dorsal packet (Fig. 1) and feeding (Fig. 2–3) over the observation period. It primarily used the wax from male mealybug pupal cocoons and the bodies of adult female mealybugs on the leaf to construct the dorsal packet (Supplemental Video S1). In several instances, the lacewing larva also scooped up live mealybug nymphs and dropped them onto the dorsal packet (Supplemental Videos S1, S5, Fig. 2–4). To construct the packet, the mandibles were used to pick up materials, then the head arched backwards to place the materials on the dorsum of the abdomen (Fig. 1). While adding materials to the packet but not feeding, the lacewing occasionally would get live mealybug nymphs and wax stuck to



Figure 1. *Ceraeochrysa claveri* larva loading the dorsal packet with *Nipaecoccus nipae* mealybug wax and live nymphs.



Figure 2. *Ceraeochrysa claveri* larva feeding on a *Nipaecoccus nipae* female. A live first-instar mealybug (yellow) is present on the right side of the dorsum of the lacewing.



Figure 3. *Ceraeochrysa claveri* larva feeding on a nymph of *Nipaeococcus nipae*. A live first-instar mealybug (yellow) is present on the right side of the dorsum of the lacewing.

the mandibles. It would continue to try to move the materials onto the packet, but at one point, scraped the mouthparts onto the leaf to remove a live mealybug nymph that was stuck (Supplemental Video S1 at 1:09). The lacewing larva fed on all life stages of the mealybug and was able to suck up the contents of a first-instar mealybug in less than 45 seconds (Supplemental Video S2). Though dead mealybugs and exuviae ended up in the dorsal packet, the lacewing did not specifically place the mealybugs it fed on in the packet. Instead, it typically would scrape these off the mandibles and leave them on the leaf (Supplemental Video S2 at 0:46).

No reflex bleeding was observed in the first- and second-instar mealybug nymphs. When the lacewing larva attempted to pluck wax from an adult female, a globule of bright orange fluid was released from the posterior ostioles (Supplemental Videos S3–S4). As the ostiolar fluid was released, the mealybug slightly raised the abdomen and expanded the most posterior anal lobe wax filaments (Supplemental Video S3). Upon contacting the ostiolar fluid, the lacewing retreated and rubbed its mouthparts on the leaf to remove the fluid. The adult mealybug never attempted to escape and the ostiolar fluid secretion was the only defensive mechanism observed. Once it stopped cleaning the mouthparts, the lacewing larva went back to gathering wax from a nearby male cocoon in one instance and in the second instance of contacting the ostiolar fluid, walked away from the area (Supplemental Videos S3–S4). During the observation period, the lacewing fed on another adult female that had already dispensed an ostiolar fluid previously, as indicated by the darkened dry red globule (Supplemental Video S5; Fig. 2), but



Figure 4. A screenshot from Supplemental Video S3 of the lacewing larva contacting the ostiolar fluid (orange) with its left mandible. Live first-instar mealybugs (yellow) are on top of both the lacewing larva and the adult mealybug.



Figure 5. The *Ceraeochrysa claveri* cocoon, with *Nipaecoccus nipae* wax and other debris incorporated. **a)** Prior to emergence. **b)** After emergence.

this female did not release more ostiolar fluid on contact. Upon pupation, the debris from the dorsal packet was incorporated into the cocoon (Fig. 4). Cocoon spinning to adult eclosion took 22 days (Fig. 5).

Discussion

This study provides evidence for and video documentation of the use of dorsal ostioles (i.e., reflex bleeding) as defense in *Nipaecoccus nipae* and adds to growing evidence that the ostiolar secretions in mealybugs can be effective defensive mechanisms against natural enemies (Gillani and Copeland 1999; Tapajós et al. 2016; Carvalho et al. 2023). On contact with the ostiolar fluid, the lacewing larva rubbed its mouthparts on the leaf substrate to remove the secretion. This, to my knowledge, is also the first published video documentation of the construction of the dorsal packet in *C. claveri*. The loading of the dorsal packet follows other descriptions where materials are gathered in the mouthparts and the head arches backwards to position the materials on the dorsum (Eisner et



Figure 6. The *Ceraeochrysa claveri* adult. a–b) A close-up of the head and thorax. c) Next to the empty cocoon.

al. 2002; Eisner and Silberglied 1988). Mealybug wax and other debris is also incorporated into the cocoon. The contents of the dorsal packet and cocoon are probably chosen opportunistically given the polyphagous nature of this species. Based on photos provided in Daquila et al. (2023) of a naked cocoon, prey remains are not or cannot be incorporated into the cocoon when larvae are fed solely on moth eggs in a laboratory setting.

In the mealybug *Pseudococcus longispinus*, abdominal flipping and pushing away lacewing predators were both defensive mechanisms used in conjunction with reflex bleeding (Gillani and Copeland 1999). Similarly, *Phenacoccus peruvianus*, *Planococcus citri*, *Planococcus ficus*, *Pseudococcus calceolariae*, and *Pseudococcus viburni* all exhibited abdominal flipping and made attempts to walk away to escape when attacked by a parasitoid wasp (Bugila et al. 2014). However, none of these behaviors were observed in the *Nipaecoccus nipae* here, though the abdomen did slightly raise when the ostiolar fluid was released (Supplemental Video S2). Reflex bleeding from the ostioles was the only defensive behavior observed with adult females. The grooming response by the lacewing

larva after getting ostiolar fluid on the mouthparts is consistent with other studies of mealybug and lacewing interactions where lacewing mouthparts were compromised by the fast-drying fluids (Tapajós et al. 2016), though the wiping behavior observed here was not detailed in those studies. Herein, dorsal packet construction was risky, as the lacewing contacted the ostiolar fluids while building the packet. The lacewing larva also contacted ostiolar fluid multiple times on the same individual mealybug during the observation period, suggesting that the ostiolar fluid was not a strong enough deterrent for learned avoidance.

Ostiolar fluid in *Nipaeococcus nipae* was discharged orange and dried a bright red (Fig. 2, Supplemental Video S5). *Nipaeococcus nipae* body contents are also orange, which is evident through the cuticle when the wax is stripped off (Fig. 3). Other species, such as *Pseudococcus longispinus*, are reported to have clear and colorless ostiolar fluid (Gillani and Copeland 1999), also corresponding with the color of their internal body contents. For predators with long wavelength color vision, it is possible that the orange, then dried red, ostiolar fluid could relay additional aposematic benefits to the mealybugs. It has been postulated that the bright red carminic acid of cochineal bugs, *Dactylopius confusus* (Cockerell, 1893) could function as an aposematic deterrent to visually oriented predators (Eisner et al. 1980). To my knowledge, the role of aposematic defense has not been tested in any of the Coccoomorpha, despite red, orange, and yellow coloration occurring frequently across the group.

One surprising observation was the number of live mealybug nymphs placed in the packet by the lacewing larva. Interestingly, the lacewing discarded the bodies of nymphs it ate and did not add those to the packet, possibly because they were pierced onto the mouthparts and challenging to remove. This contrasted with *Ceraeochrysa cincta* which used the wax and bodies of eaten *Leptococcus eugeniae* mealybugs to construct the packet (Eisner and Silberglied 1988). Given the heavy infestation of mealybugs, it was difficult for the larva to access wax that was not teeming with first- and second-instar mealybugs. If anything, incorporation of live mealybugs seemed to impede the dorsal packet construction because the mealybugs crawling around and off the dorsum of the lacewing likely knocked off parts of the packet. It is known that coccoid crawlers utilize more mobile animals such as flying insects, birds, and mammals for phoretic dispersal (Washburn and Frankie 1981; Klein et al. 1992; Poinar 2004; Magsig-Castillo et al. 2010; Shcherbakov 2022). Lacewings could facilitate dispersal if larvae are frequently including live insects in their packets and moving between different host plants.

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Supplemental Materials

Supplemental Video S1. *Ceraeochrysa claveri* larva loading the dorsal packet with the wax and live nymphs of *Nipaeococcus nipae*. Video available on YouTube (<https://youtu.be/As95aTckQZs>), Open Science Framework (<https://osf.io/sg8n9>), and Archive.org (<https://archive.org/details/ceraeochrysa-claveri>).

Supplemental Video S2. The *Ceraeochrysa claveri* lacewing larva feeds on a first-instar *Nipaeococcus nipae* nymph, piercing it with the mouthparts and extracting the body contents. Once finished, the lacewing larva scrapes the mealybug body off onto the leaf and discards it. Video available on YouTube (<https://youtu.be/qqBj1Tdtjp4>), Open Science Framework (<https://osf.io/u5h4n>), and Archive.org (<https://archive.org/details/ceraeochrysa-claveri>).

Supplemental Video S3. Reflex bleeding from the left posterior ostiole by the coconut mealybug, *Nipaeococcus nipae*. The *Ceraeochrysa claveri* lacewing larva touches the globule of ostiolar fluid, retreats and begins to wipe its mouthparts on the substrate to remove the ostiolar fluid. The video is first given at normal speed (1×) and then a portion of the clip is slowed to 0.5× and repeated to show the contact with the ostiolar fluid. Video available on YouTube (<https://youtu.be/NjWfO1jJlwQ>), Open Science Framework (<https://osf.io/ghck5>), and Archive.org (<https://archive.org/details/ceraeochrysa-claveri>).

Supplemental Video S4. Reflex bleeding from both posterior ostioles by the coconut mealybug, *Nipaeococcus nipae*. The *Ceraeochrysa claveri* lacewing larva touches the globule of ostiolar fluid, retreats and begins to wipe its mouthparts on the substrate to remove the ostiolar fluid. The video is first given at normal speed (1×) and then a portion of the clip is slowed to 0.5× and repeated to show the contact with the ostiolar fluid. Video available on YouTube (<https://youtu.be/atqNRImAWiY>), Open Science Framework (<https://osf.io/ym43k>), and Archive.org (<https://archive.org/details/ceraeochrysa-claveri>).

Supplemental Video S5. The *Ceraeochrysa claveri* larva feeding on an adult female *Nipaeococcus nipae* mealybug. It is unclear whether the mealybug is still alive, spent ostiolar fluid has dried on the dorsum (dark red). A first-instar *Nipaeococcus nipae* crawler can be seen moving around on the dorsum of the lacewing larva. Video available on YouTube (<https://youtu.be/D5AjjcL70zk>), Open Science Framework (<https://osf.io/gj97r>), and Archive.org (<https://archive.org/details/ceraeochrysa-claveri>).

