

## **Detection and Identification of Two New Native Hymenopteran Parasitoids Associated with the Exotic *Sirex noctilio* in North America**

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Source: Proceedings of the Entomological Society of Washington, 114(2):238-249. 2012.

Published By: Entomological Society of Washington

DOI: <http://dx.doi.org/10.4289/0013-8797.114.2.238>

URL: <http://www.bioone.org/doi/full/10.4289/0013-8797.114.2.238>

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**DETECTION AND IDENTIFICATION OF TWO NEW NATIVE  
HYMENOPTERAN PARASITOIDS ASSOCIATED WITH THE  
EXOTIC *SIREX NOCTILIO* IN NORTH AMERICA**

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*Abstract.*—*Rhyssa crevieri* (Provancher), a primary parasitoid of Siricidae wasps, and the Holarctic poemeniine ichneumonid, *Pseudorhyssa nigricornis* (Ratzeburg), a cleptoparasitoid of Siricidae via its parasitoids (Ichneumonidae: Rhyssinae), were reared from two stands of Scots pine (*Pinus sylvestris* L.) and red pine (*P. resinosa* Ait.) infested with the exotic siricid *Sirex noctilio* F. near Tully (Onondaga Co.), New York, in 2010. Previously, *P. nigricornis* has been recorded from the primary siricid parasitoids *Rhyssa persuasoria* (in Europe and North America) and *R. howdenorum* Townes and Townes and *R. lineolata* (Kirby) (in North America). Peak emergence of *P. nigricornis* occurred in early May concurrently with *R. persuasoria* and *R. crevieri*. A second peak occurred in late May, which overlapped peak emergence of *R. lineolata* and *Megarhyssa nortoni* (Cresson). Although 14 individuals of two native siricids, *Sirex nigricornis* F. and *S. edwardsii* Brullé, emerged from sampled trees, the number of *S. noctilio* recovered was far higher (372), suggesting cleptoparasitism of the exotic woodwasp rather than native siricids. Approximately 26% of rhyssine parasitoids in pine stands were cleptoparasitized by *P. nigricornis*. This study marks the first association of *R. crevieri* and *P. nigricornis* with *S. noctilio* in North America. A diagnosis, color images of characters, and a key are provided to aid in the identification of all parasitoids in this study.

*Key Words:* cleptoparasitism, *Rhyssa persuasoria*, *Rhyssa lineolata*, *Rhyssa crevieri*, *Megarhyssa nortoni*, morphological characters, identification key, rearing data

DOI: 10.4289/0013-8797.114.2.238

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*Sirex noctilio* F. (Hymenoptera: Siricidae) is a relatively large wood-boring wasp native to Eurasia and North Africa (Borchert

et al. 2007). Its primary hosts are stressed trees within the genus *Pinus* (Spradbery and Kirk 1978). However, under outbreak population levels, *S. noctilio* possesses the ability to attack relatively healthy trees (Spradbery 1973), disperse rapidly

(Neumann et al. 1987, Tribe and Cillie 2004, Corley and Villacide 2009), and cause great economic damage (Haugen 1990, Hurley et al. 2007). Previous invasions have been documented throughout the southern hemisphere (Hurley et al. 2007). In 2004, a single adult female was captured in Fulton, NY, eliciting concerns for native North American pine forests (Hoebeke et al. 2005).

In areas where *S. noctilio* has become an economically important invasive, *Rhyssa*, *Megarhyssa* (Ichneumonidae: Rhyssinae), and *Ibalia* (Cynipoidea: Ibalidae) parasitoids have been introduced for biological control (Miller and Clark 1935, 1937; Rawlings 1951; Zondag 1959; Zondag and Nuttall 1961; Cameron 1965; Nuttall 1972; Taylor 1976, 1978; Murphy 1998). Species of *Rhyssa* and *Megarhyssa* attack late-instar larvae (Murphy 1998) by drilling into wood after hosts (Chrystal and Myers 1928a, b). Ibalid wasps attack eggs and early-instar siricid larvae (Murphy 1998) using drill shafts left by ovipositing siricids.

The parasitoid guild of native siricid woodborers in eastern North American conifers (Taylor 1976, Murphy 1998) includes primary parasitoids of the ichneumonid genera *Rhyssa* [*R. crevieri* (Provancher), *R. lineolata* (Kirby), *R. howdenorum* Townes and Townes, and *R. persuasoria* (L.)] and *Megarhyssa* [*M. nortoni* (Cresson)], and the ibalid genus *Ibalia* [*I. leucospoides ensiger* (Norton)]. This parasitoid community also includes a secondary parasitoid or cleptoparasitoid, the Holarctic poemeniine ichneumonid *Pseudorhyssa nigricornis* (Ratzeburg). Two recently published studies (Long et al. 2009, Eager et al. 2011) have documented the hymenopteran parasitoids associated with *S. noctilio*-infested pine trees in North America as *Ibalia l. ensiger*, *Rhyssa persuasoria*, *R. lineolata*, and *Megarhyssa nortoni*.

The genus *Pseudorhyssa* contains four species: the Eurasian *P. alpestris* (Holmgren) (northwest and central Europe and Japan), *P. acutidentata* Kusigemati (Japan), and *P. maculiventris* Sheng and Sun (China), as well as the Holarctic *P. nigricornis* (Fitton et al. 1988, <http://www.taxapad.com/global.php>). Species of *Pseudorhyssa* cleptoparasitize rhyssine Ichneumonidae, consuming the primary parasitoid larvae and feeding on the siricid larvae paralyzed by the primary parasitoid (Kerrich 1966, Spradbery 1969). Although most of the literature dealing with *P. nigricornis* uses the name *P. maculicoxis* (Kreichbaumer), Horstmann (1999) concluded *P. maculicoxis* should be synonymized with *P. nigricornis*.

Several studies indicate *P. nigricornis* is associated exclusively with conifer-feeding siricid larvae via their rhyssine parasitoids (Spradbery 1969, Schimitschek 1974, Kusigemati 1984). In Europe, *P. nigricornis* (cited as *P. maculicoxis*) is well documented as a cleptoparasitoid of the siricids *Sirex juvencus* L., *S. cyaneus* F., and *S. noctilio* F. via the Holarctic *R. persuasoria* (L.) (Spradbery 1969, 1970). The North American range of *P. nigricornis* includes Quebec south to western North Carolina, west to Alberta and California and southwest to northern Arizona (Townes and Townes 1960; Kirk 1974, 1975; Carlson 1979). Kirk (1974, 1975) documented the association of *P. nigricornis* with *R. persuasoria* in Arizona and with *R. persuasoria*, *R. lineolata*, and *R. howdenorum* in western North Carolina. Porter (2001) noted an abundance of *R. howdenorum* and *P. nigricornis* (cited as *P. maculicoxis*) on loblolly pine (*Pinus taeda* L.) on the Eastern Shore of Maryland; the siricids *Urocerus cressoni* Norton, *S. nigricornis* F., and *S. edwardsii* Brullé on the same trees were the likely hosts of *R. howdenorum*.

Female *P. nigricornis* are receptive to males two or three days post emergence (Spradbery 1969). Gravid females observe *R. persuasoria* drilling for siricid larvae and, following completion of drilling, use the drill shafts to access and cleptoparasitize hosts (Spradbery 1969, Townes 1969). Females of *P. nigricornis*, however, do not necessarily have to observe drilling by the primary parasitoid, as they can locate drill shafts several days after their completion (Spradbery 1969). The ovipositor of *P. nigricornis* is smaller in cross-section and less sclerotized than primary rhyssine attackers, which facilitates successful access to drill shafts and siricid hosts (Spradbery 1969).

Oviposition by *P. nigricornis* occurs close to primary parasitoid eggs and, following eclosion, a battle ensues between larvae of *P. nigricornis* and those of the primary parasitoid (Spradbery 1969, 1970). First-instar larvae of *P. nigricornis* are heavily armored and larger than rhyssine larvae, with exaggerated, sickle-shaped mandibles, and paired caudal appendages that aid in defeating primary species (Spradbery 1969, 1970). During the initial interaction, *P. nigricornis* larvae rear on their hind, paired appendages to kill rhyssine larvae with their large mandibles (Spradbery 1969). No rhyssine larvae, irrespective of instar, prevailed against attacking first instars of *P. nigricornis*. After consuming the rhyssine larva, *P. nigricornis* consumes the siricid host paralyzed by the adult rhyssine before emerging the following spring (Spradbery 1969).

Although two previous studies (Long et al. 2009, Eager et al. 2011) documented several ichneumonid parasitoids associated with *S. noctilio* in North America, neither recorded *P. nigricornis* or *R. crevieri* from infested trees. Here, we summarize and illustrate diagnostic characters and provide a key to aid in identification of rhyssine

parasitoids and the cleptoparasitoid *P. nigricornis* associated with *S. noctilio*. We also provide emergence phenologies for *S. noctilio* and the complex of primary rhyssine parasitoids, including the previously unreported *R. crevieri* and the cleptoparasitoid *P. nigricornis*.

#### METHODS AND MATERIALS

In April 2010, pine trees in two pure stands of *P. resinosa* Ait. and *P. sylvestris* L. near Tully, NY, were examined thoroughly for the diagnostic resin beads associated with *S. noctilio* oviposition drills along the bole. Within each stand, five *P. resinosa* and five *P. sylvestris* trees with clear signs of infestation were felled. Trees ranged from 14.5 to 23.0 cm diameter at breast height (dbh), with crown conditions ranging from recently dead with a few brown needles to dying with sparse green needles.

Each tree was subsampled using methods developed by Eager et al. (2011). Nine 0.5 m bolts were removed systematically from each of the ten felled trees. If trees were < 10 m tall, the whole tree was taken. All sample bolts were transported to a rearing facility at the State University of New York, College of Environmental Science and Forestry (SUNY ESF), Syracuse, NY. Ends of bolts were sealed with Waxlor™ end sealant (Willamette Valley Company) to prevent desiccation and placed in cardboard emergence tubes. Tubes were held at ambient environmental conditions in an outdoor insectary. All emerging insects were collected and recorded multiple times per day. To reduce noise when reporting emergence phenologies, daily data were summed over weekly time periods.

Identity of all rhyssine Ichneumonidae and *Pseudorhyssa* reared in this study was confirmed morphologically using keys in Townes and Townes (1960) and in Kerrich (1966) and Wahl (1993),

respectively, and/or by comparison with identified research specimens housed in the Cornell University Insect Collection (Ithaca, NY) and the United States National Museum of Natural History (Washington, DC). Reared specimens of *S. noctilio*, its ichneumonid parasitoids, and *P. nigricornis*, are deposited in the SUNY ESF Entomology Museum Collection (Syracuse, NY), Cornell University Insect Collection (Ithaca, NY), and the University of Georgia Museum of Natural History Collection of Arthropods (Athens, GA).

Percent cleptoparasitism by *P. nigricornis* was calculated as the number of *P. nigricornis* divided by the total number of rhyssines plus *P. nigricornis*.

## RESULTS

### Diagnosis

Species of the Rhyssinae and the genus *Pseudorhyssa* are easily recognized by the presence of strong transverse ridges on the mesoscutum (Fig. 11). No other Nearctic ichneumonid has this unique and distinctive feature. The following morphological characters differentiate *P. nigricornis* from any species of *Rhyssa*. Conspicuous yellow or cream markings on the head, thorax, propodeum, and hind margins of the gastral segments (Figs. 1, 2) characterize species of *Rhyssa*, whereas the head, thorax, propodeum, and gaster in *P. nigricornis* lack any yellow or cream markings (Fig. 3). *Pseudorhyssa nigricornis* is further distinguished by the fore wing with vein cu-a joining at the bifurcation of M and Cu (Fig. 4), the occipital carina of the head capsule is complete mediodorsally (Fig. 8), the last visible tergite of the female gaster is broadly rounded apically (Fig. 6), and tergite 2 of the gaster (both sexes) possesses a moderately deep, smooth anterolateral groove on each side of the midline (Fig.

10). In contrast, species of *Rhyssa* are recognized by the fore wing with vein cu-a joining Cu distal to the bifurcation of M and Cu (Fig. 5), the occipital carina is incomplete mediodorsally (Fig. 9), the last visible tergite of the female gaster is extended into a polished, truncate horn (Fig. 7), and tergite 2 of the gaster lacks defined anterolateral grooves. Also, gastral segment 1 in *Pseudorhyssa* has a sharp lateral longitudinal carina extending from the spiracle to the posterior margin, while in species of *Rhyssa* gastral segment 1 lacks this distinct lateral longitudinal carina (Wahl 1993).

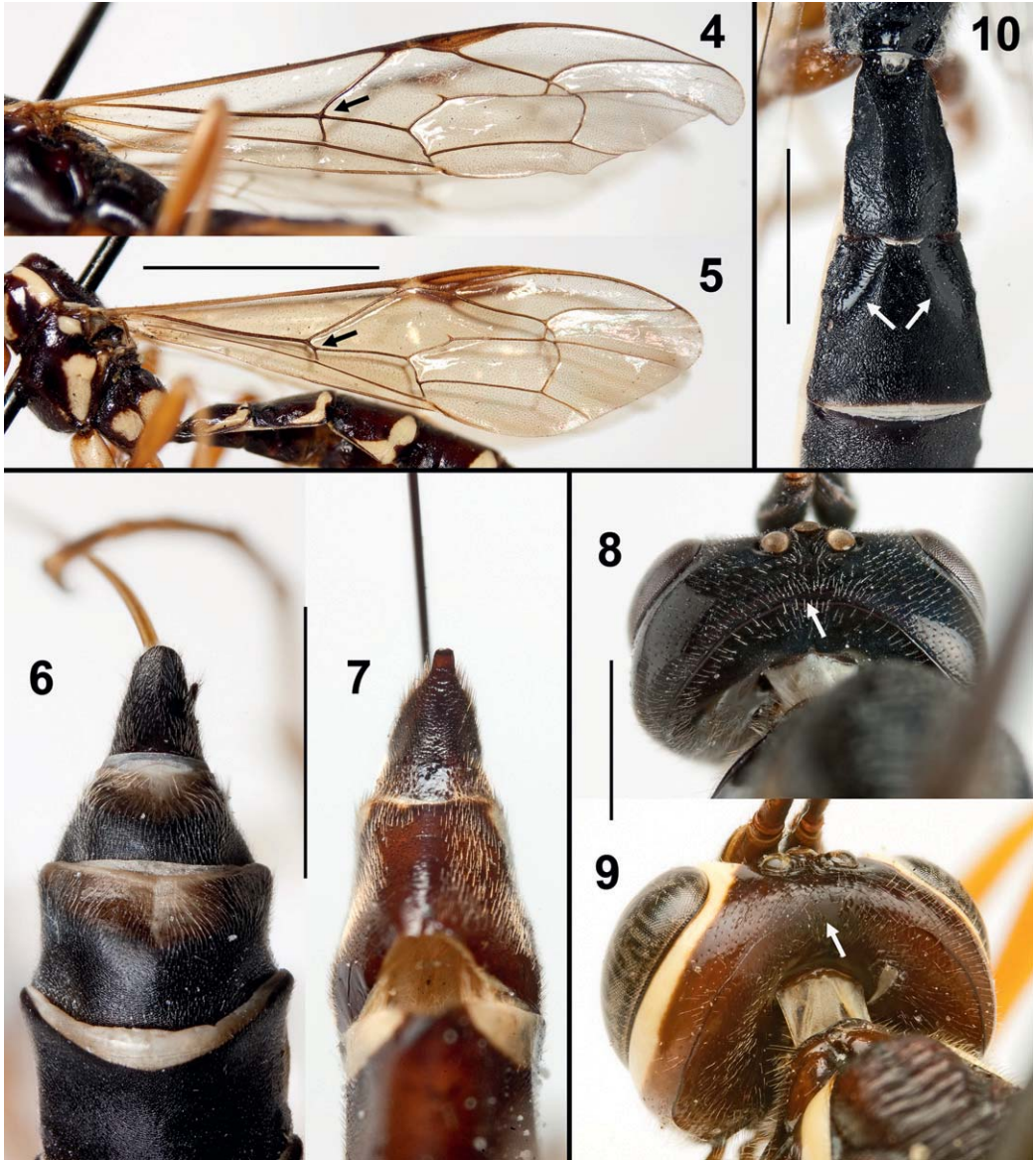
The Palearctic *Pseudorhyssa alpestris*, also reared from *S. noctilio* in Europe (Schimitschek 1974), has not been detected in North America. It differs from *P. nigricornis* by dorsal segments 1-3 of the gaster usually with a distinct reddish-brown mark near the posterior margin and by the face of the female often with obscure brownish marks (Fitton et al. 1988). In contrast, the gaster and face of the female of *P. nigricornis* are black without any brownish markings.

Among the species of *Rhyssa* reared in this study, *R. persuasoria* is readily recognized by the flagellum of the antenna being entirely black (Fig. 2). In both *R. crevieri* and *R. lineolata*, the flagellum of the antenna has a broad white band (Fig. 1), except in occasional small males (Townes and Townes 1960). Coloration distinguishes these two latter species. In *R. crevieri*, the white mark on the metapleuron is subtriangular (Fig. 12), prolonged forward along the upper margin. This subtriangular mark varies substantially in females and is often absent or much reduced in some males. The hind coxa has no white mark dorsobasally (Fig. 12) or sometimes a very small white mark limited to its constricted base. In contrast, the white mark on the metapleuron in *R. lineolata* is rounded





Figs. 1–3. Habitus, lateral view. 1, *Rhyssa lineolata*. 2, *Rhyssa persuasoria*. 3, *Pseudorhyssa nigricornis*. Scale bar = 5 mm.

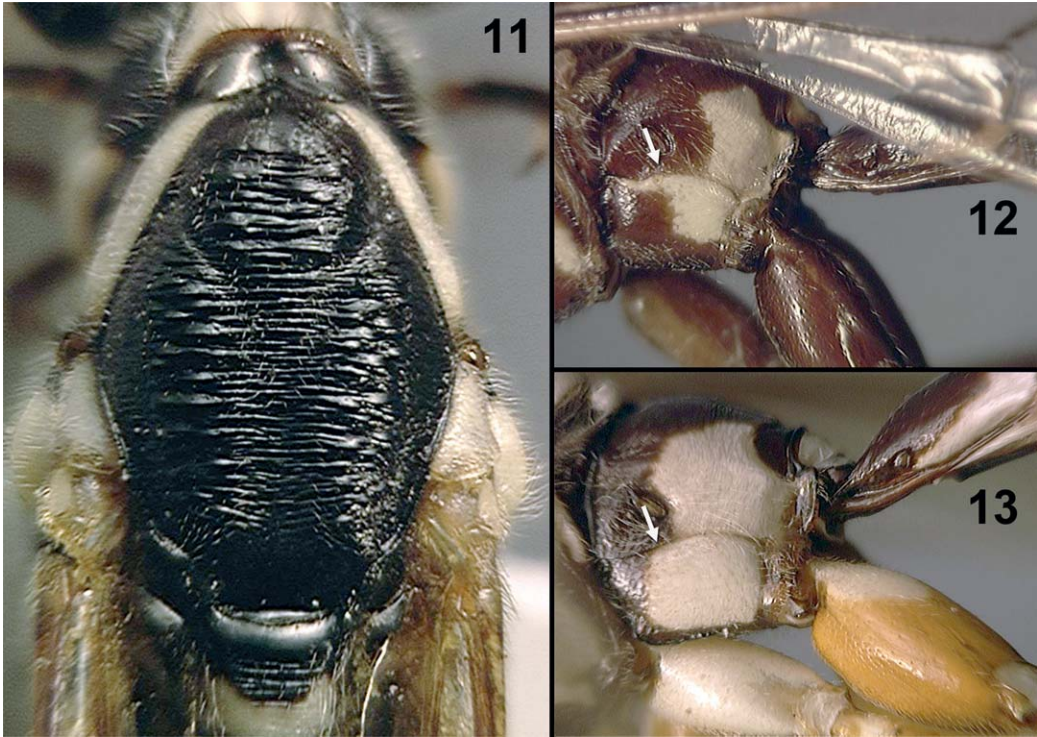


Figs. 4–10. Parasitoid characters. 4–5, Fore wing. 4, *Pseudorhyssa nigricornis*; note vein cu-a at bifurcation of M and Cu (arrow). 5, *Rhyssa lineolata*; note vein cu-a joining Cu distal to bifurcation of M and Cu (arrow). 6–7, Apex of gastral segments, dorsal view. 6, *Pseudorhyssa nigricornis*. 7, *Rhyssa lineolata*. 8–9. Upper part of head, posterior view. 8, *Pseudorhyssa nigricornis*; note occipital carina complete mediodorsally (arrow). 9, *Rhyssa lineolata*; note occipital carina incomplete mediodorsally (arrow). 10. Base of gastral segments, dorsal view, of *Pseudorhyssa nigricornis*; note deep anterolateral grooves on tergite 2 (arrows).

(Fig. 13), constricted next to the upper margin. This mark is absent or reduced in some males. The hind coxa of *R. lineolata* has a white mark dorsobasally (Fig. 13),

usually in the form of a small dash but in larger females often enlarged and irregular in shape or covering the entire upper surface of the coxa. Although both species





Figs. 11–13. Thoracic characters. 11, *Rhyssa lineolata*, mesoscutum; note strong transverse ridges. 12–13, Color markings of metapleuron and hind coxa. 12, *R. crevieri*. 13, *R. lineolata*.

are recognized currently as valid, a footnote in the “Catalog of Hymenoptera North of Mexico” (Carlson 1979) states: “It remains to be proven that *crevieri* is distinct from *lineolata*.”

The following key, based on characters given in the diagnosis above, allows for the separation of all rhyssine ichneumonids and *Pseudorhyssa* reared from *Sirex noctilio*-infested trees in the north-eastern U.S.

**Key to Species of Ichneumonidae With a Strongly Transversely Rugose Mesoscutum (Fig. 11)**

(Adapted from Fitton et al. 1988 and Townes and Townes 1960)

1. Occipital carina complete mediodorsally (Fig. 8). Female: last visible tergite of gaster not extended as horn (Fig. 6). Gastral tergite 2 with

- deep anterolateral grooves (Fig. 10) . . . . .  
 . . . *Pseudorhyssa nigricornis* (Ratzeburg) [synonyms: *Pseudorhyssa maculicoxis* (Kreichbaumer 1889), *Pseudorhyssa sternata* Merrill 1915, and *Pseudorhyssa praealpina* (Gyorfi 1946)]
- Occipital carina incomplete mediodorsally (Fig. 9). Female: last visible tergite of gaster extended into a polished, truncate horn (Fig. 7). Gastral tergite 2 without anterolateral grooves. . . . . 2.
- 2. Clypeus with median tooth or projection. Female: sternite 2 of gaster with 2 median tubercles near middle . . . . . 3.
- Clypeus truncate. Female: sternite 2 of gaster with 2 median tubercles near base . . . . .  
 . . . . . *Megarhyssa nortoni* (Cresson) [wings unicolorous, subhyaline; stigma yellowish; female: tergites 4–6 with conspicuous, yellow, round, lateral spots on each side; thorax and gaster light brown to blackish, with conspicuous yellow markings]
- 3. First 4 tergites of gaster with narrow whitish apical margin, of even width, and continuous



- across middle, or slightly narrower or interrupted medially . . . . .
- . . . *Rhyssa howdenorum* Townes and Townes (not found in this study)
- First 4 tergites of gaster with white apical spots, not forming a continuous band across middle. . . . . 4.
- 4. Flagellum of antenna with broad white band (Fig. 1) . . . . . 5.
- Flagellum of antenna entirely black (Fig. 2) . . . . . *Rhyssa persuasoria* (L.)
- 5. Metapleuron with subtriangular white spot, prolonged forward along upper margin (Fig. 12); hind coxa without white spot dorsobasally (Fig. 12), but sometimes with small white spot at base . . . . .
- . . . . . *Rhyssa crevieri* (Provancher)
- Metapleuron with rounded white spot, constricted next to upper margin (Fig. 13); hind coxa with white spot dorsobasally (Fig. 13), often enlarged and irregular in shape. . . . .
- . . . . . *Rhyssa lineolata* (Kirby)

Emergence phenology.—Twenty adult *R. crevieri* (9 males, 11 females) and fifty-one adult *P. nigricornis* (30 males, 21 females) emerged from sample bolts taken from five of the ten felled pine trees (Table 1). Peak emergence of *P. nigricornis* overlapped with its previously recorded host, *R. persuasoria*, and with *R. crevieri*, a previously unrecorded host (Fig. 14). A second peak in *P. nigricornis* emergence (Fig. 14) overlapped with two other native rhyssines, *R. lineolata* and *Megarhyssa nortoni*. Cleptoparasitism of rhyssines by *P. nigricornis* was ~ 26%. The introduced *S. noctilio* was by far the dominant siricid with 372 individuals emerging from the infested bolts and only 14 native

*S. nigricornis* and *S. edwardsii*, < 4% of the total siricid emergence from sampled trees (Table 2, Fig. 15).

DISCUSSION

The rearing and identification of *R. crevieri* as well as *P. nigricornis* from *Sirex noctilio*-infested trees at our study site in central New York marks the first association of both this primary parasitoid and the cleptoparasitoid with *S. noctilio* in North America. Previous studies in this region (Long et al. 2009, Eager et al. 2011) recorded only the rhyssines *R. persuasoria* and *R. lineolata*. However, morphological similarity between *R. crevieri* and *R. lineolata* may explain why *R. crevieri* went unnoticed in both studies. Both species contain broad, white bands on the antennae, except for some small males (Townes and Townes 1960), and similar white highlights on the rest of the body. Despite these similarities, differences in emergence phenologies of these parasitoids (Fig. 14) provide further support for their separate species status.

It is less likely that *P. nigricornis* would be misidentified as a species of *Rhyssa* based on distinguishing morphological characteristics as noted in the key. Timing of sampling may account for the absence of this species in one of the prior studies. Long et al. (2009) collected samples from *Sirex*-infested trees in late June, which, according to our emergence phenology (see Fig. 14), is late for recovery of *Rhyssa* and the associated cleptoparasitoid. In

Table 1. Tree data associated with *Sirex noctilio*-infested pines harboring *Rhyssa crevieri* and *Pseudorhyssa nigricornis* near Tully, NY, in 2010.

Tree species	Height (m)	DBH (cm)	Crown condition	No. <i>R. crevieri</i>	No. <i>P. nigricornis</i>
<i>P. resinosa</i>	11.3	17.5	sparse green needles	0	1
<i>P. resinosa</i>	16.2	18.5	needles all brown	1	7
<i>P. resinosa</i>	12.7	23	few brown needles	13	19
<i>P. sylvestris</i>	9.0	13	sparse green needles	1	0
<i>P. sylvestris</i>	8.9	17	sparse green needles	5	24

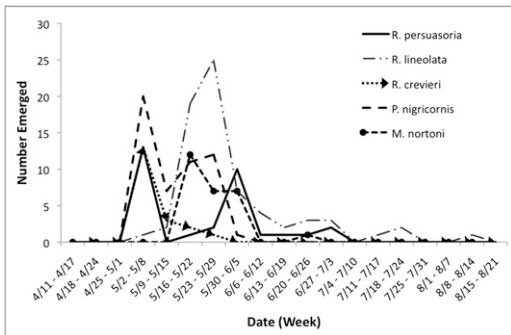


Fig. 14. Emergence phenology of *Pseudorhyssa nigricornis*, *Rhyssa persuasoria*, *R. lineolata*, *R. crevieri*, and *Megarhyssa nortoni* reared from pine trees felled near Tully, NY, in 2010.

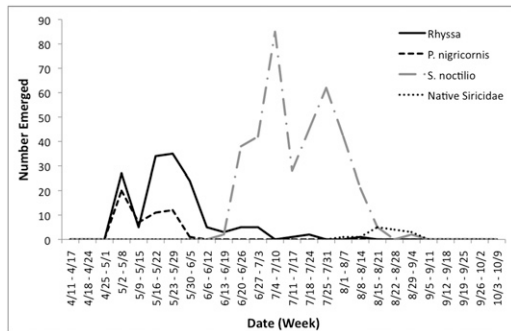


Fig. 15. Emergence phenology of pooled rhyssine primary parasitoids (*Rhyssa persuasoria* + *R. lineolata* + *R. crevieri* + *M. nortoni*), *Pseudorhyssa nigricornis*, *Sirex noctilio*, and native Siricidae populations near Tully, NY, in 2010.

another study (Eager et al. 2011), collections from the same field site used in our study (Heiberg Forest) did not yield *P. nigricornis*, perhaps because it focused exclusively on larval sampling. Characteristics distinguishing *P. nigricornis* larvae from rhyssine larvae are not obvious (Spradbery 1970) and individuals of this species could have been easily overlooked. Alternatively, *P. nigricornis* may exhibit a density dependent relationship with its rhyssine hosts as Eager (2010) recorded relatively low numbers of rhyssines in 2009. In 2011, sampled trees at Heiberg Forest also had low numbers of rhyssines and failed to yield any *P. nigricornis* (C. Standley, unpublished).

Table 2. Number of emerged *Pseudorhyssa nigricornis*, rhyssine Ichneumonidae, and species of Siricidae during the 2010 flight season from 0.5 meter logs removed from four trees near Tully, NY.

Species	No. emerged
<i>Pseudorhyssa nigricornis</i>	51
<i>Rhyssa lineolata</i>	70
<i>Rhyssa crevieri</i>	20
<i>Rhyssa persuasoria</i>	31
<i>Megarhyssa nortoni</i>	27
<i>Sirex noctilio</i>	372
<i>Sirex nigricornis</i>	8
<i>Sirex edwardsii</i>	6

In North America, *P. nigricornis* has been associated with primary parasitoids of the native siricids *Sirex abbotii* Kirby (= *cyaneus* F.), *S. nigricornis* F., and *S. cyaneus* in the southeastern U.S. (Kirk 1974) and of *S. cyaneus*, *S. californicus* (Ashmead), and *S. longicauda* Middlekauff in the southwestern U.S. (Kirk 1975). The strong overlap in emergence phenology of *P. nigricornis* with the four rhyssine species suggests that all (*R. persuasoria*, *R. lineolata*, *R. crevieri*, and possibly *M. nortoni*) may be suitable hosts. Initial peak emergence of *P. nigricornis* (early May in 2010) was concurrent with both *R. persuasoria* and *R. crevieri*, while the later peak coincided with *R. lineolata* and *M. nortoni* (Fig. 14). Emergence phenologies of *P. nigricornis* supports utilization of *R. persuasoria* and *R. lineolata* as reported by Spradbery (1969) and Kirk (1974). Phenologies also indicate *R. crevieri* is likely being exploited and it is possible *P. nigricornis* is utilizing *M. nortoni*. When *M. nortoni* is excluded from calculations, percent cleptoparasitism of the remaining rhyssines increases from 26 to 30%.

Our data suggest *P. nigricornis* may be a significant source of mortality for *R. persuasoria*, *R. lineolata*, and *R.*

*crevieri* (Table 2). As each *P. nigricornis* uses only a single rhyssine host, emergence of equivalent numbers of adults of each species indicate that mortality of rhyssines from *P. nigricornis* is not trivial and that the ability of *R. persuasoria* to check the growth of *S. noctilio* populations (see Taylor 1978) could be compromised. The importance of cleptoparasitism in the population dynamics of *S. noctilio* in North America was not previously known and research toward a more comprehensive understanding of the host-parasitoid relationships in this system is warranted.

#### ACKNOWLEDGMENTS

We thank Elizabeth Keyser and Andrew Underwood for field and lab assistance, Kent Loeffler (Department of Plant Pathology, Cornell University, Ithaca, NY) and Joseph V. McHugh (Department of Entomology, University of Georgia, Athens) for color photographic images, and Andrew Bennett (Canadian National Collection of Insects, Ottawa), A. G. Wheeler, Jr. (Clemson University, Clemson, SC) and one anonymous reviewer for critical comments and suggestions for improving an early draft of the manuscript. The New York Department of Environmental Conservation provided field vehicles critical for data collection. This project was funded by a McIntire-Stennis Formula Grant to M. K. Fierke, D. Parry and D. C. Allen.

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