Facultative commensalism of gastropods (Mollusca: Gastropoda) in Neoponera verenae Forel, 1922 (Formicidae: Ponerinae) nests

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Abstract

Ants are a ubiquitous, diverse, and ecologically dominant group and use different types of substrates for nesting. Ant nests offer protection and food in a temperature- and humidity-stable environment. Such an environment attracts numerous organisms that live in association with these social insects. The occurrence and interactions of some myrmecophilous groups have been widely studied, such as those of coleopterans and lepidopterans. Other groups have been neglected in this regard, such as gastropods. This study presents a series of observations of the interactions between gastropods and the Neotropical ponerine ant *Neoponera verenae*. A total of 56 individuals belonging to four families, seven genera, and eight species of terrestrial gastropods were found in ant nests established in three types of substrates (dry cocoa pod, soil, and decaying wood trunk). The most frequent gastropod family was Achatinidae (n = 41), followed by Scolodontidae (n = 13), Helicinidae (n = 1), and Vitrinidae (n = 1). The most frequent genera were *Allopeas* and *Leptinaria* (both from Achatinidae), which together accounted for 57.1% of the observed specimens. Young and adult individuals of *Leptinaria* sp.1 were found in ant nests. Neither aggressive nor predatory behaviors were recorded in interactions between ants and gastropods. Gastropods mainly made use of the shelter provided by ant nests, their favorable and stable microclimatic conditions, and the abundant food resources stored in waste chambers. Our study includes unpublished records of ant nest commensals and presents hypotheses on the close interactions between gastropods and ants.

Introduction

The association of diverse taxonomic groups with social insect colonies is a frequent phenomenon. Such interactions can be observed in termite (Costa et al. 2009; Cristaldo et al. 2012), bee (Fliszkiewicz et al. 2012), and ant (Hölldobler and Wilson 1990; Araújo et al. 2019; Castaño-Meneses et al. 2019) nests. As stated by Moreira et al. (2020), ant nests are remarkably stable habitats in terms of humidity and temperature (homeostasis), providing optimum conditions for numerous organisms to complete their life cycle or part of it. These conditions attract a wide variety of invertebrates and even some vertebrates to live inside or near ant nests (Donisthorpe 1927; Parmentier 2020; Hölldobler and Kwapich 2022). Myrmecophiles, in general, need to overcome the defenses of the ant nest (Hölldobler and Wilson 1990) to gain access to shelter and resources (Eguchi et al. 2005; Hughes et al. 2008; Hölldobler and Kwapich 2022).

Ants represent the most diverse and ecologically dominant group of social insects (Wilson 1971; Hölldobler and Wilson 1990; Wilson and Hölldobler 2005a, b; Kass et al. 2022), showing varied nesting habits. Ants can establish their nests on the ground (Eldridge 1993; Delabie et al. 2007), on seeds (Silva et al. 2009), on fruits (Botelho et al. 2017), on hollow branches and wood fragments in the leaf litter layer (Delabie et al. 1997; Carvalho and Vasconcelos 2002), in association with epiphytes (Da Rocha et al. 2015), under the bark of trees (Weir and Kiew 1986; Delabie et al. 1997), in the tree canopy (Klimes et al. 2012; Ribeiro et al. 2013), and even as non-permanent bivouacs, as occurs in army ants (Schneiria 1971). In the Neotropical region, studies investigating ant species that build carton nests, or establhish their nests in cocoa pods or at the basal region of epiphytes revealed a particularly rich fauna associated with the ant genera *Camponotus*, *Eciton*, and *Neoponera* (Rettenmeyer et al. 2011; Lachaud and Lachaud, 2014; Castaño-Meneses et al. 2015, 2019; Araújo et al. 2019; Rocha et al. 2020).

After crossing the defense barriers of ant nests, myrmecophilous organisms may act as predators, scavengers, temporary commensals, social parasites, ectoparasites, or endoparasites (Lapeva-Gjonova 2013; Maruyama et al., 2013), and may depend on ants during all or part of their life cycle (Wheeler 1910; Hölldobler and Wilson 1990). Myrmecophiles comprise a broad range of taxa, mostly arthropods or more rarely vertebrates and gastropods (Hölldobler and Wilson 1990; Witte et al. 2002). Myrmecophilous groups such as beetles and butterflies have received special attention, being described in extensive studies (Fiedler 1991; Rojo De La Paz 2000; Maruyama et al., 2013; Zakharov and Yanushev 2019; Sazhnev and Turbanov 2020). Other taxa, however, have been neglected (Hsu et al. 2020), having only a few casual observations, as is the case of gastropods (Castaño-Meneses et al. 2015, 2019; Araújo et al. 2019).

Gastropod–ant interactions typically fall into one of the following three categories: (i) there are several reports of the use of dead gastropod shells by ants of different species for nesting (e.g., see Jahyny et al.2003; Jahyny 2010; Bogusch et al.2018; Tlueste and Birkhofer 2021); (ii) there are observations of gastropod shells abandoned inside ant nests or in refuse piles, suggesting predation of mollusks by ants, observations of active predation (e.g., see Páll-Gergely and Sólymos 2009; Bertrand 2010), and observations of shells mistaken for other resources and carried to the nest (e.g., see Urbanski 1965); and (iii) there are a few rare observations of active gastropods inside ant nests, such as those described by Eguchi et al. (2005), Witte et al. (2002), and the current study.

Interactions between gastropods and ant colonies vary according to the species involved, gastropod size, and recognition/camouflage strategies (Witte et al. 2002; Eguchi et al. 2005). The use of shells for nest building has been reported in natural and anthropized environments in several Myrmicinae species, such as *Myrmica sabuleti* (Meinert, 1860), *Temnothorax crassispinus* (Latreille, 1798), *Temnothorax nigrips* (Mayr, 1855), and *Temnothorax parvulus* (Schenck, 1852) (Bogusch et al. 2018). As for the second type of interaction which is documented for Myrmicinae too, studies analyzing nests of the genus *Messor* in Turkey and Spain found evidence of predation on Eupulmonata shells (Bertrand 2010; Páll-Gergely and Sólymos 2009). Two species of the genus *Curvella* (Gastropoda: Eupulmonata: Achatinidae) were identified among individuals collected from *Myrmicaria natalensis eumenoides* Gerstacker, 1859 ant nests in Tanzania (Verdcourt 2002). An interaction study conducted in Bulgaria reported that *Strigillaria thessalonica* Rossmässler, 1839 individuals were carried by *Messor rufitarsis* Fabricius, 1804 workers to the ant nest, likely because of the similarity between gastropod shells and Poaceae seeds (Urbanski 1965). The third type of interaction is commensalism, whereby symbionts coexist peacefully with ants inside the nest via social integration mechanisms and enjoy the protection provided by the colony (Hölldobler & Wilson 1990; Witte et al. 2002; Moreira et al. 2020). The first observation of the occurrence of such complex interactions between gastropods and ants characterized by interspecific adaption mechanisms was made in Malaysia (Witte et al. 2002). In the cited study, *Allopeas myrmekophilos*

R.Janssen, 2002 was observed inside colonies of *Leptogenys processionalis distinguenda* Emery, 1887 (Ponerinae). These gastropods lived inside temporary ant nests without being disturbed and were carried by ant workers whenever the colony changed location (Witte et al.2002; Witte et al.2008). Secretions produced by *A. myrmekophilos* during interactions with *L. distinguenda* workers are believed to mediate ant attraction. Gastropods were recorded in ponerine ant nests in different Brazilian environments (Peixoto et al. 2010; Castaño-Meneses et al. 2015, 2019; Araújo et al. 2019; Moleiro et al. 2021). However, there is no confirmation that these gastropods were actual myrmecophiles, given the lack of information about interactions between these organisms and their respective hosts.

Neoponera verenae Forel, 1922 is a medium-sized (8–9 mm) ponerine ant found in a range of habitats. These ants use branches, trunks, dry fruits, decayed wood, and soil as substrate for nest establishing (Delabie et al. 2008). As for their feeding behavior, *N. verenae* ants are mainly predators and scavengers (Traniello and Hölldobler 1984; Wild 2002; Mackay and Mackay 2010; Araujo et al. 2019). In humid climate environments, *N. verenae* is frequently found nesting in litter (Delabie et al. 2015), whereas, in other environments, their nests may be built in the soil, holes, intact and decaying trunks, and dry fruits (Wild 2005; Delabie et al. 2008; Mackay and Mackay 2010). Ongoing studies investigating the diversity of myrmecophiles associated with *N. verenae* indicated the presence of considerable numbers of gastropods inside ant nests and the occurrence of interactions between gastropods and ant workers within the colony. This study aimed to describe interactions between gastropods and *N. verenae* and propose hypotheses to explain them.

Materials And Methods

A field study was conducted in Ilhéus, Bahia State, Brazil, between November 2021 and April 2022. Collections were carried out at experimental sites of the Cocoa Research Center (CEPEC, CEPLAC) (14°46'5.66"S 39°13'18.55"W) and in a forest fragment on the campus of the State University of Santa Cruz (UESC) (14°47'53"S 39°10'20"W). The climate of the region is equatorial (Af type) (Köppen 1936), with average temperatures ranging from 20 to 25 °C and annual precipitation of 2000 to 2400 mm (Santana et al. 2003). A total of 28 nests of *N. verenae* were collected from three different substrates, namely cocoa pods found on the soil (n = 19), decaying trunks (n = 6), and soil (n = 3). All nests were evaluated for the presence or absence of gastropods.

Nests were located by active search supported by baits (sardines in comestible oil and apples with honey) distributed at each site, which allowed us to follow *N. verenae* foragers back to the nest. Nests built in tree trunks and cocoa pods were rapidly collected in their entirety and placed in plastic bags. For collection of ant nests built in the soil, we applied the method proposed by Moreira et al. (2020). All biological material was taken to the Laboratory of Social Arthropods (LABAS, UESC) for screening and identification of myrmecophiles. The occurrence of gastropods and their interactions with ants inside the nests (trunks, dry cocoa pods, and soil) were recorded on photographic and film material in the field and at the laboratory. Additional observations were made at the sites where gastropods were found. Nest population data (numbers of workers, sexually mature individuals, and immature individuals) were also collected.

In the laboratory, the biological material was screened, and gastropods were individually fixed in 70% alcohol and stored in labeled flasks. Gastropods were identified at the most accurate taxonomic level possible. Specimens were deposited in the collection of the Professor Maury Pinto de Oliveira Museum of Malacology at the Federal University of Juiz de Fora, Minas Gerais, Brazil. Gastropod nomenclature and classification followed the MolluscaBase (2023). *N. verenae* specimens were deposited in the Formicidae collection of the Myrmecology Laboratory, Cocoa Research Center (CPDC), Executive Commission for Cocoa Cultivation Planning (CEPLAC) (Delabie et al. 2020).

Results

Of the 28 nests collected, 7 (25%) contained gastropods. Sixteen gastropod individuals were observed in two nests dug in the soil, 36 in three nests found in fallen tree trunks, and 4 in two nests found in fallen cocoa pods. The 56 gastropods sampled belonged to four families, namely Achatinidae (41), Scolodontidae (13), Helicinidae (1), and Vitrinidae (1). Information on the abundance, location, substrate type, and size range of sampled gastropod individuals is presented in Table 1.

Table 1:Terrestrial gastropods found in nests of *Neoponera verenae*: nest, location, nest-building substrate, family, species, abundance, and size

The family Achatinidae had the highest richness, with five species (*Allopeas* sp., *Allopeas micra* d'Orbigny, 1835, *Beckianum beckianum* Pfeiffer, 1846, *Dysopeas muibum* Marcus & Marcus, 1968, and *Leptinaria* sp.), occurring on all three types of nesting substrates. The second most abundant family, Scolodontidae, was represented by a single species (*Happia* sp.), observed inside nests built in tree trunks and soil. The families Helicinidae and Vitrinidae were represented by one individual each, found in nests built in the soil (*Helicina* sp.) and in a cocoa pod (*Vitrina* sp.) (Table 1). The genera *Leptinaria* and *Allopeas* were foundin six and three of the seven ant nests, respectively, representing together 57.1% of all observed gastropods. Representatives of *Allopeas* were present in nests built in tree trunks and soil, whereas *Leptinaria* individuals were found in the three nesting substrates (Table 2). *Leptinaria* sp. was the most abundant (n = 15 individuals) and the most constant species (n = 6 nests). This species was found in the three nesting substrates. The second most abundant species was *Happia* sp., with 13 individuals found in a nest located in a tree trunk and one found in a soil nest (Table 1). Some species were particularly abundant in specific nest substrates, such as *Allopeas* sp. (n = 8) in soil nests (all individuals were observed in the third chamber) and *B. beckianum* (n = 8) and *Happia* sp. (n = 11) in trunk nests. The species *D. muibum*, *Helicina* sp., and *Vitrina* sp. were represented by a single individual each.

Observed interactions

To determine the maturity of gastropods, we assessed characteristics such as shell size, number of shell whorls, and lip thickness. In *N. verenae* nests, we identified from young (partially developed shells) to adult gastropods. In soil nests, most of the gastropods were found in the deepest chambers, where ant workers tend to immature individuals (eggs and larvae). Gastropods were distributed in different points of chambers and did not form aggregates, nor were they in close contact with immature ants. In trunk nests, by contrast, gastropods were distributed near immature individuals (eggs, larvae, and pupae), in close contact with them. Gastropods were also found near refuse, where they were observed to be moving on top of carcasses' fragments from different types of prey (Coleoptera, Diptera, and other unidentifiable carcasses of small invertebrates). Nests built in cocoa pods were not compartmentalized; thus, it was not possible to establish a definite location of occurrence of gastropods. The majority of gastropods were immature and had a length of less than 1.5 mm.

Adults of *Allopeas* sp., *A. micra*, *B. beckianum*, *D. muibum*, *Happia* sp., and *Leptinaria* sp. were found to be interacting with workers, larvae, pupae, and eggs of *N. verenae* (Fig. 1). Workers touched gastropods with their antennae and legs (Fig. 1c). No aggressive behavior was observed: workers approached the gastropods, remained in contact for some time (tens of seconds), and then continued with their activities. This kind of interaction occurred with different workers and was frequent. The observed gastropods were always in motion and sometimes maintained contact with ant larvae, eggs, and pupae. Sometimes, gastropods remained immobile for long periods near aggregates of immature ants. No predation of gastropods by ants or of immature ants by gastropods was observed.

In nest chambers, gastropods moved freely, as also reported by Witte et al. (2008). In some cases, we observed mucus and foam production, possibly related to locomotion, recognition, feeding, and, perhaps, defense (Fig. 1a and b). The chambers where gastropods were active had high apparent humidity, and, in these spaces, other groups of invertebrates, such as mites and Collembola, were simultaneously present.

Fig. 1: A-F: Interactions of *Neoponera verenae* with terrestrial gastropods. (a) *Leptinaria* sp. producing foam inside the nest. (b) *Leptinaria* sp. next to immature ants. (c) Ants making antennal contact with snails. (d–e) Snail in soil nests interacting with workers and immature ants. (f) Snail in decaying trunk nest found on the ground.

Discussion

Gastropods were found in seven *N. verenae* nests established in different substrates (soil, tree trunks, and cocoa pods). Previous studies reported the occurrence of gastropods in nests of *Diacamma*, *Mayaponera*, and *Neoponera* (Verdcourt 2002; Witte et al. 2002; Eguchi et al. 2005; Araújo et al. 2019; Castaño-Meneses et al. 2019). Terrestrial gastropods were identified taxonomically in a few of these studies, but no study had yet described the interactions between groups of organisms in nests, which makes our study a pioneering effort in this regard. It should be noted that we identified a large variety of gastropod species, all of which are true myrmecophiles according to the definition of Witte et al. (2002). Witte et al. (2002) identified a single species of myrmecophilous gastropod (*A. myrmekophilos*) and Eguchi et al. (2005) identified four species (Subulinidae sp. 1, Subulinidae sp. 2, Subulinidae sp. 3, and Pupinidae sp.). Witte et al. (2002) defined true myrmecophilous gastropods as those that (i) live inside ant nests in the same chambers as immature ants, (ii) do not suffer injuries when in contact with workers, (iii) are transported when the colony changes location, and (iv) secrete mucus of a different texture than that used for locomotion when interacting with workers.

There are few records of gastropods being carried by workers into nests, and some reports of gastropods actively penetrating nests. These behaviors were observed by Neckheim and Boer (2019), who documented the occurrence of gastropods being taken into nests of the Formicinae *Formica rufa* Linnaeus,1761 and gastropods actively entering nests. In Turkey, some gastropods were found to serve as food resources for ants, such as the Myrmicinae *Messor caducus* (Victor, 1839) and *Messor oertzeni* (Victor, 1839), with an impressive predation rate of 60% (Páll-Gergely and Sólymos 2009). Non-prey individuals have shells that are likely unbreakable or insurmountable to ants or emit chemical signals that prevent predation (Páll-Gergely and Sólymos 2009).

Our observations of gastropods in *N. verenae* nests indicated non-predatory behavior. Gastropods were found to settle in nests without being attacked. Absence of agonistic behavior of ants toward gastropod tenants was also observed by Vaisman and Mienis (2011) in nests of *Messor ebeninus* Santschi, 1927. One factor possibly influencing the ant–gastropod relationship is the size of gastropods. Small individuals tend to go unnoticed in ant nests, such as *Allopeas gracile* Hutton, 1834, *Paropeas achatinaceum* Pfeiffer, 1846, and *Subulina octona* Bruguière, 1789, which were ignored by *L. processionalis distinguenda* (Witte et al. 2002). Other mollusks rely on physical protection provided by the shell and secretions (mucus) to defend themselves against ant attacks (Witte et al. 2002). However, in *N. verenae* nests,gastropods ranging in size from 1.4 to 9.5 mm were observed (see Table 1), suggesting that mollusk size was not a determining factor for coexistence in ant nests.

Among the type of nests analyzed, those established in decaying trunks had the highest number of individuals, followed by soil nests. The high number of gastropods in trunk and soil nests is possibly associated with the larger size of nests (variable not tested here). These substrates are more conducive to the presence of these organisms compared with fallen cocoa pods, which are notably smaller in size.

The most represented family in this study, Achatinidae, was also observed in ant nests studied by Witte et al. (2002), Castaño-Meneses et al. (2019), and Araújo et al. (2019). In this family, *Leptinaria* sp. was the most frequent species. Individuals were collected from the three substrates, with representatives at different phases of the life cycle. This finding suggests that the gastropod uses ant nests at all stages of its biological cycle, supporting its status as a true myrmecophile. Species from the family Achatinidae exhibit diversified strategies during their life cycle; some are oviparous, whereas others are ovoviviparous, with the possibility of uniparental reproduction (Dundee 1986; Almeida and Bessa 2001;d'Ávila and Bessa 2005a, b; Pilate et al. 2013; d'Ávila et al. 2018). Factors such as food availability, temperature, physical space, population density, humidity, and photoperiod are determinant for terrestrial mollusk development (Albuquerque de Matos 1989). The abundance of gastropods in *N. verenae* nests might be linked to the effect of these abiotic and biotic factors and availability of nesting sites offered by *N. verenae*.

The frequency of occurrence of gastropods near refuse suggests that these organisms feed on prey remains and other food items left by workers. According to Castaño-Meneses et al. (2015), there is an accumulation of organic matter in ant nests, composed of debris, stored food, and excretions of several natures. These resources can be used by different groups of organisms living in the same environment, leading to close relationships with ants. *Allopeas* sp., *A. micra*, *B. beckianum*,and *Leptinaria* sp. produced foam/mucus when near refuse (Fig. 1a and b), apparently more abundantly than individuals of the same species that were further from refuse. *N. verenae* nests do not have a clear internal division; workers were found in all areas of the nest, even when gastropods were in contact with refuse.

Mucus produced by terrestrial gastropods has adhesive and lubricant properties that allow individuals to attach to the substrate (Cilia and Fratini 2018). Furthermore, mucus decreases the chances of dehydration, repels possible predators, and helps in grasping food (Hamalainem and Jarvinem 2012; South 1992). The high production of foamy mucus by gastropods associated with *N. verenae* might be related to the need to reinforce their odor after contact with ant prey inside nests. A hypothesis is that the mucus allows gastropods to move around the nests without being attacked by ants. According to Parmentier (2020), chemical residues are fundamental for nestmate recognition; these residues are composed of a colony-specific mixture of low-volatility signals present in the cuticle. Mimicking the chemical profile of the host can result in complete acceptance of gastropods by the colony. Thus, individuals with the same odor are treated as colony members, whereas individuals with different odors are rejected (van Zweden and d'Ettorre 2010).

Foamy mucus or large quantities of common mucus may be an anti-predatory defense strategy (Rollo and Wellington 1979; Pakarinen 1994; Mair and Port 2002). The production of mucus foams at the shell opening in the gastropods *Helicina adspersa* (Pfeiffer, 1839), *Chondropoma pictum* (Pfeiffer, 1839), *Aegista vermis* (Reeve, 1852), and *Plectotropis mackensii* (Adams & Reeve, 1859) was reported as a strategy to avoid predation by coleopterans of the family Lampyridae (Madruga Rios and Hernández Quinta 2010; Sato 2019). Predation by different beetle species was low among *Arion fasciatus* (Nilsson, 1823) and *Deroceras reticulatum* (Müller, 1774) individuals that produced high amounts of dorsal gland mucus, differing significantly from predation on stressed *D. reticulatum* (reduced ability to produce mucus) (Pakarinen, 1994; Mair and Port, 2002).

The increase in mucus production by *Allopeas* sp., *A. micra*, *B. beckianum*,and *Leptinaria* sp. when near refuse might be a defense response against predation attempts by other myrmecophilous invertebrates also present in the nests. None of the aforementioned gastropods have an operculum (corneous or calcareous anatomical structure that serves as a type of trapdoor of the shell opening, protecting the gastropod); thus, it is possible that the foam-like mucus served as a barrier to protect the shell opening. Sato (2019) analyzed the predation success of the firefly *Pyrocoelia atripennis* Lewis, 1896 on gastropod species with and without operculum and with and without the ability to produce foamy mucus. Fireflies were unable to predate gastropods capable of producing the mucus cap, even when they did not have an operculum.

The relationships observed between gastropods and adult and immature ants were harmonious, without apparent aggressions. According to Witte et al. (2002), the more frequent the direct contact with aggressive ants without damage to gastropods, the more gastropods benefit from protection against other eventual predators. Given this, it is understood that these gastropods share ant nests for benefits related to shelter, food, and environmental stability (temperature and humidity), without being disturbed by the hosts.

This study presents original data on interactions between gastropods and ants, focusing mainly on the family Achatinidae, the most abundant group in our sample. However, there are still questions to be clarified, such as the degree of interaction between gastropods and immature ants and the possible role of chemical signals in these interactions. Finally, the level of interaction between gastropods and *N. verenae* observed here is unprecedented. Future studies should explore gastropod behavior, evolution, and chemical nature of mucus in ant–gastropod interactions. Furthermore, this study reported several species that live in ant nests and interactions that are new to science.

Declarations

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Conflicts of interest

The authors declare no competing interests.

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Availability of data and material (data transparency)

All data are available in the text and in the appendix

Authors' contributions

CSFM & JHCD contributed to study conception and design. Material preparation, data collection and analysis were performed by MDS, IMC, JTS and SD. The first draft of the manuscript was written by MDS, CSFM and JHCD and all authors commented on previous versions of the manuscript. All authors are accountable for the content and approved the final version of manuscript.

Consent to participate (include appropriate statements)

Consent for publication (include appropriate statements)

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Tables

Table 1: Terrestrial gastropods found in nests of *Neoponera verenae*: nest, location, nest-building substrate, family, species, abundance, and size

Nest	Substrate	Coordinates	Family	Species	Number of individuals (n) and average size (mm)
Nest 01	Fallen trunk	S 14° 47.654’ W 039° 10.263’	Achatinidae	*Leptinaria* sp.	1 (6,8)
Nest 02	Fallen trunk	S 14° 45.367’ W 039° 13.819’	Achatinidae	*Leptinaria* sp. (immature) *Dysopeas muibum* *Allopeas micrum*	1 (2,9) 1 (3,5) 1 (5,0)
Nest 03	Fallen trunk	S 14° 45.358’ W 039° 13.815’	Achatinidae	*Leptinaria* sp. *Leptinaria* sp. (immature) *Beckianum beckianum* *Allopeas* sp. *Allopeas micrum*	2 (8,7) 3 (2,3) 8 (5,5) 4 (4,9) 4 (4,9)
			Scolodontidae	*Happia* sp. *Happia sp.* (immature)	9 (4,0) 2 (1,4)
Nest 04	Dried cocoa fruit	S 14° 45.421’ W 039° 13.937’	Achatinidae	*Leptinaria* sp. (immature) *Leptinaria* sp.	2 (1,5) 1 (7,9)
Nest 05	Dried cocoa fruit	S 14° 45.438’ W 039° 13.920’	Vitrinidae	*Vitrina* sp. (immature)	1 (1,4)
Nest 06	Soil Chamber 01	S 14° 47.694’ W 039° 10.266’	Helicinidae	*Helicina* sp.	1 (5,1)
	Soil Chamber 03		Achatinidae	*Allopeas* sp. *Leptinaria* sp.	8 (4,9) 1 (9,5)
			Scolodontidae	*Happia* sp.	2 (4,1)
Nest 07	Soil Chamber 04	S 14° 47.561’ W 039° 10.398’	Achatinidae	*Leptinaria* sp.	4 (5,5)

Table 2 not available with this version.

Supplementary Files

Videos 1, 4, and 5 not available with this version.

Figures

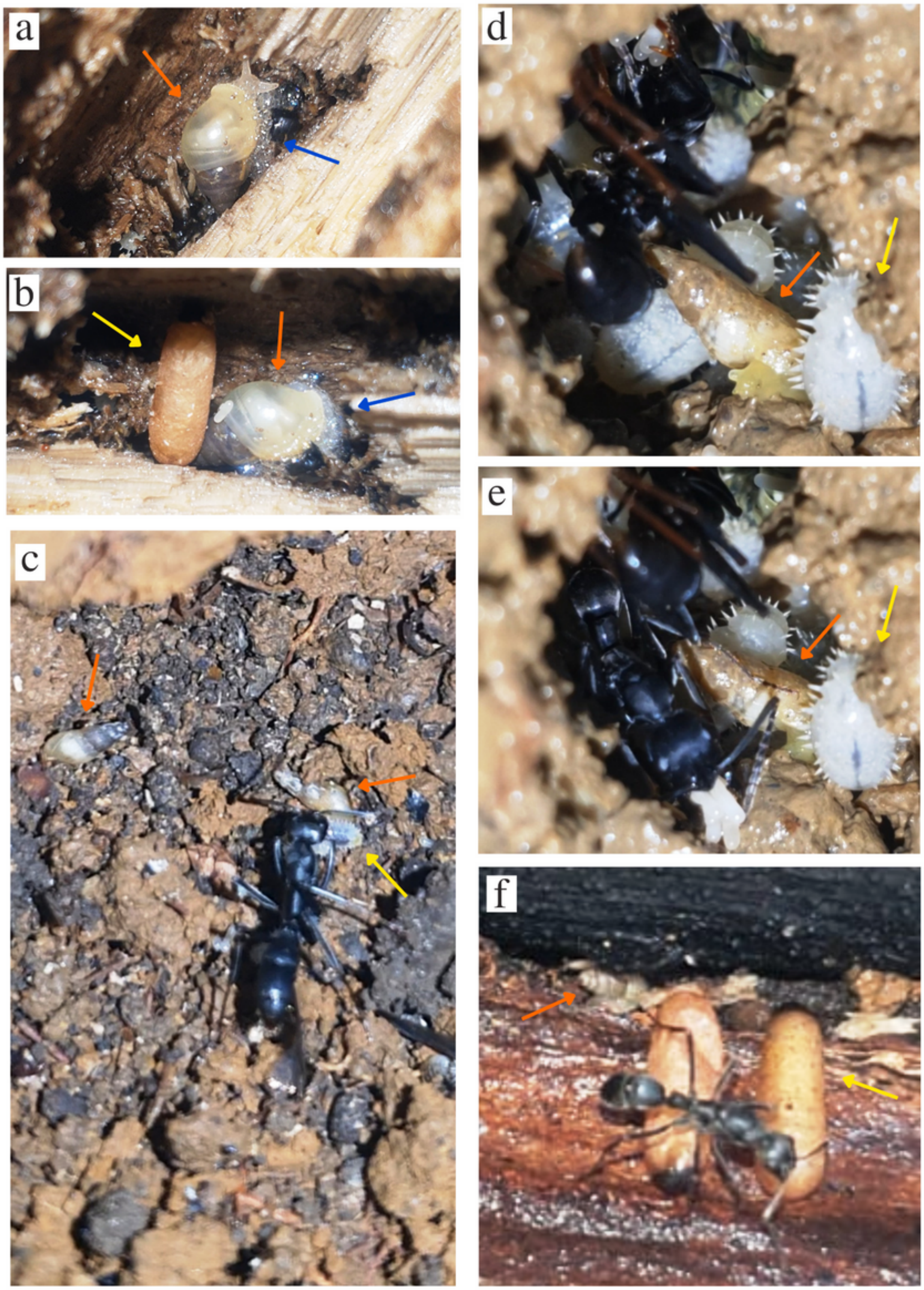

Figure 1

A-F: Interactions of *Neoponera verenae* with terrestrial gastropods. (a) *Leptinaria* sp. producing foam inside the nest. (b) *Leptinaria* sp. next to immature ants. (c) Ants making antennal contact with snails. (d–e) Snail in soil nests interacting with workers and immature ants. (f) Snail in decaying trunk nest found on the ground.

Supplementary Files

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