Phoretic Arthropods of the Red Imported Fire Ant in Central Louisiana

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ABSTRACT More than 4,665 phoretic arthropods comprising 29 species were collected from alates of the red imported fire ant, *Solenopsis invicta* Buren, preparing to fly from nests in Pineville, LA. A wide variety of taxonomic groups were represented, including two insect and 17 mite families. Most arthropods fell into two classes: 1) those that may be truly phoretic with more than four specimens collected (13 species) and 2) those seeming to be accidentally phoretic with one to three specimens collected (16 species). The latter group may be the result of gathering "accidental" mites from adjacent sources, such as grass, soil, tree bark; thus, practically any very small arthropod may use phoresy as a dispersal mechanism. The arthropod with perhaps the highest total numbers was *Cyphoderus similis* Folsom, a wingless insect, and the only known Collembola phoretic species. Eight new species of mites found in this study were recently described, with several other species future candidates for descriptions. Results indicate the more common species may actively persist in nests for the entire year. At least 11 species from six families may feed on fungi within nests. These and common associates from other families carry hyperphoretic spores of fungi that live inside fire ant nests. All three of the laelapid associates may be important predators or parasitoids of individuals within the nests. The collembolan is possibly a general feeder, and *Histiostoma* spp. are filter feeders that consume microorganisms. *S. invicta* is native to Argentina, and we speculate that some of the common mites associated with this ant species also may have originated in Argentina.

KEY WORDS mites, phoresy, red imported fire ant, *Solenopsis invicta*, alate

Since its unfortunate introduction into the United States in the 1930s at Mobile, AL (Creighton 1930), the red imported fire ant, *Solenopsis invicta* Buren, which was formerly referred to in literature as *Solenopsis saevissima richteri* Forel (Buren 1972), has sparked much consternation and research. This small insect, originally from Argentina (Caldera et al. 2008), has spread throughout the Southeast. Much research has been done on the fire ant's biology, ecology, and control measures; however, few studies have been conducted on the mites associated with the red imported fire ant, specifically on the monogyne (single queen) colonies found in Louisiana.

The red imported fire ant is known to produce nuptial flights year-round, with the most intense flights occurring in May, June, and July (Markin et al. 1971). Morrill (1974), however, noted that fire ants in Mississippi began heavy flights in April and continued through August, with a peak in June. The number of flights that occurred during the year varied considerably, with most flights occurring during late morning or early afternoon (Tschinkel 2006).

The occurrence of nuptial flights serves two main purposes. Primarily, flights provide a means of dispersal, because females can fly or be carried long distances by wind. In addition, genetic mixing is greatly increased in mating flights in which alates from many mounds participate (Markin et al. 1971). As speculated by Hermann et al. (1970), successful phoresy on alates would be a possible dissemination mechanism for the establishment of populations of myrmecophilous arthropods associated with fire ant colonies. Many studies and observations have shown that mites are known for their phoretic behavior and are transported by using other insects as a vehicle of distribution (Moser 1976). Hermann et al. (1970) conducted a study in 1964 and 1965 to collect swarming alate male and female ants and noted at least three species of mites, one collembolan, and one psocid phoretic on the collected *S. invicta* alates. The authors of that study also noted, but did not sample, phoretic mites on postswarming female alates. Other investigators studied mites and various other myrmecophile arthropods associated within fire ant colonies (Hunter and Costa 1971, Wojcik 1990). Evans et al. (1961) also noted immature stages of certain mite species on insects during periods of host dispersal with the most pronounced cases involving the deutonymphs of acarid and uropodid species, and their phoretic use of hosts for transportation from one area to another. Accord-

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ing to Hermann et al. (1970), alate female ants harbored the largest numbers of mites, whereas males, in general, usually lacked myrmecophilous associates. They discovered mites on the head, thorax, abdomen, and walking appendages of ants. Collembola also were seen associated with the wings. On occasion, the investigators found alate females so laden with mites that it was impossible for them to become airborne.

Only a few species of mites associated with *S. invicta* have been described. *Gymnolaelaps shealsi* Hunter & Costa (Hunter and Costa 1971) was collected from *S. invicta* in Mississippi. *Oplitis carteretensis* Hunter & Farrier, *Oplitis communis* Hunter & Farrier, and *Oplitis virgilinus* Hunter & Farrier, were all described; *Oplitis moseri* Hirschmann was redescribed from *S. invicta* colonies located in the Carolinas (Hunter and Farrier 1975, 1976).

Caesarodispus klepzigi Khaustov & Moser; *Petalomium hofstetteri* Khaustov & Moser; *Imparipes louisianae* Ebermann & Moser; *Scutacarus nanus* Ebermann & Moser; *Scutacarus tertius* Ebermann & Moser; *Gaeolaelaps invictianus* Walter & Moser; and *Histiostoma blomquisti* Wirth & Moser, all of which were found in this study, were described earlier by Ebermann and Moser (2008), Khaustov and Moser (2008), Walter and Moser (2010), and Wirth and Moser (2010) to provide names for this publication.

Because relatively little information is known of the arthropod species associated with alates of *S. invicta*, this study was conducted to compile a list of the arthropod species currently believed to be phoretic on *S. invicta* in central Louisiana.

Materials and Methods

Twenty-two nests were marked in the J.C.M.'s suburban yard in Pineville, LA. Nests were checked daily for a 16-mo period, 16 May 2004, through 25 September 2005. Some nests died during the 2 yr, and some moved. Consequently, all 22 nests were not sampled at every particular date. In the southern United States, *S. invicta* alates fly between 1130 and 1500 hours; daily flights are triggered only after a suitable amount of rain and with acceptable minimum flight temperatures (Tschinkel 2006). Although the duration of flight lasted ≈2.5 h, alates from each of the individual nests did not fly at the same time. Alates of some nests would fly early in the period, some in the middle, and some at the end of the flight period. Once alates began to fly from a nest, the period of flight for that nest usually lasted 15–30 min.

Not every nest produced alates on dates favorable for flights, and because of this, usually only 8–10 of the viable nests were able to be sampled on those days during which flights took place. Due to the limited time available, and because alates did not necessarily take off from every nest during the approximate 2.5-h flight period, no attempt was made to collect all of the alates flying daily from each of the study nests producing flying alates on that particular day. Instead, an estimated 10 min were spent collecting a sample of as many alates as possible from each nest before moving on to survey and collect from each of the other active nests. Several rounds of each nest were made during the flight period to assure that all nests had been sampled. Although not ideal, we believe that, given the amount of time and labor available, this method produced a reasonable sample of the relative number of alates that flew from nests in this particular yard.

Alates were plucked from nest surfaces using forceps as the winged females and males prepared to fly, usually from the tips of grass leaves. Female and male alates were placed into separate 1 ml vials of ethanol at the time of collection. When possible, several alate and dealate queens that had landed after mating flights were also collected and placed into ethanol vials. Worker ants were gathered serendipitously as they attempted to protect the flying alates.

Male and female alates, workers, and associated arthropods were cleared in a lactophenol solution and then examined under a stereoscope. Phoretic mites and various arthropods collected from the ants were removed and mounted onto slides in Berlese's medium. The mites were separated from the other arthropods and sent to family specialists for identification and descriptions (Table 1).

Time of flight, air temperature, and precipitation also were noted for each flight date. Additional weather measurements, such as wind speed and prior rainfall, were obtained from National Weather Service Forecast Office records for Alexandria, LA.

To determine whether the ant colonies sampled were monogyne (single queen) or polygyne (multiple queens), worker ants were collected from the colonies and sent to the U.S. Department of Agriculture–Agricultural Research Service, Gainesville, FL, where the ant samples were genetically analyzed.

Results and Discussion

During the 16-mo collection period, ant mating flights were recorded on 54 different dates. Alates flew every month, except in April 2005, when the absence of rain prohibited flight initiation. But our later observations also noted flying alates in April 2006, confirming statements by others that flights occur in all months of the year (Tschinkel 2006). Peak flights occurred from May to August (Fig. 1; Table 2). Ninety-five percent of the flights occurred within 72 h of previous precipitation. Ants flew in air temperatures ranging from 22°C (72°F) to 39°C (102°F), with the average temperature being 31°C (88°F). Wind velocity never exceeded 21.7 m/h (13.5 miles/h), with an average wind speed of 17.6 m/h (10.9 miles/h). Flights occurred between 1145 and 1530 hours (CDT), with peak flights between 1200 and 1400 hours. DNA analyses reported all of the nests sampled as monogyne colonies.

A combined total of 208 mating flights occurred, with 4,731 ants collected during these flights. Of these, 1,375 were female alates, 2,352 male alates, and the remaining 1,004 were worker ants, which were often collected serendipitously while protecting the alates. Of the alates, 37% were females and 63% were males.

Table 1. Phoretic arthropod associates of *S. invicta*

Phoretic myrmecophile[a]	Determined by	No. attached to ants by caste	No. found in lactophenol sediments	No. found in alcohol sediments	Total no. found
Acarina group					
Laelapidae	D. E. Walter				
Cosmolaelaps n. sp. nr. *clavige* (Michael), ♀[b]		11 8 on ♀ alates; 3 on ♂ alates	9	57	77
Gaeolaelaps invictianus Walter & Moser, ♀		86 6 on ♀ alates; 80 on ♂ alates	42	258	386
Androlaelaps n. sp., ♀[b]		5 3 on ♀ alates; 2 on ♂ alates	5	29	39
Ascidae	E. E. Lindquist				
Blattisocius tarsalis (Berlese) ♀		0	0	1	1
Proctolaelaps n. sp. *proctofissus* group ♀[b]		0	0	2	2
Phytoseiidae	E. E. Lindquist				
Amblyseiinae sp., ♀		0	1	0	1
Uropodidae	J. C. Moser				
Oplitis moseri Hirschmann, ♀		107 56 on ♀ alates; 49 on ♂ alates; 2 on workers	133	1663	1903
Trachyuropoda whitkombi Hirschmann, ♀		85 4 on ♀ alates; 81 on ♂ alates	84	404	573
Tydeidae	W. C. Welbourn				
Lorria sp., ♀		0	0	1	1
Tydeidae sp., ♀		0	0	1	1
Pygmephoridae	A. A. Khaustov				
Pediculaster n. sp., ♀[b]		0	0	1	1
Microdispidae	A. A. Khaustov				
Caesarodispus klepzigi Khaustov & Moser, ♀		0	3	6	9
Neopygmephoridae	A. A. Khaustov				
Petalomium hofstetteri Khaustov & Moser, ♀		5 4 on ♀ alates; 1 on ♂ alates	9	18	32
Scutacaridae	E. Ebermann				
Imparipes louisianae Ebermann & Moser, ♀		72 47 on ♀ alates; 25 on ♂ alates	106	373	551
Scutacarus andrassy Mahunka, ♀		0	1	1	2
Scutacarus n. sp. nr. *deserticolus* Mahunka, ♀[b]		0	0	2	2
Scutacarus nanus Ebermann & Moser, ♀		0	7	1	8
Scutacarus tertius Ebermann & Moser, ♀		4 on workers	5	7	16
Tarsonemidae	W. L. Magowski				
Xenotarsonemus n. sp., ♀[b]		0	0	6	6
Tetranychoidea	W. C. Welbourn				
Petrobia sp., ♀		0	1	2	3
Eriophyoidea	J. W. Amrine				
Cecidophyes n. sp., ♀[b]		0	0	2	2
Acaridae	B. M. OConnor				
Rhizoglyphus n. sp., DN[b]		1 on ♂ alate	0	0	1
Forcellinia n. sp., DN[b]		0	0	1	1
Histiostomatidae	S. Wirth				
Histiostoma blomquisti Wirth & Moser, DN		38 32 on ♀ alates; 3 on ♂ alates; 3 on workers	155	415	608
Histiostoma n. sp. #2, DN[b]		0	1	1	2
Tectocepheidae	R. A. Norton				
Tectocepheus velatus (Michael), ♀		0	0	1	1
Other Arthropods					
Insecta					
Collembola	J. C. Moser				
Collembola sp. [specimen lost]		0	0	1	1
Cyphoderidae	K. A. Christiansen				
Cyphoderus similis Folsom, ♀		25 3 on ♀ alates; 22 on ♂ alates	51	357	433+
Cecidomyiidae	R. J. Gagné				
Lestremiinae: Micromyini sp., ♂		0	0	1	1

Most slides and or specimens in alcohol are deposited in the USDA Forest Service collection at Pineville, LA, but some were kept by the specialists. Slide duplicates of the more common species also may have been given or loaned to other interested parties.

[a] Stage of phoretic arthropod: ♀, adult female; ♂, adult male; and DN, deutonymph.

[b] Specimens labeled n. sp. are undescribed, and are being retained by us or the specialists for future descriptions.

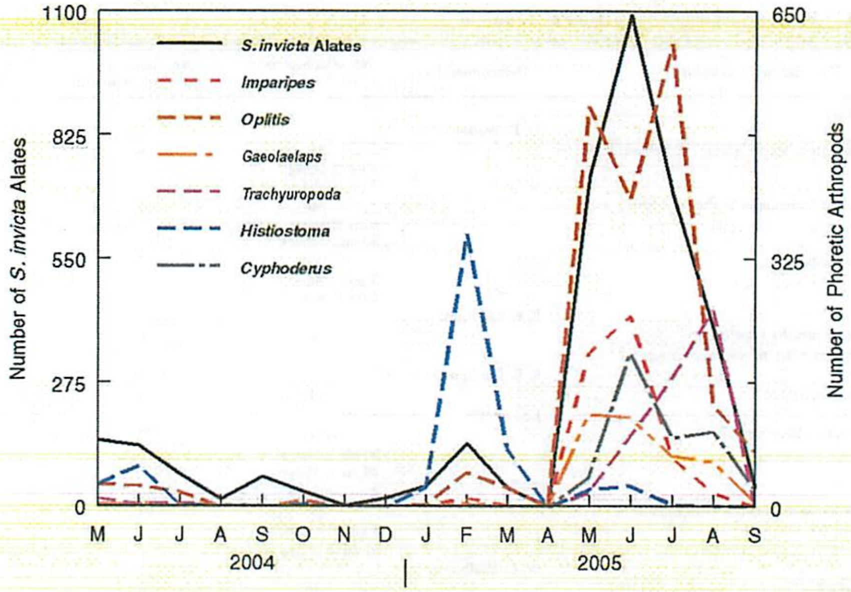

Fig. 1. Monthly totals of *S. invicta* alates and six of the most frequently collected phoretic arthropods. (Online figure in color.)

A sample of 430 mites representing the 10 commonly seen arthropod species revealed that 38% rode females and 62% rode males, which was statistically the same as the percentage of female to male alates. However, for unknown reasons, this ratio of arthropods phoretic on each alate sex differed widely from the above for at least six of the following common individual arthropod species, and chi-square analyses indicate these differences are significant: *Gaeolaelaps invictianus*, six individuals on female alates, 80 on male alates; *Oplitis moseri*, 56 on females, 49 on males; *Trachyuropoda whitkombi* Hirschmann, four on females, 81 on males; *Imparipes louisianae*, 46 on females, 26 on males; *Histiostoma blomquisti* Wirth & Moser, 32 on females, three on males; and *Cyphoderus similis* Folsom, three on females, 22 on males (Table 3).

In total, 29 species of myrmecophilous arthropods were phoretic on alates and workers of *S. invicta* in central Louisiana; 27 of these were mite species, and two species were insects (Table 1). In addition, we observed an immature spider (Araneae: Salticidae sp.) attack and kill a male alate that was preparing to fly from a blade of grass (Fig. 2). These 29 phoretic arthropod species belong to a wide variety of taxonomic groups (18 insect and mite families) (Table 1). Most arthropods were loosely attached to the ant cuticle surfaces (Fig. 3) and detached as soon as they were collected and placed into cryogenic vials full of alcohol; lesser numbers of arthropods were released from the ants after they were removed from the vials and placed into the lactophenol. The collembolan *C. similis* is usually found only in association with ants (Christiansen and Bellinger 1998); this may be a species complex of morphologically identical sibling species (K. Christiansen, personal communication). It is also probably a general feeder (K. Christiansen, personal communication). The data here of *C. similis* riding *S. invicta* seem to be the first documentation of a species of Collembola phoretic on a flying insect, although there are several records of collembolan species riding nonflying termites and crabs (Jacquemart 1980, Mari Mutt 1994).

Based on numbers of total individuals/species in Table 1, it seems that phoretic arthropods fall into two groups—those that may be "truly phoretic" with more than four specimens collected (13 species) and those seeming to be "accidentally phoretic," with only one to three specimens collected (16 species). We postu-

Table 2. Number of nests involved in mating flights each month by the 22 ant nests during the 16-mo study

Yr	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
2004	xxx[a]	xxx	xxx	xxx	5	10	4	1	3	2	1	1
2005	2	11	3	0	32	67	40	20	6	xxx	xxx	xxx

Data indicate peak mating flights for central Louisiana occur in the summer, starting in May and continuing through August.

[a] No sampling conducted in these months.

Table 3. Chi-square analyses of the six most commonly found mite species on *S. invicta* male and female alates

Species of mite	No. male alates	No. female alates	χ^{2a}	*P*
Cyphoderus similis	22	3	6.62	<0.0100
Gaeolaelaps invictianus	80	6	32.57	<0.0000
Histiostoma blomquisti	3	32	44.05	<0.0000
Imparipes louisianae	26	46	21.99	<0.0000
Oplitis moseri	49	56	11.80	<0.0006
Trachyuropoda whitkombi	81	4	37.29	<0.0000

[a] The chi-square test was performed testing each individual mite species against the overall total of *S. invicta* male (2,352) and female (1,375) alates, with a df = 1.

Fig. 2. Two *S. invicta* females preparing to lift off for nuptial flight. (Online figure in color.)

late here that the truly phoretic species may indicate mite species permanently associated with this ant, and phoretic on alates from within the nests. Most of those caught less than four times may represent accidental phoresy, and were picked up by alates from all sorts of adjacent sources, such as grass, soil, and tree bark. Because these accidental species represent a number of different taxonomic groups (Table 1), these data suggest that practically any mite species, and perhaps those of some wingless arthropod species, might use phoresy as a dispersal mechanism.

Phoretic arthropods were acquired every month except November and December, indicating that most of the truly phoretic arthropods are present in nests throughout the year (Fig. 1). Although most of the common phoretic arthropods were collected during peak spring populations of the flying alates (Fig. 1), this does not necessarily indicate that the actual num-

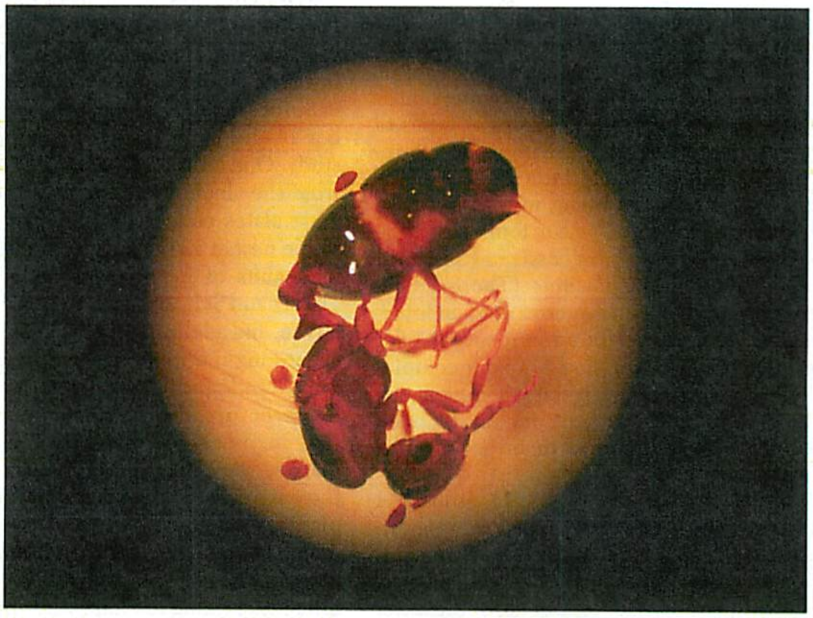

Fig. 3. Female *S. invicta* alate with four female *O. moseri* attached with chelicerae. (Online figure in color.)

Fig. 4. Ascospores and ascus of unidentified fungus inside female of *I. louisianae.* (Online figure in color.)

bers of phoretic arthropod populations in the nests were highest at that time. In reality, populations of the latter may peak in midwinter, because *S. invicta* populations are highest within nests at that time and lowest in midsummer (Tschinkel 2006). Indeed, the phoretic populations of *H. blomquisti,* which peak in February, may actually mimic its high nest populations in winter (Fig. 1).

Ants that nest in soil must cope with the huge range of bacteria, fungi, and other microorganisms for which soil is a fecund medium (Tschinkel 2006). Baird et al. (2007) found 58 bacterial and 35 fungal taxa from mound soil, mound plant debris and ant bodies (presumably workers) of black (*Solenopsis richteri* Forel)/hybrid imported fire ants in northeastern Mississippi, microorganism numbers that presumably are similar to those of *S. invicta.* The large numbers of types of hyperphoretic spores that ride some phoretic arthropods of *S. invicta* alates (Fig. 4) indicate that many bacterial and fungal taxa are being moved by these arthropods. Baird et al. (2007) also found that the fungal insect pathogens *Beauveria bassiana* (Balsamo) Vuillemin and *Paecilomyces lilacinus* (Thom) R. A. Samson were present. Only one microsporidian infection and several yeasts were found in a survey of *S. invicta, S. geminata, S. richteri,* and *S. xyloni* colonies from 285 sites across six southern states (Jouvenaz et al. 1977). We note here that at least one unidentified ascomycete fungal species seems to be an internal pathogen of mites (Fig. 5).

Of the 29 phoretic associates (Table 1), at least 11 mite species that belong to the families Pygmephoridae, Microdispidae, Neopygmephoridae, Scutacaridae, Tarsonemidae, and possibly the Uropodidae, may feed on fungi within nests. Most, if not all, of the latter families contain species associated with fungi (Cross 1965; Ebermann 1981, 1991; Ebermann and Hall 2003). Ebermann and Moser (2008) and Khaustov and Moser (2008) speculated that of the above-mentioned 11 species, one species each of Neopygmephoridae and Microdispidae, and five species of Scutacaridae may feed on fungi inside nests of *S. invicta.* Travis (1941) noted scutacarids riding workers. The mites stood erect, bobbed up and down, and tapped the ants with their first pair of legs. Perhaps this stimulated the ant mouthparts and anal openings to excrete liquids, upon which mites were observed feeding.

We found no specimens of the predatory pyemotid *Pyemotes tritici* (Lagreze-Fossat & Montagne), a mite suggested as a biological insecticide for the control of fire ants (Bruce and LeCato 1980).

Surprisingly, *Xenotarsonemus* sp. was the only member of the large family Tarsonemidae found in this study. One larva and five phoretic females were taken from the alcohol sediments of the vial containing female alates collected while preparing to fly from a single nest at 1355 hours, 22 February 2005. The feeding habits of *Xenotarsonemus* are unknown. Ewing (1939) and Schaarschmidt (1959) noted that the eggs, larvae, and adults of other species were green in color, suggesting that this was evidence of ingested chlorophyll. Lindquist (1986) noted that "this evidence, plus the structure of their chelicerae, leaves little doubt that members of this genus feed on green plant matter; they may be algophagous, fungivorous, or they may feed on mosses or herbaceous vascular plants, or a combination of these." However, Wojciech Magowski (personal communication) excludes vascular plant tissues (such as grasses or foliage) as being too hard for their small mouthparts. Hence, unless this species feeds on some nongreen

Fig. 5. Hyperphoretic spores from body of female *G. invictianus*. (Online figure in color.)

tissue inside the nest, it seems that this mite may be another accidental phoront.

At least two species of the Laelapidae, *Gaeolaelaps invictianus* and *Androlaelaps* n. sp. (Table 1), may be important predators of *S. invicta* individuals within the nests. Species of *Gaeolaelaps* are large and aggressive, preying on smaller arthropods (Walter and Proctor 1999). *Gaeolaelaps aculeifer* (Canestrini) and *Gaeolaelaps oreithyiae* Walter & Oliver are aggressive predators of nematodes and arthropods, and will attack animals that are many times their size by seizing an area of soft cuticle with their chelicerae and eventually chewing through (Walter and Oliver 1989). *Gaeolaelaps invictianus* (Table 1) may act as a generalist predator-inquiline in *S. invicta* colonies (Walter and Moser 2010). Another laelapid genus, *Cosmolaelaps*, has been reported from nests of several species of ants (Gwiazdowicz 2008). Michael (1891) demonstrated that *C. vacua* (Michael) fed on dead ants. A closely related species, *Cosmolaelaps* sp. nr. *claviger* (Michael) (Table 1), was common in our nests, and also may feed on dead insects.

The feeding habits of the uropodid *Oplitis moseri* Hirschmann are unknown, although *O. arboricavi* Hunter & Farrier and *O. communis* Hunter & Farrier are reported to ride on *Solenopsis geminata* (F.) workers (Taber 2000). *Oplitis communis*, is reported from both *S. geminata* and *S. invicta; O. arboricavi* only from *S. geminata, O. carteretensis* also from *S. invicta* (Hunter and Farrier 1975). *O. moseri* is sometimes eaten by the host ants when food is scarce (O'Neal and Markin 1973). The feeding habits of *Trachyuropoda whitkombi* Hirschmann are unknown. Other uropodids such as *Trichouropoda australis* feed on fungi (Kinn 1983), but others such as *T. lamellosa* are nematode predators (Kinn 1987). Certain uropodids may be true parasites or parasitoids of ants (Krantz et al. 2007, Le Breton et al. 2007).

Solenopsis invicta is native to Argentina (Caldera et al. 2008), and we speculate that most of the common mites associated with this ant species also may have originated there. *Oplitis moseri* (Hirschmann) and *Trachyuropoda whitkombi* (Hirschmann), at least, have been documented from *S. invicta* nests from that country (Hirschmann 1972, 1975).

Wirth and Moser (2010) observed a maximum of 14 deutonymphs of *Histiostoma blomquisti* on female alates, whereas as many as 200+ deutonymphs covered the entire bodies of *S. invicta* nest queens. These 200+ nonfeeding deutonymphs were distributed all over the queen's body, and were constantly crawling around and changing positions. *S. invicta* workers licked the queen's bare cuticle around the deutonymphs, but the mites were never removed. The mite could not be cultured.

Stefan Wirth (personal communication) also found deutonymphs and a female of *H.* sp. #2 present in queen chambers of artificial nests of *S. invicta* queens. The female mite fed on rotting wood and leaves.

In central Louisiana, the large number of phoretic mite species seems to be an important component of *S. invicta* nests. These mite species occupy many ecological niches in *S. invicta* nests, such as regulating the nest soil fungi, and acting as predators, parasitoids, or both of each other and the ants. Moreover, the many microorganism species hyperphoretic on these mites may also be essential to the nest biology, as well as possibly affecting the vigor of both the ants and the mites.

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