# Distribution and Abundance of Fire Ant Decapitating Flies (Diptera: Phoridae: *Pseudacteon*) in Three Regions of Southern South America

LUIS A. CALCATERRA,[1] SANFORD D. PORTER,[2] AND JUAN A. BRIANO[1]

Ann. Entomol. Soc. Am. 98(1): 85–95 (2005)

**ABSTRACT** The distribution and abundance of fire ant decapitating flies (Diptera: Phoridae: *Pseudacteon* Coquillett) were studied in three regions of southern South America, primarily from September 2002 to September 2004. A total of 2,421 flies belonging to 14 *Pseudacteon* species were found at 51% of the 662 fire ant mounds examined at 125 collecting sites. Flies occurred in a variety of habitats at altitudes from sea level to 2,280 m. *Pseudacteon obtusus* Borgmeier (large form) was found at the highest altitude and at the most western longitude. Flies were active between 16 and 37°C, 20 and 90% RH, and 0 and 11.6 km/h wind speed. *Pseudacteon curvatus* Borgmeier showed the highest abundance and one of the broadest geographical distributions. *Pseudacteon tricuspis* Borgmeier, *P. litoralis* Borgmeier, the large form of *P. obtusus*, *P. nudicornis* Borgmeier, and *P. nocens* Borgmeier also were widely distributed. These species seem to be the most generalized within *saevissima*-group. *Pseudacteon solenopsidis* Schmitz was only collected attacking isolated workers. A new *Pseudacteon* species was discovered in northwestern Argentina. Seven fly species were reported for the first time on a new fire ant host in this region. *Pseudacteon cultellatus* Borgmeier was found for the first time on *Solenopsis invicta* Buren in Corrientes province in northeastern Argentina, where up to nine fly species have been found to cooccur. Males of *P. tricuspis* and *P. obtusus* were the only males normally attracted to disturbed fire ant colonies.

**KEY WORDS** *Pseudacteon*, parasitoid, *Solenopsis*, biological control, Argentina

THE GENUS *Pseudacteon* Coquillett (Diptera: Phoridae) is widespread throughout the world. *Pseudacteon* species has been collected in South America, North America, Europe, Asia, Australia, and Indonesia (Coquillett 1907, Disney 1994, Brown and Feener 1998, Disney and Michailovskaya 2000, Folgarait et al. 2005). All *Pseudacteon* flies are almost certainly parasitoids of individual worker ants (Hymenoptera: Formicidae) (Disney 1994, Feener and Brown 1997). The adult female inserts an egg into the thorax of a live worker ant (Porter et al. 1995a). The egg hatches and the larva migrates to the head of the ant. At pupariation, the phorid consumes all the tissue inside the ant's head, killing the ant. An adult phorid emerges from the ant's mouth ≈5 or 6 wk after the egg was laid (Porter et al. 1995a; Folgarait et al. 2002a, b). All species of *Pseudacteon* flies with lobed ovipositors have only been collected attacking ants in the genus *Solenopsis* Westwood (Disney 1994, Porter et al. 1995a, Porter 1998b, Porter and Alonso 1999). Some *Pseudacteon* flies with simple ovipositors attack other ant genera (*Linepithema*, *Neivamyrmex*, *Crematogaster*, *Dorymyrmex*, *Liometopum*, *Azteca*, *Camponotus*, *Formica*, *Lasius*, *Paratrechina*, *Myrmica*, and *Pseudolasius*) (Disney 1994, Brown and Feener 1998).

Approximately 30 New World species of *Pseudacteon* are parasitoids of *Solenopsis* fire ants. Nine of them attack ants in the *Solenopsis geminata* species-group, and 20 attack fire ants in the *Solenopsis saevissima* species-group (Borgmeier and Prado 1975, Williams 1980, Porter 1998a, Brown and Morrison 1999, Pesquero 2000, and Porter and Pesquero 2001, Pitts 2002, Brown et al. 2003). Fire ants in the *saevissima* species-group occur in different regions of South America from the Amazon Basin of Brazil, west to the Andes and south through the Province of Buenos Aires in Argentina. Regional morphological variation has been reported in some *Pseudacteon* by Porter and Pesquero (2001), such as *P. tricuspis* Borgmeier and *P. curvatus* Borgmeier. Some cases may be intraspecific clinal variation, whereas others may be true sibling species isolated by geography or host preferences. Different biotypes of the same species or sibling species are likely adapted to attack different fire ant species (Porter 1998a, Porter and Briano 2000, Porter and Pesquero 2001).

So far, four *Solenopsis* fire ant species [*S. richteri* Forel, *S. invicta* Buren, *S. saevissima* (Smith), and *S. interrupta* (Santschi)] have been reported to be

[1] USDA–ARS South American Biological Control Laboratory, Bolivar 1559 (1686) Hurlingham, Buenos Aires province, Argentina.
[2] USDA–ARS, Center for Medical, Agricultural and Veterinary Entomology, P.O. Box 14565, Gainesville, FL 32604.

natural hosts of *Pseudacteon* species in Argentina and Brazil (Porter et al. 1995a, Orr et al. 1997, Porter 1998a, Folgarait and Gilbert 1999, Porter and Pesquero 2001, Brown et al. 2003). Because of their parasitic lifestyle, *Pseudacteon* species are of great interest as biocontrol agents against the imported fire ants, *S. invicta* and *S. richteri*, in the United States. Interactions between *Pseudacteon* flies and fire ants have been studied in Brazil (Porter et al. 1995b; Orr et al. 1995, 1997; Porter 1998a, 2000) and in Argentina (Feener and Brown 1992; Folgarait and Gilbert 1999; Feener 2000; Porter and Briano 2000; Folgarait et al. 2002a, b; Wuellner et al. 2002a). These studies indicate that the presence of phorid flies inhibits fire ant recruitment to food resources and allow other ants in the community access to those resources.

At present, three *Pseudacteon* species (four biotypes) have been released in the United States against fire ants. *P. tricuspis* from Brazil was successfully released in Texas (Gilbert and Patrock 2002) and Florida in 1997 (Porter et al. 1999), and it is well established in eight states (Porter et al. 2004). *P. tricuspis* from Formosa was released in Texas, but its establishment was not confirmed yet. *P. curvatus* from Argentina was released in 2000 (Porter et al. 2004). One biotype of *P. curvatus* from Las Flores, Buenos Aires, is established on hybrids fire ants at several locations in Alabama and Mississippi (Graham et al. 2003, Vogt and Streett 2003) and a second biotype from Formosa just established on the red imported fire ant near Gainesville, FL (Vazquez et al. 2005). Several trial releases of *P. litoralis* Borgmeier are in progress near Gainesville (S.D.P., unpublished data). However, because imported fire ants inhabit a relatively large area in the United States, it will be necessary to import additional species or biotypes from South America to expand the breadth and magnitude of their impact on imported fire ants.

South American *Pseudacteon* flies have been only reported from a few localities of Argentina and Brazil, especially from places close to Buenos Aires and Sao Paulo where fly populations were suitable to conduct studies (Williams et al. 1973, Fowler et al. 1995, Pesquero et al. 1996, Orr et al. 1997, Folgarait et al. 2003). However, the distribution and abundance of most of the species are poorly known (Williams 1980, Folgarait et al. 2005). Williams (1980) only reported the overall abundance of *Pseudacteon* species for a wide area of Brazil, whereas Folgarait et al. (2005) reported information on occurrence of species for a wider geographic range, including Argentina and Brazil, but not abundance. The objective of this work was to detail the geographical occurrence and abundance of *Pseudacteon* species in three regions of southern South America, including several unexplored areas. Data from this study will be used to collect flies for export to quarantine facilities in the United States and to locate field sites with dense populations of flies to conduct long-term studies.

## Materials and Methods

**Area Surveyed.** Field surveys were conducted in east central, northeastern, and northwestern Argentina, southern Paraguay, and a small area in southern Bolivia, beginning in 1995, but more intensively from September 2002 to September 2004. The surveys were mainly carried out during the warm seasons (late September to late April) when *Pseudacteon* flies are generally more abundant (Fowler et al. 1995; Pesquero et al. 1995, 1996; Folgarait et al. 2003). A total of 662 fire ant mounds were sampled in 125 collecting sites where flies were found. Most of the sites were sampled only once.

Fly collections were divided in three regions according to 1) the most frequent fire ant hosts, as described by Trager (1991) and Pitts (2002), and 2) phytogeographical information provided by Cabrera and Willink (1980). Region 1 included east central Argentina (southern Entre Ríos and northeastern Buenos Aires province), Pampeana phytogeographical province (horizontal plains with grassland and xeric woodland), where *S. richteri* Forel is the predominant species. Region 2 included northeastern Argentina (eastern Formosa, eastern Chaco, Santa Fe, northwestern Corrientes, and Misiones provinces) and southern Paraguay (Itapua, Alto Paraná, Concepción, and Caaguazú districts). Collecting sites in this region corresponded mainly to the Chaco (a mosaic of ecosystems combining woods with savanna) and Paranaense (subtropical forest with patches of evergreen coniferous forests and savannas in the plateaus, and grasslands) phytogeographical provinces. *S. invicta* and secondarily *S. macdonaghi* Santschi are the dominant species in this region. Region 3 included northwestern Argentina (southern Catamarca, Tucumán, western Santiago del Estero, southeastern Jujuy, and central Salta provinces) and a small area in southern Bolivia (Tarija district), which corresponded mainly to the phytogeographical province of Las Yungas. Data from the phytogeographical province of the Monte (La Rioja and San Luis provinces) was not included because no flies were found in that province. However, a few sites corresponded to the Chaco phytogeographical province (Cabrera and Willink 1980). Las Yungas is one of the largest areas of mountain rainforest in the world in which a large number of endemic species occur (Stattersfield et al. 1998). *S. interrupta* is the most common fire ant species reported for this region. The most important collecting sites in each region were mapped (Fig. 1).

**Collection Method.** The regions were surveyed by sampling along main and secondary roads. Collecting sites included roadsides, pastures, camping areas, and parks. The occurrence of *Solenopsis* mounds (nests) within the *saevissima* species-group (Pitts 2002) was recorded in each site. In each stop, several nests were opened and disturbed to attract phorid flies. The search for flies was stopped 20 min after nest disturbance because this is often the maximum time in which the flies occur (Porter 1998b). All flies attracted to the mounds were collected using hand aspirators.

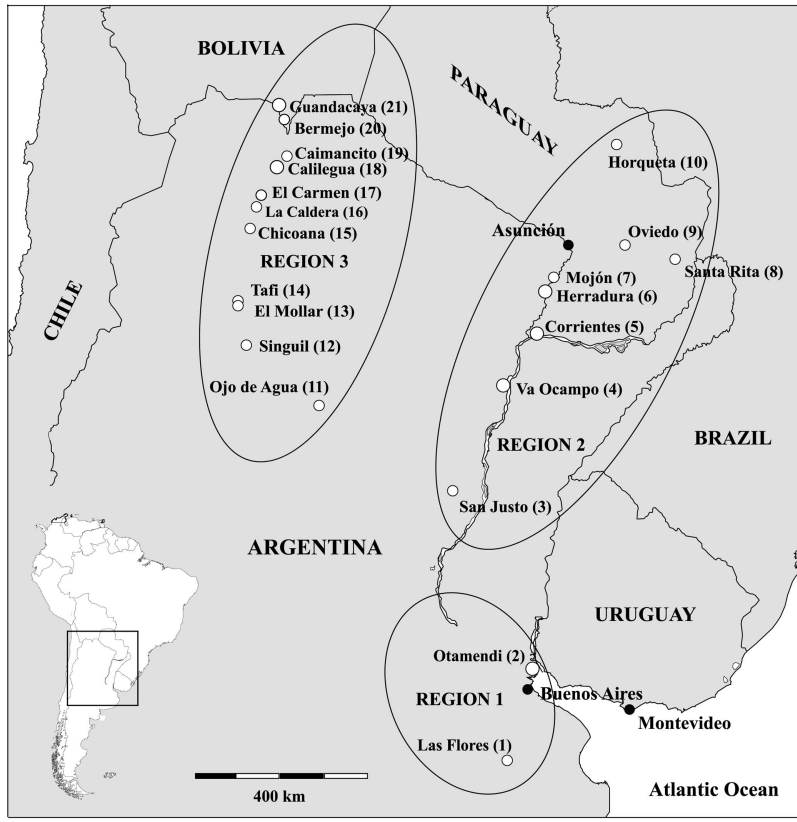


**Fig. 1.** Regions surveyed within southern South America. The main localities where *Pseudacteon* flies were collected are numbered (the number in parentheses refers to sampling areas in Table 1).

Fire ant samples were taken from most of the colonies examined and were preserved in 80% ethanol for taxonomic identification. Temperature, humidity, speed wind, altitude, and geographic position were recorded for each site where flies were found. Weather variables were measured on top of the ant mounds by using a portable weather station Kestrel 3000, whereas altitude and geographical position were recorded using a GPS unit Garmin III.

Some flies also were collected from trays containing worker ants to attract flies in five localities (see Table 1) as part of a study of preference of *Pseudacteon* flies for different fire ant hosts. Attack trays (12–15) containing 2 g of worker ants were placed on ground for 2 h in each locality. Most attracted females were collected with an aspirator and identified to species with 10× hand lens in the field, or they were preserved in 80% ethanol for taxonomic identification under a dissecting microscope with available keys (Porter and Pesquero 2001). Additionally, the most common *Pseudacteon* species collected in each region were measured (mesonotum width) under a dissecting microscope to compare average body sizes of flies from different regions and/or different fire ant hosts.

Voucher specimens of collections made in Argentina, Paraguay, and Bolivia were deposited at the Museo de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, and the USDA–ARS–South American Biological Control Laboratory, Hurlingham, Buenos Aires province, Argentina.

**Data Analysis.** Only females were considered when analyzing the distribution and abundance of flies because males of most species are not attracted to fire ants in the field. The occurrence of each fly species refers to the number (%) of sites where each species occurred. Similarly, the abundance of each species refers to the number of individuals found. The two forms of *P. obtusus* Borgmeier (large and small) mentioned by Porter and Pesquero (2001) were considered separately in this analysis because preliminary studies based on amplified fragment length polymorphism analysis suggest that they are different species (Porter and Gilbert 2005).

Three indices were used to characterize and/or compare the *Pseudacteon* species diversity in the three regions surveyed: the richness or number of species collected by region, the Shannon diversity index (H′), and Sorensen's quantitative index of community similarity ($SQ = 2pN/aN + bN$, where $aN$ is the total number of individuals in site A, $bN$ is the total number of individuals in site B, and $pN$ is the sum of the lower of the two abundances recorded for species found in both sites. Index range varies between 0.0 for no similarity and 1.0 for complete similarity) (Magurran

**Table 1. Distribution and abundance of decapitating flies in southern South America**

| Country/province[a] Locality[b] | No. collecting sites (w/flies) | No. mounds examined (% w/flies) | No. *Pseudacteon* female flies collected[c] (no. males) | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *cur* | *lit* | *noc* | *tri* | *obt*[d] | *dis* | *cul* | *obt*[e] | *nud* | *sol* | *bor* | n. sp. | *com* | *bul* | Total |
| **Region 1 (east central Argentina)** | | | | | | | | | | | | | | | | | |
| Argentina | | | | | | | | | | | | | | | | | |
| Buenos Aires | | | | | | | | | | | | | | | | | |
| Las Flores (1) | 2 | 20 (100) | 24 (1) | | | 2 (16) | | | | | | | | | | | 26 (17) |
| Otamendi (2) | 6 | 40[f] (26) | 224 | 1 | | 15 (38) | | | 3 | | 1 | | 7 | | 1 | | 252 (38) |
| Others | 6 | 20 (35) | 27 | | | | | | 1 | | 1 | | 3 | | | | 32 |
| Entre Rios | | | | | | | | | | | | | | | | | |
| Several | 5 | 25 (44) | 7 | 12 | 5 | 1 (3) | 1 (3) | | | 2 | | | | | | | 28 (6) |
| Subtotal | 19 | 105 (44) | 282 (1) | 13 | 5 | 18 (57) | 1 (3) | | 4 | 2 | 2 | | 10 | | 1 | | 338 (61) |
| **Region 2 (northeastern Argentina and Paraguay)** | | | | | | | | | | | | | | | | | |
| Argentina | | | | | | | | | | | | | | | | | |
| Santa Fe | | | | | | | | | | | | | | | | | |
| San Justo (3) | 2 | 27[f] (67) | 3 | 35 | | 22 (9) | 2 (3) | | | 1 | | 3[g] | | | | | 66 (12) |
| Villa Ocampo (4) | 3 | 15 (60) | | 20 | 1 | 2 (5) | 9 (1) | | | 8 | | | | | | | 40 (6) |
| Others | 18 | 60 (55) | | 14 | 2 | 17 (28) | 26 (22) | | | 5 | | | | | | | 64 (50) |
| Chaco | | | | | | | | | | | | | | | | | |
| Several | 3 | 25 (20) | | 2 | | 1 (4) | 2 (1) | | | | | | | | | | 5 (5) |
| Corrientes | | | | | | | | | | | | | | | | | |
| Corrientes (5) | 2 | 20[f] (75) | 4 | 17 | 25 | 8 (16) | 6 (8) | | 111 | 5 | 1 | 1 | | | | | 178 (24) |
| Others | 4 | 79 (8) | | 3 | | 1 (5) | 2 | | 3 | 1 | | | | | | | 10 (5) |
| Formosa | | | | | | | | | | | | | | | | | |
| Herradura (6) | 3 | 37[f] (78) | 39 | 217 | 143 | 40 (63) | 54 (25) | | | 26 (1) | 10 | | | | | | 529 (89) |
| Mojón de Fierro (7) | 1 | 20[f] (85) | 4 | | 3 | 16 (35) | 28 (24) | | | 12 | | | | | | | 63 (59) |
| Others | 18 | 86 (43) | 2 (2) | 4 | 2 | 24 (51) | 12 (22) | | | | | 19[g] | | | | | 63 (75) |
| Misiones | | | | | | | | | | | | | | | | | |
| Several | 8 | 17 (47) | 2 | 4 | | 7 (20) | | | | | | | | | | | 13 (20) |
| Paraguay | | | | | | | | | | | | | | | | | |
| Itapua | | | | | | | | | | | | | | | | | |
| Several | 3 | 7 (43) | | 1 | | 1 | 1 | | | 1 | | | | | | | 4 |
| Alto Parana | | | | | | | | | | | | | | | | | |
| Santa Rita (8) | 1 | 5 (40) | | | | 2 | 2 (1) | | | | | | | | | | 4 (1) |
| Caaguazú | | | | | | | | | | | | | | | | | |
| Coronel Oviedo (9) | 1 | 3 (33) | | | 1 | | | | | | | | | | | | 1 |
| Concepción | | | | | | | | | | | | | | | | | |
| Horqueta (10) | 1 | 1 (100) | 1 | | | 4 (3) | | | | | | | | | | | 5 (3) |
| Subtotal | 68 | 402 (46) | 55 (2) | 317 | 177 | 145 (239) | 144 (107) | | 114 | 59 (1) | 11 | 23 | | | | | 1,045 (349) |
| **Region 3 (northwestern Argentina and Bolivia)** | | | | | | | | | | | | | | | | | |
| Argentina | | | | | | | | | | | | | | | | | |
| Sgo. Del Estero | | | | | | | | | | | | | | | | | |
| Va. Ojo de Agua (11) | 1 | 4 (75) | 31 | | | | | | | | | | | | | 1 | 32 |
| Catamarca | | | | | | | | | | | | | | | | | |
| Singuil (12) | 2 | 6 (100) | 58 | | | | | | | | | | | | | | 58 |
| Others | 5 | 11 (64) | 14 | | | | | | | | | | | | | | 14 |
| Tucumán | | | | | | | | | | | | | | | | | |
| El Mollar (13) | 3 | 6 (67) | | | | | 5 (16) | | | | | | | | | | 5 (16) |
| Tafí del Valle (14) | 4 | 11 (91) | | | | | 7 (35) | | | | | | | | | | 7 (35) |
| Others | 5 | 10 (80) | 12 | | | | | 3 | | | 7 | | | | | | 22 |
| Salta | | | | | | | | | | | | | | | | | |
| Several (15–16) | 5 | 38 (58) | 74 | 6 | 15 | 7 (11) | 1 (1) | 14 | | | | | | 2 | | | 118 (12) |
| Jujuy | | | | | | | | | | | | | | | | | |
| El Carmen (17) | 2 | 16 (69) | 42 | 5 | | | | 4 | | | | | | 2 | | | 53 |
| Calilegua (18) | 3 | 9 (59) | 9 | 26 | | 2 (1) | | 3 | | | 1 | | | | | | 41 (1) |
| Caimancito (19) | 1 | 4 (25) | | | | | | | | | | | | 2 | | | 2 |
| Bolivia | | | | | | | | | | | | | | | | | |
| Tarija | | | | | | | | | | | | | | | | | |
| Bermejo (20) | 1 | 4 (100) | 29 | 1 | | | | 43 | | | | | | | | | 73 |
| Guandacaya (21) | 6 | 17 (100) | 3 | 7 | | 19 (31) | | 73 | | | 5 | | | | | | 107 (31) |
| Subtotal | 38 | 144 (72) | 272 | 45 | 15 | 28 (43) | 13 (52) | 140 | | | 13 | | | 6 | | 1 | 533 (95) |
| Total | 125 | 662 (51) | 609 (3) | 375 | 197 | 191 (339) | 158 (162) | 140 | 118 | 61 (1) | 26 | 23 | 10 | 6 | 1 | 1 | 1,916 (505) |

[a] Districts for Paraguay and Bolivia.

[b] Numbers in parentheses refer to localities shown in Fig. 1.

[c] *Pseudacteon* species: *cur* = *curvatus*, *lit* = *litoralis*, *noc* = *nocens*, *tri* = *tricuspis*, *obt* = *obtusus*, *dis* = *Pseudacteon* sp. near *disneyi*, *cul* = *cultellatus*, *nud* = *nudicornis*, *sol* = *solenopsidis*, *bor* = *borgmeieri*, n. sp. = *Pseudacteon* new species, *com* = *comatus*, *bul* = *bulbosus*.

[d] Large form of *P. obtusus* matching original species description (Borgmeier 1963).

[e] Small form of *P. obtusus*.

[f] Females were reared from ants exposed to fly attacks in trays in the field.

[g] Females reared from naturally parasitized ants.

1988). The similarity index was calculated using the relative percentage of abundance of each species, because sampling effort was different among regions. The indexes were calculated using BIO-DAP (Thomas 2000), a software package based on the worked examples in Magurran (1988).

## Results and Discussion

Most of the *Pseudacteon* species were common and/or abundant in the regions surveyed in southern South America, whereas a few were restricted to specific regions and hosts. We found 2,421 flies belonging to 14 *Pseudacteon* species in 51% (338/662) of the fire ant mounds examined at 125 collecting sites, where at least one *Pseudacteon* individual was detected (Table 1). However, the highest occurrence of flies was in northwestern Argentina and Bolivia, with almost twice as many colonies attracting flies (72%) as in east central Argentina (44%) and northeastern Argentina and Paraguay (46%). It is unknown whether this reflects natural abundances or better collecting conditions. The 14 species collected represented 65% of the *Pseudacteon* species known to attack *saevissima* group in South America (Brown 2000, Pesquero 2000, Porter and Pesquero 2001, Folgarait et al. 2005).

**Geographical Distribution.** *Pseudacteon* flies were broadly distributed across a wide range of habitats and climates, with the exception of extremely arid areas. However, more abundant populations were found near permanent body of waters (such as large rivers or lagoons) or forest habitats. They were found between 23° 15′ and 35° 89′ S, between 65° 46′ and 54° 26′ W, and up to 2,280 m of altitude. The distribution range for almost all species extended to northeastern through southeastern Brazil (Williams et al. 1973, Williams 1980, Fowler et al. 1995, Orr et al. 1997, Folgarait et al. 2005). The large form of *P. obtusus* was found at the highest altitude and at the most western longitude (Santa Cruz, near El Mollar and Tafí del Valle, Tucumán province; Table 1). This represents the westernmost record for *Pseudacteon* species attacking fire ants and the first report of fly occurrence for the ecotone between the Las Yungas and Prepuneña phytogeographical provinces (a transition zone compound by grasslands between the 1000- and 2,500-m altitude, and with 400 and 700 mm of annual rainfall). Fire ant colonies were found up to 66° 14′ W and 3,064 m of altitude.

Climates in the areas of *Pseudacteon* fly distribution were highly variable, ranging from semiarid temperate and subtropical highlands in the west, to temperate and subtropical lowlands in the east, with and without dry winter seasons (Cabrera and Willink 1980). The collecting localities of Argentina have an average annual rainfall of 870 mm, ranging from 393 to 1,222 mm (Fig. 1) (De Fina 1992).

Little is known about physical factors that limit the distribution of *Pseudacteon* flies (Folgarait et al. 2003, 2005), but presumably there are thermal and moisture limits, as well as limits associated with plant cover (Porter 1998b). This could explain why we did not find flies (and only few fire ants) in La Rioja and San Luis (Argentina), where annual rainfall is <400 mm, mean temperatures during the warm season are >27°C (De Fina 1992), and plant cover is scarce. Most parts of both provinces belong to the Monte phytogeographical province, one of the most arid areas of Argentina (Cabrera and Willink 1980). Red imported fire ants (*S. invicta*) do not seem to infest areas with low precipitation (<500 mm) and without irrigation in the United States (Korzukhin et al. 2001). Why we did not find flies in most of southern Paraguay is unknown because the climatic conditions seem to be suitable for phorids.

A new *Pseudacteon* species was discovered in four localities of the Argentinean northwestern (region 3): El Carmen and Caimancito in Jujuy province, and Chicoana and La Caldera in Salta province (Fig. 1). The six individuals collected are near *P. solenopsidis* (Schmitz) or *P. borgmeieri* Schmitz, but they differ in the shape of the apex of the ovipositor and the absence of large ventral hairs near the ovipositor (L.A.C., unpublished data).

Seven species are reported for the first time in northwestern Argentina and Bolivia: *P. curvatus*, *P.* sp. near *disneyi*, *P. tricuspis*, *P. litoralis*, *P. nudicornis* Borgmeier, *P. obtusus* (large form), and *P. nocens* Borgmeier. Most individuals were darker than those collected in the other two regions, especially *P. curvatus.* One individual of *P. bulbosus* Brown also was found in the Santiago del Estero province (Fig. 1). *P. bulbosus* was previously reported by Brown et al. (2003) attacking *S. interrupta* in this province. It is the southernmost collecting site of this region and corresponds to the Chaco phytogeographical province. The hosts of flies in this region were often fire ant species with larger workers than those in the other two regions (Porter 1998a, Porter and Pesquero 2001). *Pseudacteon* flies have not been previously reported attacking larger species of fire ants such as *S. quinquecuspsis* Forel, *S. interrupta,* or *S. macdonaghi* in the field, with the exception of *P. bulbosus* (Brown et al. 2003). An individual of the phorid genus *Apocephalus* Coquillett also was collected hovering over a fire ant mound in this region of Argentina. It is not known whether this fly is a fire ant parasite. *Apocephalus normenti* Prado and *A. coquilletti* Malloch were reported hovering over mounds of the fire ants *S. richteri* (Prado 1980) and *S. xyloni* (MacCook) (Greene 1938), respectively.

The number and abundance of *Pseudacteon* species in most of the collecting sites might be underestimated because only a few sites were sampled throughout the year and at different times of the day. Nevertheless, the number of flies and species found in the three regions surveyed in this work (primarily in Argentina) is similar to the results of the study conducted by Williams (1980), in which 2,848 specimens belonging to 14 *Pseudacteon* species were collected in a wide area in Brazil. In that same study, three other fly species also were mentioned for Brazil, and three more species were reported later (Pesquero 2000, Brown 2000). Of these 20 fly species reported for Brazil, eight,

*Pseudacteon affinis* Borgmeier, *P. convexicauda* Borgmeier, *P. dentiger* Borgmeier, *P. lenkoi* Borgmeier & Prado, *P. pradei* Borgmeier, *P. wasmanni* (Schmitz), *P. fowleri* Pesquero, and *P. conicornis* Borgmeier, were not found in our surveys.

One likely explanation for the absence in Argentina of the eight species collected in Brazil is that some of them attack almost exclusively *Solenopsis* species that do not occur in our study sites, such as *S. saevissima.* Sixteen *Pseudacteon* species have been reported hovering over *S. saevissima* mounds (Disney 1994); however, only nine were confirmed. *P. tricuspis, P. litoralis, P. curvatus, P. obtusus, P. nudicornis, P. wasmanni, P. pradei,* and *P. borgmeieri* in Sao Paulo state, Brazil (Pesquero et al. 1993, Fowler et al. 1995, Orr et al. 1997), and *P. conicornis* in Rio de Janeiro, Brazil (Brown 2000). The host of *Pseudacteon lenkoi, P. dentiger, P. fowleri,* and *P. affinis* is not clear, but they seem to be more common (Folgarait et al. 2005) in the Cerrado phytogeographical province (a mosaic of grasslands, tree savannahs, and woodlands with patches of semideciduous forest). However, only two of the *Pseudacteon* species reported in our study (*P. bulbosus* and the new *Pseudacteon* species found in northwestern Argentina) were not found in Brazil. The former could be restricted to a tropical dry forest of Chaco, whereas the latter might be restricted to an ecofloristic zone of the Yungas (Stattersfield et al. 1998).

**Weather Conditions.** Although differences were observed across species, phorid flies were active at a wide climatic range. They were found between 16 and 37°C, 20 and 90% RH, and 0 and 11.6 km/h wind speed (average of 7.5 km/h). *P. tricuspis* was found at the highest temperature (37°C) and the lowest relative humidity (20%), whereas *P. nocens* was active at the lowest temperature (16°C) and the lowest relative humidity (20%). However, *P. litoralis, P. curvatus,* and the small form of *P. obtusus* were active at 17°C. *P. curvatus* and *P. bulbosus* also were found at low relative humidity (30%), whereas *P. nocens* and *P. litoralis* at the highest one (90%). Studies conducted by Morrison et al. (1999), Folgarait and Gilbert (1999), Folgarait et al. (2003), and Wuellner and Saunders (2003) reported that most *Pseudacteon* species were inactive with temperature <20°C and *P. borgmeieri* <14°C.

**Sex Ratio.** A total of 505 males were collected hovering over fire ant workers, 99.2% of which were either *P. tricuspis* (339) or the large form of *P. obtusus* (162). Males of these species were regularly observed taking females out of the air and mating with them as they fell to the ground. The ratio of males to females was ≈2:1 for *P. tricuspis* and ≈1:1 for *P. obtusus* (large form). The primary sex ratio in the field is unknown, but these values are in the range of what is found in laboratory colonies (S.D.P., unpublished data). Males of other *Pseudacteon* species are rarely or never attracted to fire ants. Three *P. curvatus* males were collected but these were almost certainly accidental as this species does not mate on the wing over fire ants (Wuellner et al. 2002a). Only one male of what seemed to be the small form of *P. obtusus* was collected indicating that this fly, unlike its larger relative, may not mate over fire ant colonies.

**Species Richness and Abundance.** The number of *Pseudacteon* species found was similar in the three regions sampled, in spite of the fact that the sampling efforts varied among the regions. A total of 10, nine, and nine species were collected from 19, 68, and 38 collecting sites in regions 1, 2, and 3, respectively. Individual regions contained 60–70% of the total species found (14). Although more colonies attracted flies in northwestern Argentina and Bolivia than other regions surveyed, overall abundance of flies was proportional to the number of collecting sites in each region. A total of 338, 1,045, and 533 female flies were collected in regions 1, 2, and 3, respectively (Table 1). The east central (region 1) and northeastern Argentina (region 2) shared the highest number of species (8). One might expect greater similarity between these two regions than between regions 1 and 3 or 2 and 3, because of their proximity and higher number of species shared. However, considering relative abundance of the fly species (Fig. 2), regions 1 and 3 were actually the most similar (SQ = 0.602). Similarity between these two regions was three times higher than in the other paired comparisons (SQ = 0.198 between regions 1 and 2, whereas SQ = 0.206 between regions 2 and 3). Northeastern Argentina had the highest species diversity ($H' = 1.794$), followed by northwestern ($H' = 1.402$) and east central ($H' = 0.747$) Argentina. The high diversity in region 2 might be explained by the fact that this region was the most intensively surveyed, and, consequently, seasonal differences in occurrence and abundance of species might have been compensated. The low diversity in region 1 could be explained by its higher environmental homogeneity (only the Pampeana phytogeographical province).

Six *Pseudacteon* species occurred in all three regions: *P. curvatus, P. litoralis, P. tricuspis, P. obtusus* (large form), *P. nudicornis,* and *P. nocens,* whereas two other species occurred only in region 1 and 2: *P. cultellatus* Borgmeier and *P. obtusus* (small form). The few specimens of *P. nocens* and *P. obtusus* (small form) collected in region 1 were from an area where *S. invicta* and *S. richteri* overlap (Ross and Trager 1990). Consequently, these flies could have been parasitizing either fire ant species. Host preference tests suggested that *S. richteri* is a natural host of both fly species (L.A.C., unpublished data).

*P. borgmeieri* and *P. comatus* Borgmeier occurred only in region 1. *P. solenopsidis* occurred only in region 2, whereas *P.* sp. near *disneyi, P. bulbosus,* and the new *Pseudacteon* species were restricted to region 3. *P. borgmeieri, P. comatus,* and *P. solenopsidis* also were reported for northeastern Argentina and/or southern Brazil (Orr et al. 1997, Folgarait et al. 2004). It is important to note that most of the 21 *P. solenopsidis* females from Formosa and Santa Fe (Fig. 1) emerged in the laboratory from naturally parasitized workers. These workers were probably parasitized on foraging trails because the flies are almost never attracted to

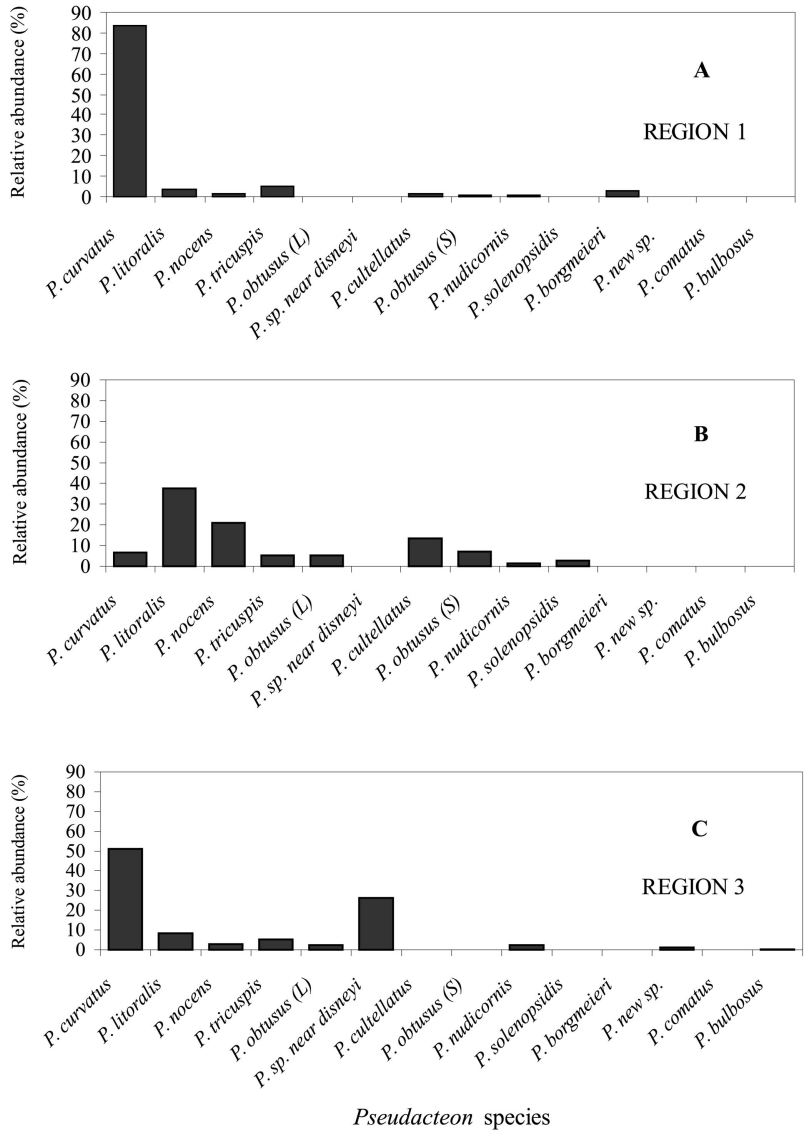


**Fig. 2A-C.** Abundance of *Pseudacteon* flies in the three regions surveyed in South America.

disturbed colonies (Orr et al. 1997, Wuellner et al. 2002b). The only *P. solenopsidis* female from Corrientes was collected while attacking an isolated fire ant worker. *P. solenopsidis* is probably attracted to the individual ants responding to trail pheromones, whereas the other species are attracted to the alarm pheromones emitted by disturbed colonies (Morrison and King 2004). The presence of *P. solenopsidis* was underestimated because of its behavior. Additional surveys, including baits, are necessary to have a good indication of its occurrence and abundance.

In general, *P. curvatus* was the most abundant and the second most common species during this study (Table 2). *P. litoralis* was the most abundant and one of the most common species found in northeastern Argentina and Paraguay (the region most intensively sampled; Fig. 2). *P. tricuspis* was abundant and the most common distributed species (47.2% of all the sites surveyed). *P. nocens*, *P. cultellatus*, and *P.* sp. near *disneyi* were locally abundant, but never common (with the exception of *P.* sp. near *disneyi* that was the second most common species found in northwestern Argentina). As explained above, *P. solenopsidis* was less abundant and rarely collected only in region 2. The new *Pseudacteon* species, *P. comatus*, and *P. bulbosus* were all rarely collected and scarce.

*P. cultellatus* was only found attacking *S. richteri* in Buenos Aires and *S. invicta* in Corrientes. This is the first report of *P. cultellatus* being attracted naturally to *S. invicta* in the field. Flies of *P. cultellatus* developed successfully from *S. invicta* colonies attacked in Corrientes (L.A.C., unpublished data). Flies collected in

**Table 2. Percentage of collecting sites with a given *Pseudacteon* species**

| *Pseudacteon* sp. | Region 1 *n* = 19 | Region 2 *n* = 68 | Region 3 *n* = 38 | Total *n* = 125 |
|---|---|---|---|---|
| *P. curvatus* | 100 (282) | 17.6 (55) | 63.2 (272) | 44.0 (609) |
| *P. litoralis* | 31.6 (13) | 42.7 (317) | 39.5 (45) | 40.0 (375) |
| *P. nocens* | 15.8 (5) | 16.2 (177) | 5.3 (15) | 12.8 (197) |
| *P. tricuspis* | 42.1 (18) | 57.4 (45) | 31.6 (28) | 47.2 (191) |
| *P. obtusus* (large) | 5.3 (1) | 57.4 (44) | 21.1 (13) | 38.4 (158) |
| *P.* sp. near *disneyi* | 0 | 0 | 47.4 (140) | 14.4 (140) |
| *P. cultellatus* | 10.5 (4) | 4.4 (114) | 0 | 4.0 (118) |
| *P. obtusus* (small) | 5.3 (2) | 22.0 (59) | 0 | 12.8 (61) |
| *P. nudicornis* | 10.5 (2) | 5.9 (11) | 21.0 (13) | 11.2 (26) |
| *P. solenopsidis* | 0 | 4.4 (23) | 0 | 2.4 (23) |
| *P. borgmeieri* | 26.3 (10) | 0 | 0 | 4.0 (10) |
| *P.* new species | 0 | 0 | 10.5 (6) | 3.2 (6) |
| *P. comatus* | 5.3 (1) | 0 | 0 | 0.8 (1) |
| *P. bulbosus* | 0 | 0 | 2.6 (1) | 0.8 (1) |

Number of flies collected are shown in parentheses.

Corrientes on *S. invicta* are similar in the shape of their ovipositor to those collected on *S. richteri* in Buenos Aires, but different from those mentioned by Porter and Pesquero (2001) in the state of Goiás (Brazil). *Pseudacteon* sp. near *disneyi* was found in northwestern Argentina and Bolivia, whereas *P. disneyi* Pesquero have been previously reported in the states of Sao Paulo and Goiás, Brazil (Pesquero 2000).

All the species that we found in northeastern Argentina and Paraguay also were reported for the same phytogeographical province (Paranaense) in Brazil (Williams et al. 1973, Williams 1980, Fowler et al. 1995, Pesquero et al. 1996, Orr et al. 1997, Folgarait et al. 2005) and in similar percentage of sites to the ones reported by Folgarait et al. (2005). The occurrence of *P. bulbosus* had been reported for northwestern Argentina (Brown et al. 2003). Although in our case the host species is not *S. interrupta* and would be *S. electra* or a new *Solenopsis* species (L.A.C., unpublished data).

**Local Assemblages.** Up to nine sympatric *Pseudacteon* species were found on *S. invicta* near Corrientes city, on the coast of the Paraná River (Table 1 and Fig. 1), being the highest number of *Pseudacteon* species found at a single site. Also, abundant and species-rich fly communities were found attacking *S. invicta* at Herradura, Formosa province (seven species), and Villa Ocampo, Santa Fe province (five species), and attacking *S. richteri* at Otamendi, Buenos Aires province (seven species). The numbers of species found in these communities agrees with previous reports, where five to eight *Pseudacteon* species occur at the same site (Porter et al. 1995a, Pesquero et al. 1996, Fowler 1997, Orr et al. 1997). Communities of up to five *Pseudacteon* species also were found in northwestern Argentina (Calilegua, Jujuy province) and southern Bolivia (Guandacaya, Tarija district; Fig. 1), although the fire ant hosts have not been determined yet.

**Fly Activity.** Overall abundance of flies in these communities was variable throughout the year with peak populations occurring in the spring and fall in northeastern Argentina, and in the summer in east central Argentina. Peaks of abundance were not recorded for each species, but it is likely that they vary according to temperature and humidity (Pesquero et al. 1996; Morrison et al. 1999, 2000; Folgarait et al. 2003; Wuellner and Saunders 2003). In the native range, Fowler et al. (1995) reported peak populations for the seven *Pseudacteon* species during the spring in Sao Paulo, Brazil, whereas Folgarait et al. (2003) found different annual peaks of abundance for six species studied in Buenos Aires, Argentina, where seasonality is more pronounced. *P. curvatus* was dominant in summer, *P. borgmeirei* in winter, and *P. tricuspis*, *P. obtusus*, *P. nudicornis*, and *P. comatus* in fall. Morrison and Porter (2005) also found the highest abundance of *P. tricuspis* in the United States during autumn.

**Table 3. Size of *Pseudacteon* species (mesonotum width in mm)**

| *Pseudacteon* sp. | Region 1 $\bar{x} \pm$ SD (*n*) | Region 2 $\bar{x} \pm$ SD (*n*) | Region 3 $\bar{x} \pm$ SD (*n*) | San Paulo $\bar{x} \pm$ SD (*n*) |
|---|---|---|---|---|
| *P. litoralis* | 0.55 ± 0.06 (9) | 0.57 ± 0.06 (157) | 0.58 ± 0.04 (21) | 0.55 ± 0.05[a]<br>0.57 ± 0.03[b] |
| *P. tricuspis* | 0.60 ± 0.06 (7) | 0.53 ± 0.06 (82) | 0.43 ± 0.07 (25) | 0.50 ± 0.04[a]<br>0.49 ± 0.03[b] |
| *P. obtusus* (large) | — | 0.52 ± 0.04 (100)<br>0.60[c] | 0.49 ± 0.05 (10) | |
| *P. nocens* | — | 0.50 ± 0.06 (106)<br>0.60[c] | — | |
| *P. borgmeieri* | 0.48 ± 0.06 (12) | — | — | 0.45 ± 0.04[b] |
| *P. solenopsidis* | — | 0.50 ± 0.04 (14) | — | 0.47 ± 0.04[b] |
| *P. curvatus* | 0.39 ± 0.04 (51) | 0.36 ± 0.05 (44) | 0.35 ± 0.03 (79) | 0.33 ± 0.04[a] |
| *P.* sp. near *disneyi* | — | — | 0.36 ± 0.04 (50) | |
| *P. obtusus* (small) | — | 0.36 ± 0.04 (37) | — | 0.35 ± 0.04[b] |
| *P. nudicornis* | 0.37 (1) | 0.35 ± 0.07 (9) | 0.34 ± 0.03 (14) | 0.34 ± 0.02[b] |
| *P. cultellatus* | 0.31 ± 0.05 (3)<br>0.36 ± 0.05[d] | 0.33 ± 0.02 (31) | — | |

Fly sizes are compared with those reported in the literature for the same regions and San Paulo, Brazil.
[a] Morrison et al. 1997.
[b] Orr et al. 1997.
[c] Folgarait et al. 2002b.
[d] Folgarait and Gilbert 1999.

Fly species activity was different through the day. *P. litoralis* and *P. nocens* were mainly collected during the early morning and late afternoon, whereas *P. tricuspis*, *P. obtusus* (both morphs), and *P. curvatus* were mainly collected from late morning to early afternoon. This agrees with Pesquero et al. (1996), who showed the same activity pattern in Brazil for *P. tricuspis* and *P. litoralis. Pseudacteon* species were not active after dark, although *P. litoralis* and *P. nocens* were active at dusk. They disappeared from the attack trays at that moment, in spite of the fact that temperature and humidity were suitable for phorid activity.

**Fly Sizes.** *P. litoralis* was the largest species collected (Table 3), followed by *P. tricuspis*, the large form of *P. obtusus*, *P. nocens*, *P. solenopsidis*, and *P. borgmeieri*. Four other fly species were smaller: *P. curvatus*, *P.* sp. near *disneyi*, the small form of *P. obtusus*, and *P. nudicornis. P. cultellatus* was the smallest species. Surprisingly, the fly species collected in northwestern Argentina and Bolivia, with the exception of *P. litoralis*, were smaller than the flies collected in the other regions, in spite of the size of the host workers observed in field (presumably *S. interrupta* or *S. electra*) seem to be bigger than those examined in the other regions. The sizes of the flies collected in this study are similar to those cited in the literature (Morrison et al. 1997, Orr et al. 1997, Folgarait and Gilbert 1999, Folgarait et al. 2002b) (Table 3).

**Fire Ant Hosts.** *Pseudacteon* species found in most of the sites were not matched to specific hosts because flies collected hovering over a host might not necessarily develop successfully in that species. Matching *Pseudacteon* species to *Solenopsis* hosts will require morphological comparisons among species and the confirmation that the flies can develop successfully in the host ants where they were collected. Nevertheless, several fly species were confirmed as natural parasites of the black and red imported fire ants in Argentina by field observations and tests of oviposition (field choice tests) and development (L.A.C., unpublished data). *Solenopsis richteri* is host to at least 10 *Pseudacteon* species (*P. curvatus*, *P. litoralis*, *P. tricuspis*, both forms of *P. obtusus* (large and small), *P. cultellatus*, *P. nudicornis*, *P. borgmeieri*, *P. comatus*, and *P. nocens*). *S. invicta* is host to at least 10 fly species (*P. curvatus*, *P. litoralis*, *P. tricuspis*, *P. nocens*, both forms of *P. obtusus*, *P. cultellatus*, *P. nudicornis*, *P. borgmeieri*, and *P. solenopsidis*). Other *Solenopsis* species in northwestern Argentina and Bolivia seem to be hosts for nine species (*P. curvatus*, *P. litoralis*, *P. tricuspis*, *P. obtusus* [large form], *P. nudicornis*, *P.* sp. near *disneyi*, *P. nocens*, *P. bulbosus*, and the new species of *Pseudacteon*).

Based on our observations and previous reports (Pesquero et al. 1993, Fowler et al. 1995, Orr et al. 1997, Brown 2000), only five fly species (*P. curvatus*, *P. litoralis*, *P. tricuspis*, *P. nudicornis*, and the large form of *P. obtusus*) are capable of attacking at least four fire ant species. These species seems to be the most generalized within the *saevissima*-group, parasitizing all the fire ant hosts known. However, the ability of most fly species to develop successfully in each of the hosts from which they were collected must be confirmed.

## Acknowledgments

We thank Neil Tsutsui, Edward LeBrun, Guillermo Logarzo, Joe Keiper, and one anonymous reviewer for valuable comments and criticism. We acknowledge Lucas Nuñez, Mariana Emiliozzi, and Joaquín Sacco for field assistance and Brian Brown for confirming the identity of the new *Pseudacteon* species.

## References Cited

**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., 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. 2000.** Five natural history notes on Neotropical phorid flies. Phorid Newsl. 8: 1–2.

**Brown, B. V., and D. H. Feener, Jr. 1998.** Parasitic phorid flies (Diptera: Phoridae) associated with army ants (Hymenoptera: Formicidae: Ecitoninae, Dorylinae) and their conservation biology. Biotropica 30: 482–487.

**Brown, B. V., and L. W. Morrison. 1999.** New *Pseudacteon* (Diptera: Phoridae) from North America that parasitizes the native fire ant, *Solenopsis geminata* (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. 92: 308–311.

**Brown, B. V., P. Folgarait, and L. Gilbert. 2003.** A new species of *Pseudacteon* attacking *Solenopsis* fire ant (Hymenoptera: Formicidae) in Argentina. Sociobiology 41: 685–688.

**Cabrera, A. L., and A. Willink. 1980.** Biogeografía de América Latina. OEA. Serie de Biología 13. Washington, DC.

**Coquillett, D. W. 1907.** A new phorid genus with horny ovipositor. Can. Entomol. 39: 207–208.

**De Fina, L. A. 1992.** Aptitud agroclimática de la República Argentina. INTA, Academia Nacional de Agronomía y Veterinaria, Buenos Aires, Argentina.

**Disney, R.H.L. 1994.** Scuttle flies: the Phoridae. Chapman & Hall, London, United Kingdom.

**Disney, R.H.L., and M. V. Michailovskaya. 2000.** New species of *Pseudacteon* Coquillett (Diptera: Phoridae) from the Far East of Russia. Fragm. Faun. 43: 35–45.

**Feener, D. H. 2000.** Is the assembly of ant communities mediated by parasitoids? Oikos 90: 79–88.

**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. Am. 85: 80–84.

**Feener, D. H., Jr., and B. V. Brown. 1997.** Diptera as parasitoids. Annu. Rev. Entomol. 42: 73–97.

**Folgarait, P. J., and L. E. Gilbert. 1999.** Phorid parasitoids affect foraging activity of *Solenopsis richteri* under different availability of food in Argentina. Ecol. Entomol. 24: 163–173.

**Folgarait, P. J., O. A. Bruzzone, and L. E. Gilbert. 2002a.** Development of *Pseudacteon cultellatus* (Diptera: Phoridae) on *Solenopsis invicta* and *Solenopsis richteri* fire ants (Hymenoptera: Formicidae). Environ. Entomol. 31: 403–410.

**Folgarait, P. J., O. A. Bruzzone, R. Patrock, and L. E. Gilbert. 2002b.** Developmental rates and host specificity for *Pseudacteon* parasitoids (Diptera: Phoridae) of fire ants

(Hymenoptera: Formicidae) in Argentina. J. Econ. Entomol. 95: 1151–1158.

**Folgarait, P. J., O. A. Bruzzone, and L. E. Gilbert. 2003.** Seasonal patterns of activity among species of black fire ant parasitoid flies (Pseudacteon: Phoridae) in Argentina explained by analysis of climatic variables. Biol. Control 28: 368–378.

**Folgarait, P. J., O. Bruzzone, S. D. Porter, M. A. Pesquero, and L. E. Gilbert. 2005.** Biogeography and macroecology of phorid flies that attack fire ants in southeastern Brazil and Argentina. J. Biogeogr. (in press).

**Fowler, H. G. 1997.** Morphological prediction of worker size discrimination and relative abundance of sympatric species of *Pseudacteon* (Diptera, Phoridae) parasitoids of the fire ant, *Solenopsis saevissima* (Hym., Formicidae) in Brazil. J. Appl. Entomol. 121: 37–40.

**Fowler, H. G., M. A. Pesquero, S. Campiolo, and S. D. Porter. 1995.** Seasonal activity of species of *Pseudacteon* (Diptera: Phoridae) parasitoids of fire ants (*Solenopsis saevissima*) Hymenoptera: Formicidae) in Brazil. Cientifica 23: 367–371.

**Gilbert, L. E., and R. J. Patrock. 2002.** Phorid flies for the biological suppression of imported fire ants in Texas: region specific challenges, recent advances and future prospects. Southwest. Entomol. 25: 7–17.

**Greene, C. T. 1938.** A new genus and two new species of the dipterous family Phoridae. Proc. U.S. Natl. Mus. 85: 181–185.

**Graham, L. C., S. D. Porter, R. M. Pereira, H. D. Dorough, and Amber T. Kelley. 2003.** Field releases of the decapitating fly *Pseudacteon curvatus* (Diptera: Formicidae) for control of imported fire ants (Hymenoptera: Formicidae) in Alabama, Florida, and Tennessee. Fla. Entomol. 86: 334–339.

**Korzukhin, M. D., S. D. Porter, L. C. Thompson, and S. Wiley. 2001.** Modeling temperature-dependent range limits for the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae) in the United States. Environ. Entomol. 30: 645–655.

**Morrison, L., and S. D. Porter. 2005.** Post-release host-specificity testing of *Pseudacteon tricuspis,* a phorid parasitoid of *Solenopsis invicta* fire ants. Biocontrol (in press).

**Morrison, L. W., and J. R. King. 2004.** Host location behavior in a parasitoid of imported fire ants. J. Insect Behav. 17: 367–383.

**Morrison, L. W., C. G. Dall'Agilo-Holvorcem, and L. E. Gilbert. 1997.** Oviposition behavior and development of *Pseudacteon* flies (Diptera: Phoridae), parasitoids of *Solenopsis* fire ants (Hymenoptera: Formicidae). Environ. Entomol. 26: 716–724.

**Morrison, L. W., E. A. Kawazoe, R. Guerra, and L. E. Gilbert. 1999.** Phenology and dispersal in *Pseudacteon* flies (Diptera: Phoridae), parasitoids of *Solenopsis* fire ants (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. 92: 198–207.

**Morrison, L. W., E. A. Kawazoe, R. Guerra, and L. E. Gilbert. 2000.** Ecological Interactions of *Pseudacteon* parasitoids and *Solenopsis* ant hosts: environmental correlates of activity and effects on competitive hierarchies. Ecol. Entomol. 25: 433–444.

**Magurran, A. E. 1988.** Ecological diversity and its measurement. Princeton University Press, Princeton, NJ.

**Orr, M. R., S. H. Seike, W. W. Benson, and L. E. Gilbert. 1995.** Flies suppress fire ants. Nature (Lond.) 373: 292–293.

**Orr, M. R., S. H. Seike, and L. E. Gilbert. 1997.** Foraging ecology and patterns of diversification in dipteran parasitoids of fire ants in south Brazil. Ecol. Entomol. 22: 305–314.

**Pesquero, M. A. 2000.** Two new species of *Pseudacteon* (Diptera: Phoridae) parasitoids of fire ants (*Solenopsis* spp.) (Hymenoptera: Formicidae) from Brazil. J. N.Y. Entomol. Soc. 108: 243–247.

**Pesquero, S., S. Campiolo, and H. G. Fowler. 1993.** Phorids (Diptera: Phoridae) associated with mating swarms of *Solenopsis saevissima* (Hymenoptera: Formicidae). Fla. Entomol. 76: 179–181.

**Pesquero, M. A., S. D. Porter, H. G. Fowler, and S. Campiolo. 1995.** Rearing of *Pseudacteon* spp. (Diptera: Phoridae), parasitoids of fire ants (*Solenopsis*) (Hymenoptera: Formicidae). J. Appl. Entomol. 119 677–678.

**Pesquero, M. A., S. Campiolo, H. G. Fowler, and S. D. Porter. 1996.** Diurnal pattern of ovipositional activity in two *Pseudacteon* fly parasitoids (Diptera: Phoridae) of *Solenopsis* fire ants (Hymenoptera: Formicidae). Fla. Entomol. 79:455–457.

**Pitts, J. P. 2002.** A cladistic analysis of the *Solenopsis saevissima* species-group (Hymenoptera: Formicidae). Ph.D. dissertation, University of Georgia, Athens.

**Porter, S. D. 1998a.** Host-specific attraction of *Pseudacteon* flies (Diptera: Phoridae) to fire ant colonies in Brazil. Fla. Entomol. 81: 423–429.

**Porter, S. D. 1998b.** Biology and behavior of *Pseudacteon* decapitating flies (Diptera: Phoridae) that parasitize *Solenopsis* fire ants (Hymenoptera: Formicidae). Fla. Entomol. 81: 292–309.

**Porter, S. D. 2000.** Host specificity and risk assessment of releasing the decapitating fly, *Pseudacteon curvatus* as a classical biocontrol agent for imported fire ants. Biol. Control 19: 35–47.

**Porter, S. D., and L. E. Alonso. 1999.** Host specificity of fire ant decapitating flies (Diptera: Phoridae) in laboratory oviposition tests. J. Econ. Entomol. 92: 110–114.

**Porter, S. D., and J. A. Briano. 2000.** Parasitoid-host matching between the little decapiting fly *Pseudacteon curvatus* from Las Flores, Argentina and the black fire ant *Solenopsis richteri.* Fla. Entomol. 83: 422–427.

**Porter, S. D., and M. A. Pesquero. 2001.** Illustrated key to *Pseudacteon* decapitating flies (Diptera: Phoridae) that attack *Solenopsis saevissima* complex fire ants in South America. Fla. Entomol. 84: 691–699.

**Porter, S. D., and L. E. Gilbert. 2005.** Assessing host specificity and field release potential of fire ant decapitating flies (Phoridae: *Pseudacteon*). *In* R. G. Van Driesche, T. Murray, and R. Reardon [eds.], Assessing host ranges to parasitoids and predators used for classical biological control: a guide to best practice. U.S. Dep. Agric. Forest Service, Morgantown, WV (in press).

**Porter, S. D., L. A. Nogueira de Sá, and L. W. Morrison. 2004.** Establishment and dispersal of the fire ant decapitating fly *Pseudacteon tricuspis* in north Florida. Biol. Control 29: 179–188.

**Porter, S. D., M. A. Pesquero, S. Campiolo, and H. G. Fowler. 1995a.** Growth and development of *Pseudacteon* phorid fly maggots (Diptera: Phoridae) in the heads of *Solenopsis* fire ant workers (Hymenoptera: Formicidae). Environ. Entomol. 24: 475–479.

**Porter, S. D., L. A. Nogueira de Sá, K. Flanders, and L. Thompson. 1999.** Field releases of the decapitation fly, *Pseudacteon tricuspis,* p. 102. Imported Fire Ant Conference, Charleston, SC.

**Porter, S. D., R. K. Vander Meer, M. A. Pesquero, S. Campiolo, and H. G. Fowler. 1995b.** *Solenopsis* (Hymenoptera: Formicidae) fire ant reactions to attacks of *Pseudac-*

*teon* flies (Diptera: Phoridae) in southeastern Brazil. Ann. Entomol. Soc. Am. 88: 570–575.

**Prado, A. P. 1980.** New records and descriptions of phorid flies, mainly of the Neotropical region (Diptera: Phoridae). Stud. Entomol. 19: 561–609.

**Ross, K. G., and J. C. Trager. 1990.** Systematics and population genetics of fire ants (*Solenopsis saevissima* complex) from Argentina. Evolution 44: 2,113–2,134.

**Stattersfield, A. J., M. J. Crosby, A. J. Long, and D. C. Wege. 1998.** Endemic bird areas of the world: priorities for biodiversity conservation. Birdl. Conserv. Ser. 7. Cambridge, United Kingdom.

**Thomas, G. M. 2000.** BIO-DAP. A biodiversity analysis package. http://nhsbig.inhs.uiuc.edu/www/populations.html.

**Trager, J. C. 1991.** A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). J. N.Y. Entomol. Soc. 99: 141–198.

**Vazquez, R. J., S. D. Porter, and J. A. Briano. 2005.** Field release and establishment of the decapitating fly *Pseudacteon curvatus* on red imported fire ants in Florida. Biocontrol (in press).

**Vogt, J. T., and D. A. Streett. 2003.** *Pseudacteon curvatus* (Diptera: Phoridae) laboratory parasitism, release, and establishment in Mississippi. J. Entomol. Sci. 38: 317–320.

**Williams, R. N. 1980.** Insect natural enemies of fire ants in South America with several new records. *In* Proceedings of the Tall Timbers Conference Ecology and Animal Control Habitat Management 7: 123–134.

**Williams, R. N., J. R. Panala, D. Gallos, and W. H. Whitcomb. 1973.** Fire ants attacked by phorid flies. Fla. Entomol. 56: 259–262.

**Wuellner, C. T., and J. B. Saunders. 2003.** Circadian and circannual patterns of activity and territory shifts: comparing a native ant (*Solenopsis geminata*, Hymenoptera: Formicidae) with its exotic, invasive congener (*S. invicta*) and its parasitoids (*Pseudacteon* spp., Diptera: Phoridae) at a central Texas site. Ann. Entomol. Soc. Am. 96: 54–60.

**Wuellner, C. T., S. D. Porter, and L. E. Gilbert. 2002a.** Eclosion, mating, and grooming behavior of the parasitoid fly *Pseudacteon curvatus* (Diptera: Phoridae). Fla. Entomol. 85: 563–566.

**Wuellner, C. T., C. G. Dall'aglio-Holvorcem, W. W. Benson, and L. E. Gilbert. 2002b.** Phorid fly (Diptera: Phoridae) oviposition behavior and fire ant (Hymenoptera: Formicidae) reaction to attack differ according to phorid species. Ann. Entomol. Soc. Am. 95: 257–266.

*Received 20 August 2004; accepted 9 October 2004.*