

HOST SPECIFICITY OF SEVERAL *PSEUDACTEON* (DIPTERA:
PHORIDAE) PARASITES OF FIRE ANTS (HYMENOPTERA:
FORMICIDAE) IN SOUTH AMERICA

SANFORD D. PORTER,¹ HAROLD G. FOWLER,² SOFIA CAMPIOLO,²
AND MARCOS A. PESQUERO³

¹Medical and Veterinary Entomology Research Laboratory, USDA, Agricultural
Research Service, P.O. Box 14565, Gainesville, FL 32604

²Departamento de Ecologia, Instituto de Biociencias, Universidade Estadual
Paulista, 13500, Rio Claro, SP, Brazil

³Departamento de Zoologia, Instituto de Biociencias, Universidade Estadual Paulista,
18610, Botucatu, SP, Brazil

ABSTRACT

We tested the host specificity of several parasitic *Pseudacteon* scuttle flies in South America with 23 species of ants in 13 genera. None of these ant species attracted *Pseudacteon* parasites except *Solenopsis saevissima* (F. Smith) and to a lesser extent *Solenopsis geminata* (Fab.). This result is encouraging because it indicates that the *Pseudacteon* flies tested in this study would not pose an ecological danger to other ant genera if these flies were introduced into the United States as classical biological control agents of imported fire ants. This prediction of host specificity will, of course, need to be validated with potential hosts in the United States before these flies can be released.

Key Words: Biocontrol, *Solenopsis*, Brazil

RESUMEN

Probamos la especificidad de hospedero de varias moscas parásitas del género *Pseudacteon* contra 23 especies de hormigas pertenecientes a 13 géneros en América del Sur. Ninguna de las hormigas atrajo moscas parásitas, con la excepción de *Solenopsis saevissima* (F. Smith) y, en menor escala, *Solenopsis geminata* (F.). Este resultado es alentador porque indica que las moscas *Pseudacteon* probadas en este ensayo no harían daños ecológicos a otros géneros de hormigas, si estas fueran introducidas en los Estados Unidos como agentes de control biológico contra las hormigas de fuego. Tal predicción de la especificidad de hospedero, claro, necesitaría ser valorada con hospederos potenciales en los Estados Unidos, antes que las moscas fueran liberadas.

When fire ants were introduced into the United States, they left behind almost all of their natural enemies in South America (Jouvenaz 1983). Consequently, release from natural enemies is a likely explanation for the 5- to 10-fold increase in fire ant densities reported in North America (Porter et al. 1992). A number of organisms have been considered as possible biological control agents for exotic fire ant populations, including micro-organisms, nematodes, a parasitic wasp, parasitic phorid flies, and other ants (Buren 1983, Feener & Brown 1992, Heraty et al. 1993, Jouvenaz et al. 1988, Patterson & Briano 1993).

Phorid or scuttle flies of the genus *Pseudacteon* Coquillett were proposed as biological control agents because of their dramatic impacts on fire ant foraging rates and the stereotypical defensive reactions of fire ant workers to scuttle fly attacks (Feener & Brown 1992, Porter et al. 1995a). But no matter how effective phorid flies might be in fire ant biocontrol, they cannot be released into the United States until it can be demonstrated that they will not cause ecological problems for native non-target organisms.

Available collection data indicates that individual *Pseudacteon* species are almost always specific to one genus of ants (Borgmeier 1962, 1963, 1969; Borgmeier & Prado 1975; Disney 1991, 1994; Williams & Banks 1987). The European species *Pseudacteon formicarum* (Verrall) has been reported from *Lasius* and several other ant genera (Donisthorpe 1927), but tests by Wasmann (1918) indicate that it is specific to *Lasius*. One rare South American species (*Pseudacteon convexicauda* Borgmeier) has been collected over *Solenopsis* and *Paratrechina* nests (Borgmeier 1962), but no details are given and this has not been confirmed by other collectors or the presence of developing larvae. A report that *Pseudacteon borgmeieri* Schmitz attacks both *Solenopsis* and *Camponotus* ants (Disney 1994) is based on a mistranslation of Borgmeier (1922), who actually stated that he only found this fly over *Solenopsis* nests even though he also inspected other ant nests including two species of *Camponotus*.

Sixteen South American *Pseudacteon* species have only been reported from *Solenopsis* ants (Disney 1994), including 13 with lobed ovipositors and three with unlobed ovipositors. Three additional South American *Pseudacteon* species plus several from North America have been reported attacking other ant genera. All of the new-world species reported from genera other than *Solenopsis* have unlobed ovipositors. The 20 or more new-world species of *Pseudacteon* with bilobed or trilobed ovipositors are reported to attack only *Solenopsis* ants (Borgmeier 1962, 1963, 1969; Borgmeier & Prado 1975; Disney 1991).

Many of the *Pseudacteon* species that attack fire ants in South America are broadly distributed (Borgmeier 1963, Borgmeier & Prado 1975) across the ranges of several fire ant species (Trager 1991). *Pseudacteon litoralis* Borgmeier, *Pseudacteon tricuspis* Borgmeier, *Pseudacteon obtusus* Borgmeier, *Pseudacteon wasmanni* (Schmitz) and *Pseudacteon curvatus* Borgmeier have all been collected attacking both *Solenopsis invicta* Buren and *Solenopsis saevissima* (F. Smith) (Williams 1980, Porter et al. 1995b, unpublished data). However, the fact that four *Pseudacteon* species in the United States all attack *Solenopsis geminata* (Disney 1991, Feener 1987), but not sympatric populations of the imported fire ant, *S. invicta*, suggests that some flies may also be specific to particular fire ant species or species groups (Feener & Brown 1992).

The objective of this study was to determine if the *Pseudacteon* flies that attack *Solenopsis* fire ants in South America will also attack other genera of South American ants.

MATERIALS AND METHODS

In order to test the species specificity of *Pseudacteon* flies, we collected 23 species of ants in 13 genera. These ants were separated from their nest material and placed into white plastic trays coated with fluon so they could not escape. We used either 30 by 40 cm trays that contained 10-cm petri dish nests or 13 by 30 cm trays that contained water tube nests (Banks et al. 1981). Only one type of nest and tray was used at each location. During tests, lids on the petri dish nests were removed or ants were shaken out of nest tubes to expose as many ants as possible to potential phorid attacks. The number of ants in a tray varied between several hundred and several thou-

sand depending on their size and availability. During tests, trays were carried to a test site and placed in shaded locations several m apart. All scuttle flies that appeared over the trays were collected using a double-chambered Allen aspirator (BioQuip®, Gardena, CA). This style of aspirator was particularly effective in capturing attacking flies (>90%) because the long flexible collection tube was easily maneuvered over the trays as the flies darted back and forth. A second advantage was that the inner chamber is a small vial that can be easily shaded with a hand so that the flies move into the light while the vial is being exchanged. Use of this aspirator was a considerable improvement over the snap-cap vial technique used by previous researchers (Williams 1980).

Tests were conducted using two different protocols. In the first set of tests, ants were set out for 75 min at a single location on the Rio Claro campus of São Paulo State University (UNESP-Rio Claro). Each test included one tray of fire ants (*S. saevissima*) and four to eight trays containing other species of ants. This procedure was repeated 19 times over a 27-day period from 11 December 1992 to 7 January 1993. The second set of tests was conducted in February, 1994 at five sample sites around each of two cities (Rio Claro, SP and Viçosa, MG). Sample sites were 1-10 km apart. Two clusters of 4-5 trays were set out at each site for 30-45 min; each cluster contained one fire ant colony and 3-4 other species of ants. Voucher specimens of ants and flies have been deposited with the Museu de Zoologia, Universidade de São Paulo, Brazil.

RESULTS AND DISCUSSION

The *Pseudacteon* flies in our tests were specific to the genus *Solenopsis*. In the first series of tests at the single site on the UNESP Rio Claro campus, we collected *Pseudacteon* phorids from the tray with *S. saevissima* on 74% (14/19) of the observation days. Altogether, we collected 50 *Pseudacteon* flies: 47 - *P. litoralis*, 2 - *P. tricuspis*, 1 - *P. wasmanni*. No *Pseudacteon* flies were observed flying over any of the other ants tested (number of trials is shown in parentheses): *Atta sexdens* (18), *Monomorium pharaonis* (16), *Camponotus rufipes* (14), *Paratrechina* sp. (7), *Odontomachus minutus* (6), *Myrmelachista autori* (6), *Ectatomma quadridens* (5), *Pachycondyla striata* (5), *Pheidole* sp. 2 (5), *Crematogaster* sp. (4), *Pheidole oxyopus* (4), *Camponotus abdominalis* (3), *Camponotus blandus* (2). We also collected 11 *Myrmosciarius grandicornis* Borgmeier phorid flies from trays with *Atta sexdens* on eight different occasions. Two unidentified phorids (not *Pseudacteon*) appeared to be attracted to a *Paratrechina* sp. colony on two occasions.

Results for the second set of tests at sites around Rio Claro and Viçosa were similar. We collected *Pseudacteon* phorids at 75% of the nests with *S. saevissima* (7/10 in Rio Claro and 8/10 in Viçosa). We collected 23 *Pseudacteon* phorids at the Rio Claro sites (3 - *P. curvatus*, 3 - *P. tricuspis*, 7 - *P. pradei*, 8 - *P. wasmanni*, 1 - *P. litoralis*, 1 - *P. borgmeieri*) and 12 more at the Viçosa sites (2 - *P. pradei*, 10 - *P. wasmanni*). We also collected three phorids (1 - *P. pradei*, 2 - *P. wasmanni*) that were attracted to a nest tray with black *Solenopsis geminata* (Fab.) at two of the five Viçosa sites. The other 10 species of ants tested did not attract phorid flies (the number of tray periods is shown in parentheses; two species have 10 periods because two trays were used at each site): Rio Claro Area - *Odontomachus brunneus* (5), *Acromyrmex rugosus* (10), *Pheidole* sp. (5), *Camponotus angulatus* (10); Viçosa Area - *Odontomachus haematodus* (5), *Dorymyrmex* sp. (5), *Atta sexdens* (5), *Camponotus rufipes* (5), *Camponotus* sp. 3 (5), *Paratrechina longicornis* (5).

When we compared the number of fire ant trays attracting *Pseudacteon* flies to the number of non-fire ant trays attracting *Pseudacteon*, the results were very significant, regardless of whether we analyzed results from the two tests separately or combined

(χ^2 tests, $P < 0.0001$). When we summed the numbers of scuttle flies collected from the campus tests with the numbers collected at the two multiple-site tests, four *Pseudacteon* species (*P. litoralis*, *P. wasmanni*, *P. pradei*, and *P. tricuspsis*) were significantly more likely to be caught with fire ants than with non-fire ants (χ^2 tests, $P < 0.001$, $P < 0.001$, $P < 0.002$, and $P < 0.05$, respectively). Two species (*P. curvatus* and *P. borgmeieri*) were not collected frequently enough to make a determination. The 88 flies we collected over fire ant colonies were sufficient to have detected non-fire ant attraction rates as small as 3.5% at $P < 0.05$ (i.e.; 0.965⁸⁸). Statistical sensitivity for individual ant species was, of course, dependent on the number of scuttle flies collected when a particular ant species was available for attack. Statistical sensitivity ranged from 5% for *Atta sexdens* to about 25% for ant species only tested five times around the Viçosa area. Nevertheless, even if *Pseudacteon* flies had been attracted to other ant genera at some low rate, this would not necessarily mean that they would oviposit in them or that these ants would be suitable hosts for larval development.

Both *S. saevissima* and *S. geminata* were collected in the Viçosa area. *Solenopsis saevissima* was sparsely distributed in urban and agricultural sites while *S. geminata* was only found at two urban sites. No scuttle flies were found attacking *S. geminata* at either of its collection sites, although several scuttle flies were collected while attacking a *S. saevissima* colony at one of these sites.

In order to further investigate *Pseudacteon* attacks on *S. geminata* colonies, we returned to one of the Viçosa sites where we had previously captured phorids attacking *S. saevissima* nests. Trays with *S. saevissima* and *S. geminata* were set out alternately. When the *S. saevissima* trays were present, we observed 3-5 phorids continuously flying around the trays and attacking workers. After the *S. saevissima* trays were removed and the *S. geminata* trays were set out, we observed only 1-2 phorids in the trays and the number usually declined to 0-1 after a couple of minutes. Within a minute or two after returning the *S. saevissima* trays, the number of scuttle flies increased to 3-5 again. This pattern was observed through three cycles of replacing *S. saevissima* colonies with *S. geminata* colonies. Careful observations of scuttle flies in the *S. geminata* colonies indicated that they did attempt to oviposit on some of the workers, but attempts were not very frequent, and the workers did not respond with the stiling behavior normally seen after *S. saevissima* workers have been attacked (Porter et al. 1995a). Many of the *S. geminata* workers were observed in a standard defensive posture with the head raised and the gaster curled under the thorax (Feener & Brown 1992), but general colony immobility was not observed (Porter et al. 1995a). Further tests will be necessary to determine if eggs are actually laid in *S. geminata* workers and whether they can produce viable larvae. At the end of the test, we collected four *P. pradei*, two *P. wasmanni*, and six *Pseudacteon affinis* Borgmeier over the *S. saevissima* nests.

Information from this study together with previous collection records (Borgmeier 1962, 1963, 1969; Borgmeier & Prado 1975) strongly indicate that most *Pseudacteon* parasites of fire ants will meet a critical requirement of a good biological control agent; that is, host specificity. The phorid flies tested in this study appear to be specific to a single genus of ants (*Solenopsis*) and perhaps to a specific subcomplex within that genus. These results are encouraging and should justify further and more extensive tests with ants from North America. Tests will also need to be done with other groups of insects, but it is highly unlikely that *Pseudacteon* flies would pose a threat to any arthropod group other than ants, considering their oviposition behavior, their highly specialized ovipositors, their specialized adaptations for pupation in the head capsules of worker ants (Porter et al. 1995b), and the fact that virtually all phylogenetically related phorid genera are ant parasites (Brown 1993, Disney 1994).

ACKNOWLEDGMENTS

Thanks are extended to T. M. C. Della Lucia (UVF, Viçosa) and E. F. Vilela (UVF, Viçosa) for providing logistical support and laboratory space in Viçosa. Special thanks are also extended to G. M. Rodrigues (UVF, Viçosa) for his invaluable field assistance and expertise. B. V. Brown (L.A. County Museum), D. H. Feener (Univ. of Utah), L. E. Gilbert (Univ. of Texas), and D. P. Wojcik (USDA-ARS, MAVERL) read the manuscript and provided many helpful comments. Thanks are extended to B. V. Brown for his early, but essential help with phorid identifications and to both B. V. Brown and D. H. Feener for general discussions concerning the host specificity of parasitic phorids. This work was partially funded with a grant from the U.S.-Brazil Science and Technology Initiative through the USDA-OICD-IRD. Mention of a commercial product does not imply endorsement by the authors or their employers.

REFERENCES CITED

- BANKS, W. A., C. S. LOFGREN, D. P. JOUVENAZ, C. E. STRINGER, P. M. BISHOP, D. F. WILLIAMS, D. P. WOJCICK, AND B. M. GLANCEY. 1981. Techniques for collecting, rearing, and handling imported fire ants. USDA, SEA, AATS-S-21, 9 p.
- BORGMEIER, T. 1922 (1921). Zur Lebensweise von *Pseudacteon borgmeieri* Schmitz (in litt.) (Diptera: Phoridae). Zs. Deut. Ver. Wiss. Kunst São Paulo 1: 239-248.
- BORGMEIER, T. 1962. Cinco espécies novas do genero *Pseudacteon* Coquillett. Arq. Mus. Nac. (Rio de Janeiro) 52: 27-30.
- BORGMEIER, T. 1963. Revision of the North American phorid flies. Part I. The Phorinae, Aenigmatiinae, and Metopininae, except *Megaselia* (Diptera: Phoridae). Stud. Entomol. 6: 1-256.
- BORGMEIER, T. 1969. New or little-known phorid flies, mainly of the Neotropical region (Diptera: Phoridae). Stud. Entomol. 12: 33-132.
- BORGMEIER, T., AND A. P. PRADO. 1975. New or little known Neotropical phorid flies, with description of eight new genera (Diptera: Phoridae). Stud. Entomol. 18: 3-90.
- BROWN, B. V. 1993. Taxonomy and preliminary phylogeny of the parasitic genus *Apocephalus*, subgenus *Mesophora* (Diptera: Phoridae). Syst. Entomol. 18:191-230.
- BUREN, W. F. 1983. Artificial faunal replacement for imported fire ant control. Florida Entomol. 66: 93-100.
- DISNEY, R. H. L. 1991. The fire-ant parasitoids of the *Pseudacteon spatulatus* complex (Diptera, Phoridae; Hymenoptera, Formicidae). Sociobiology 18: 283-298.
- DISNEY, R. H. L. 1994. Scuttle flies: the Phoridae. Chapman & Hall, London, 467 p.
- DONISTHORPE, H. S. J. K. 1927. The guests of British ants, their habits and life histories. George Routledge & Sons, London, 244 p.
- FEENER, D. H., JR. 1987. Size-selective oviposition in *Pseudacteon crawfordi* (Diptera: Phoridae), a parasite of fire ants. Ann. Entomol. Soc. America 80: 148-151.
- FEENER, D. H., JR., AND B. V. BROWN. 1992. Reduced foraging of *Solenopsis geminata* (Hymenoptera: Formicidae) in the presence of parasitic *Pseudacteon* spp. (Diptera: Phoridae). Ann. Entomol. Soc. America 85: 80-84.
- HERATY, J. M., D. P. WOJCICK, AND D. P. JOUVENAZ. 1993. Species of *Orasema* parasitic on the *Solenopsis saevissima*-complex in South America (Hymenoptera: Eucharitidae, Formicidae). J. Hymen. Res. 2: 169-182.
- JOUVENAZ, D. P. 1983. Natural enemies of fire ants. Florida Entomol. 66: 111-121.
- JOUVENAZ, D. P., D. P. WOJCICK, M. A. NAVES, AND C. S. LOFGREN. 1988. Observations on a parasitic nematode (Tetradonematidae) of fire ants, *Solenopsis* (Formicidae), from Mato Grosso. Pesq. Agropec. Brasil. 23: 525-528.
- PATTERSON, R. A., AND J. A. BRIANO. 1993. Potential of three biological control agents for suppression of *Solenopsis invicta*, red imported fire ant, p. 35-43 in K. B. Wildey and W. H. Robinson [eds.] Proceedings of the 1st international conference on insect pests in the urban environment. BPC Wheatons Ltd., Exeter, 498 p.

- PORTER, S. D., H. G. FOWLER, AND W. P. MACKAY. 1992. Fire ant mound densities in the United States and Brazil (Hymenoptera: Formicidae). *J. Econ. Entomol.* 85: 1154-1161.
- PORTER, S. D., R. K. VANDER MEER, M. A. PESQUERO, S. CAMPIOLO, AND H. G. FOWLER. 1995a. Reactions of *Solenopsis* fire ants to attacks of *Pseudacteon* phorid flies in southeastern Brazil. *Ann. Entomol. Soc. America* (In press).
- PORTER, S. D., H. G. FOWLER, S. CAMPIOLO, AND M. A. PESQUERO. 1995b. Rearing *Pseudacteon* phorid fly maggots (Diptera: Phoridae) in the heads of *Solenopsis* fire ant workers (Hymenoptera: Formicidae). *Environ. Entomol.* (submitted)
- TRAGER, J. C. 1991. A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). *J. New York Entomol. Soc.* 99: 141-198.
- WASMANN, E. 1918. Zur Lebensweise und Fortpflanzung von *Pseudacteon formicarum* Verr. (Diptera, Phoridae). *Biol. Zentbl.* 38: 317-329.
- WILLIAMS, D. F., AND W. A. BANKS. 1987. *Pseudacteon obtusus* (Diptera: Phoridae) attacking *Solenopsis invicta* (Hymenoptera: Formicidae) in Brazil. *Psyche* 94: 9-13.
- WILLIAMS, R. N. 1980. Insect natural enemies of fire ants in South America with several new records. *Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage.* 7: 123-134.

