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*Pseudacteon* Phorid Flies: Host Specificity and Impacts on *Solenopsis* Fire Ants

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**Abstract**

Human commerce has resulted in the spread of the imported fire ants, *Solenopsis* species, worldwide. Six species of parasitic *Pseudacteon* phorid flies that are highly host specific to the *Solenopsis saevissima* complex of *Solenopsis* fire ants have been successfully released in the southern United States. The presence of *Pseudacteon* phorid flies, in addition to having direct mortality effects on their host ants, modifies foraging behavior and disrupts interspecific competition between host species and other ant species in the community. Fire ant workers have evolved effective methods to cope with parasitism pressure, which may relieve population-level impacts of introduced phorid flies. This review focuses on the mechanisms underlying host location, host preference, and host-size selection of *Pseudacteon* phorid flies and highlights their direct and indirect effects on fire ant populations. Knowledge gained from parasitoid–ant interactions will enhance use of natural enemies as biological control agents for invasive social insects.



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## INTRODUCTION

There are about 20 species of fire ants in the genus *Solenopsis* (Formicidae, Myrmicinae) native to the New World (91, 120, 121). These *Solenopsis* species all possess a venomous burning sting, thus engendering the name fire ants. Most fire ant species are Neotropical except for three species, *S. amblychila* Wheeler, *S. aurea* Wheeler, and *S. xyloni* McCook, which are considered to be native to North America. Despite their highly aggressive character, fire ants are not particularly abundant in their native ranges. Since its accidental introduction from South America into the United States in the 1930s, the red imported fire ant, *S. invicta* Buren, has become a serious pest in agricultural, urban, and natural habitats. Because of high foraging efficiency (134), superior competitive ability (133), and escape from coevolved competitors and natural enemies (54, 110), *S. invicta* has displaced many native ants, caused population collapses of numerous arthropods, and posed significant negative impacts on biodiversity and urban environments (2, 121, 129, 141). When *S. invicta* displaced *S. richteri* Forel, the black imported fire ant, in Alabama and Mississippi, interbreeding between *S. richteri* and *S. invicta* occurred wherever the two species came into contact, resulting in the production of a fully fertile hybrid form (115, 123, 139). Generally, imported fire ants (i.e., *S. invicta*, *S. richteri*, and the hybrid) are considered one of the most important drivers of ecosystem dynamics in their introduced range (54). As aggressive predators, imported fire ants prey on both pest and beneficial species, having a mixed effect in agriculture. Further, imported fire ants are a health threat to humans, as they sting people aggressively (130).

In the past 80 years, the red imported fire ant, *S. invicta*, has spread throughout the southern United States via nuptial flights of newly mated queens and by human commerce and was further transported to Australia, New Zealand, East Asia, and the Caribbean (3, 16, 131, 132). Much of the tropical and subtropical regions of the world has been predicted to be at risk of *S. invicta* infestation (79), which was validated by the recent invasions of Taiwan and southern China (19, 144). Once established in a new environment, fire ant colonies spread rapidly in disturbed habitats and are often associated with disruption of arthropod communities (55, 106).

Although a number of highly effective insecticides are available for fire ant control (136), applying insecticides over large areas is impractical, and eradication is impossible once fire ants have become well established. Natural enemies are expected to provide sustainable, long-term control of fire ants (83, 137, 138). Fire ant–decapitating *Pseudacteon* flies are koinobiont, solitary parasitoids of worker ants (36). The adult flies live only a few days in the laboratory, but their life span in nature is unknown (67, 94). However, sugar feeding can considerably enhance the life span of adult phorid flies for approximately 4–15 days in the laboratory (1, 23, 31). Under field conditions, phorid flies may encounter and feed on nectar and/or honeydew sources, as they are capable of utilizing cotton aphid honeydew with an approximately 1-day increase in adult longevity (20, 30, 53). Host-specific *Pseudacteon* (Diptera: Phoridae) flies are promising classical biocontrol agents for fire ant populations (69, 97). In the past two decades, six phorid fly species have been imported from southern South America and released in many parts of the southern United States for fire ant control (17, 47, 92, 102, 103). Although parasitism of *Solenopsis* fire ants by *Pseudacteon* phorid flies has been well documented (67, 94, 101), very little is known about the impact of released phorid flies on fire ant populations in the field (69).

This review focuses on (a) phorid fly host-range specificity and host preferences, (b) the direct and indirect effects of phorid flies on fire ant workers and populations, and (c) biological control perspectives. We review recently published literature on these topics to gain insights into mechanistic explanations for the unique life cycle of phorid flies and their long-term impact on fire ant populations and discuss the possible ecological and evolutionary implications for social insect host–parasitoid interactions.

## PHORID SPECIES DIVERSITY IN SOUTH AMERICA

The genus *Pseudacteon* Coquillett (Diptera: Phoridae) comprises over 72 recognized species of parasitoid flies that decapitate host ants (88, 93). There are at least 22 known species of *Pseudacteon* flies (Table 1) that attack South American fire ants in the *S. saevissima* (Smith) complex, and about 23 species associated with the *S. geminata* complex (87, 88, 93, 104). Twenty *Pseudacteon* species are associated with *S. invicta* or *S. saevissima*, and 16 species are parasitoids of both fire ant species. Only

**Table 1** A list of the *Pseudacteon* species that attack South American fire ants in the *Solenopsis saevissima* species complex

Species	Hosts	Fly distribution	Reference(s)
<i>Pseudacteon affinis</i> Borgmeieri	<i>Solenopsis saevissima</i>	Eastern Brazil	(87)
<i>P. borgmeieri</i> Schmitz	<i>S. interrupta</i> , <i>S. invicta</i> , <i>S. macdonaghi</i> , <i>S. richteri</i> , <i>S. saevissima</i>	Argentina, eastern Brazil	(87)
<i>P. bulbosus</i> Brown, Folgarait et Gilbert	<i>S. electra</i> , <i>S. interrupta</i>	Northwestern Argentina	(8, 13, 87)
<i>P. calderensis</i> Calcaterra	<i>S. interrupta</i>	Northwestern Argentina	(11, 87)
<i>P. comatus</i> Borgmeieri	<i>S. interrupta</i> , <i>S. invicta</i> , <i>S. richteri</i> , <i>S. saevissima</i>	Argentina, southeastern Brazil	(87)
<i>P. conicornis</i> Borgmeieri	<i>S. saevissima</i>	Southeastern Brazil	(87)
<i>P. cultellatus</i> Borgmeieri	<i>S. interrupta</i> , <i>S. invicta</i> , <i>S. macdonaghi</i> , <i>S. richteri</i> , <i>S. saevissima</i>	Argentina, eastern Brazil	(87)
<i>P. curvatus</i> Borgmeieri	<i>S. interrupta</i> , <i>S. invicta</i> , <i>S. macdonaghi</i> , <i>S. quinquecupis</i> , <i>S. richteri</i> , <i>S. saevissima</i>	Argentina, Bolivia, southern Brazil, Paraguay	(87)
<i>P. dentiger</i> Borgmeieri	<i>S. invicta</i> , <i>S. saevissima</i>	Brazil	(87)
<i>P. disneyi</i> Pesquero	<i>S. invicta</i> , <i>S. saevissima</i>	Northwestern Argentina, Bolivia, central-southern Brazil	(87)
<i>P. fowleri</i> Pesquero	<i>S. saevissima</i>	Central-southern Brazil	(87)
<i>P. lenkoi</i> Borgmeieri et Prado	<i>S. invicta</i> , <i>S. saevissima</i>	Central-southern Brazil	(87)
<i>P. litoralis</i> Borgmeieri	<i>S. interrupta</i> , <i>S. invicta</i> , <i>S. quinquecupis</i> , <i>S. richteri</i> , <i>S. saevissima</i>	Argentina, Bolivia, southern Brazil, Paraguay	(87)
<i>P. nocens</i> Borgmeieri	<i>S. interrupta</i> , <i>S. invicta</i> , <i>S. macdonaghi</i> , <i>S. quinquecupis</i> , <i>S. richteri</i> , <i>S. saevissima</i>	Argentina, central-southern Brazil, Paraguay	(87)
<i>P. notocaudatus</i> Plowes, Folgarait et Gilbert	<i>S. invicta</i> , <i>S. interrupta</i>	Northwestern Argentina	(93)
<i>P. nudicornis</i> Borgmeieri	<i>S. interrupta</i> , <i>S. invicta</i> , <i>S. macdonaghi</i> , <i>S. richteri</i> , <i>S. saevissima</i>	Argentina, Bolivia, southern Brazil	(42, 87)
<i>P. obtusatus</i> Plowes, Folgarait et Gilbert	<i>S. interrupta</i> , <i>S. invicta</i> , <i>S. richteri</i> , <i>S. saevissima</i> , <i>S. weyrauchi</i>	Northern Argentina, southeastern Brazil, Paraguay	(13, 14, 87, 93)
<i>P. obtusus</i> Borgmeieri	<i>S. interrupta</i> , <i>S. invicta</i> , <i>S. quinquecupis</i> , <i>S. richteri</i> , <i>S. saevissima</i>	Argentina, Brazil, Paraguay	(87)
<i>P. nr. obtusus</i>	<i>S. gayi</i>	Central Chile	(14)
<i>P. pradei</i> Borgmeieri	<i>S. invicta</i> , <i>S. saevissima</i>	Southern Brazil	(87)
<i>P. solenopsidis</i> (Schmitz)	<i>S. interrupta</i> , <i>S. invicta</i> , <i>S. megergates</i> , <i>S. saevissima</i>	Northeastern Argentina, Brazil	(87)
<i>P. tricuspis</i> Borgmeieri	<i>S. interrupta</i> , <i>S. invicta</i> , <i>S. macdonaghi</i> , <i>S. quinquecupis</i> , <i>S. richteri</i> , <i>S. saevissima</i>	Argentina, Bolivia, Brazil, Paraguay	(42, 87)
<i>P. wasmanni</i> (Schmitz)	<i>S. invicta</i> , <i>S. saevissima</i>	Southern Brazil	(87)

10 species (*P. borgmeieri*, *P. comatus*, *P. cultellatus*, *P. curvatus*, *P. litoralis*, *P. nocens*, *P. nudicornis*, *P. obtusatus*, *P. obtusus*, and *P. tricuspis*) are listed as parasitizing both *S. richteri* and *S. invicta*. In addition, three larger-sized *Solenopsis* species, *S. interrupta* Santschi, *S. macdonaghi* Santschi, and *S. quinquecuspis* Forel, are hosts of some *Pseudacteon* species in South America (Table 1) (13, 42, 45).

## HOST SPECIFICITY FOR SOLENOPSIS COMPLEXES

*Pseudacteon* species associated with either complex of fire ant species can strongly discriminate between ant species in the other complex. Furthermore, fly species have not switched to the other complex even where *S. geminata* and *S. saevissima* complex ants overlap in native or in introduced ranges (71, 100). Early field investigations showed that *Pseudacteon* species attacking *Solenopsis* fire ants in South America did not parasitize ants in other genera and were attracted only to *Solenopsis* fire ants (95, 100). A series of further laboratory tests confirmed that almost all *Pseudacteon* species from southern South America are functionally specific to the *S. saevissima* complex fire ants (29, 48, 72, 96, 97, 128). Furthermore, different *Pseudacteon* species display different levels of host specificity (Table 2). Females of *P. cultellatus*, *P. litoralis*, *P. nudicornis*, *P. obtusatus*, *P. obtusus*, *P. tricuspis*, and *P. wasmanni* attack *S. geminata* Forel very rarely and do not successfully complete development (101). *P. litoralis*, *P. tricuspis*, and *P. wasmanni* were much less likely to attack native *S. geminata* workers than the imported *S. invicta* workers in no-choice laboratory tests (48). *P. nocens* attacks the native fire ants at a relatively higher frequency, at about one-sixth the frequency on *S. invicta* workers (29), but successful development of *P. nocens* parasites in *S. geminata* was very low.

The geographic origin of *Pseudacteon* species is important for understanding host specificity. Some phorid fly species and biotypes exhibit moderate to high attack rates on fire ants in the *S. geminata* complex (48, 96, 100, 128). Biotypes represent different geographic types, which match with different genotypes (genetically differentiated populations or species in some cases). The Las Flores (Argentina) biotype of *P. curvatus* associated with *S. richteri* was able to attack and develop successfully in two native fire ants—*S. geminata* and *S. xyloni*—although parasitism rates were considerably lower than those with *S. invicta* (48, 96). The Campinas (Brazil) biotype of *P. curvatus* readily attacked and parasitized both *S. invicta* and *S. geminata* workers in no-choice laboratory tests (48). The Formosa (Argentina) biotype of *P. curvatus* associated with *S. invicta* displayed a high degree of specificity toward *S. invicta* compared with the two native fire ants. In both no-choice and choice tests, rates of pupal production were much lower in *S. xyloni* compared with *S. invicta*, and zero in *S. geminata*, suggesting that the Formosa biotype is more host-specific than the Las Flores biotype (128). Like *P. curvatus*, *P. borgmeieri* readily attacks *S. geminata* (72) but attacks *S. invicta* more frequently (72). Some highly host-specific species may mistakenly parasitize native species in the *S. geminata* complex. Most attacks on native fire ants, however, fail to result in successful parasitism. Only *P. curvatus*, *P. obtusus*, *P. tricuspis*, and *P. wasmanni* have been reported to be capable of developing in *S. geminata* but apparently do so with low success (95–97, 101).

Social insects often become invasive when biological traits are altered during introduction (54), which consequently may cause the alteration of traits in introduced biological control agents that parasitize them. The introduced biocontrol agent with altered traits may still pose a threat to nontarget species. Postrelease studies mainly on *P. tricuspis* and *P. curvatus* confirmed that the diurnal activity, phenological abundance, sex ratios, and host specificity of introduced populations of *Pseudacteon* flies were consistent with findings in their native ranges (52, 76, 127). Introduced *P. tricuspis* were frequently observed at *S. invicta* mounds but never at trays containing *S. geminata* placed in the field, suggesting that these flies retain strong host preference and do not pose a threat

**Table 2** Host specificity of *Pseudacteon* flies in laboratory and field conditions

Species	Origin (host species)	Host specificity	Reference(s)
<i>Pseudacteon affinis</i>	Rio Claro, São Paulo, Brazil ( <i>Solenopsis invicta</i> )	High (field: <i>S. invicta</i> , <i>S. geminata</i> )	(100)
<i>P. borgmeieri</i>	Jundiá, São Paulo, Brazil; Reserva Ecológica Costanera Sur, Buenos Aires, Argentina	Low (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(72)
<i>P. cultellatus</i>	Brea Pozo, Santiago del Estero, Argentina; Corrientes, Argentina ( <i>S. invicta</i> )	High (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(29)
<i>P. curvatus</i>	Campinas, São Paulo, Brazil ( <i>S. invicta</i> )	Low-moderate (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(48)
	Las Flores, Buenos Aires, Argentina ( <i>S. ricbteri</i> )	Moderate-high (choice: <i>S. invicta</i> versus <i>S. geminata</i> ; choice: <i>S. invicta</i> versus <i>S. xyloni</i> ) High (no-choice: <i>S. invicta</i> versus <i>S. geminata</i> ) Low (no-choice: <i>S. invicta</i> versus <i>S. xyloni</i> )	(96)
	Formosa, Argentina ( <i>S. invicta</i> )	Moderate (choice: <i>S. invicta</i> versus <i>S. geminata</i> ) High (choice: <i>S. invicta</i> versus <i>S. xyloni</i> ) Low (no-choice: <i>S. invicta</i> versus <i>S. geminata</i> ; no-choice: <i>S. invicta</i> versus <i>S. xyloni</i> )	(128)
<i>P. litoralis</i>	Jaguariuna and Rio Claro, São Paulo, Brazil ( <i>S. invicta</i> , <i>S. saevissima</i> )	High (field: <i>S. invicta</i> + <i>S. saevissima</i> , <i>S. geminata</i> )	(95, 100)
	Campinas, São Paulo, Brazil ( <i>S. invicta</i> )	High (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(48)
	Jaguariuna and Rio Claro, São Paulo, Brazil ( <i>S. invicta</i> , <i>S. saevissima</i> )	High (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(97)
<i>P. nocens</i>	Brea Pozo, Santiago del Estero, Argentina ( <i>S. invicta</i> )	Moderate (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(29)
<i>P. nudicornis</i>	Reserva Ecológica Costanera Sur, Buenos Aires, Argentina	High (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(29)
<i>P. obtusitus</i>	Campinas, São Paulo, Brazil ( <i>S. invicta</i> )	High (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(72)
	Herradura, Argentina	High (no-choice: <i>S. invicta</i> versus <i>S. geminata</i> ) Moderate-high (no-choice: <i>S. invicta</i> versus <i>S. xyloni</i> )	(101)
<i>P. obtusus</i>	Mercedes, Corrientes, Argentina ( <i>S. invicta</i> )	High (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(29)
<i>P. pradei</i>	Jaguariuna and Rio Claro, São Paulo, Brazil ( <i>S. invicta</i> , <i>S. saevissima</i> )	Possibly high (field: <i>S. invicta</i> + <i>S. saevissima</i> , <i>S. geminata</i> )	(95, 100)
<i>P. solenopsidis</i>	Argentina and Brazil ( <i>S. invicta</i> , <i>S. saevissima</i> )	High (descriptive)	(142)
<i>P. tricuspis</i>	Jaguariuna and Rio Claro, São Paulo, Brazil ( <i>S. invicta</i> , <i>S. saevissima</i> )	High (field: <i>S. invicta</i> + <i>S. saevissima</i> , <i>S. geminata</i> )	(95, 100)
	Campinas, São Paulo, Brazil ( <i>S. invicta</i> )	High (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(48)
	Jaguariuna and Rio Claro, São Paulo, Brazil ( <i>S. invicta</i> , <i>S. saevissima</i> )	High (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(97)
<i>P. wasmanni</i>	Jaguariuna and Rio Claro, São Paulo, Brazil ( <i>S. invicta</i> , <i>S. saevissima</i> )	Moderate-high (field: <i>S. invicta</i> + <i>S. saevissima</i> , <i>S. geminata</i> )	(95, 100)
	Jundiá, São Paulo, Brazil ( <i>S. invicta</i> , <i>S. saevissima</i> )	High (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(48)
	Jaguariuna and Rio Claro, São Paulo, Brazil ( <i>S. invicta</i> , <i>S. saevissima</i> )	High (no-choice: <i>S. invicta</i> , <i>S. geminata</i> )	(97)

to native ants (78). Similarly, native phorids associated with *S. geminata* in northern Florida and Texas were never observed to attack the introduced *S. invicta* populations (9, 73, 78). The Las Flores biotype of *P. curvatus* that parasitizes *S. richteri* and hybrid fire ants has apparently been able to adapt to *S. invicta* populations in southern Georgia and northeast Louisiana, suggesting that host preference is primarily a species-level trait and life history evolution of these parasitoids may have occurred in the introduced range (17). A switch of host use by *Pseudacteon* species associated with a specific host group has not been observed despite host and parasitoid overlap in some areas of their distributions. The relative benefit of releasing the *Pseudacteon* species with high preference for the invasive fire ant species should outweigh the risk posed by these flies on the native fire ants (83).

## HOST PREFERENCE FOR SOLENOPSIS SPECIES

*Pseudacteon* phorid flies are highly specialized in their oviposition preferences, generally utilizing only a few closely related ant species as hosts. Most American fly species always prefer their original host complex, indicating a genetically controlled character. The species parasitizing the North American *S. geminata* complex, such as *P. bifidus* Brown et Morrison (9) and *P. browni* Disney, have not been found to shift to the imported fire ants, *S. invicta* or *S. richteri*, despite longtime coexistence (48).

Because they are broadly distributed across the ranges of several fire ant species in South America (13, 39, 87), most common species of decapitating flies are expected to use several different fire ant species as hosts. Consequently, biotypes of the same fly species attack different fire ant species, such as *P. curvatus* and *P. tricuspis*. Furthermore, flies from a specific location are usually capable of parasitizing several fire ant species in the *S. saevissima* complex (40, 42, 98). There is limited information about the host preferences of the different species and biotypes of phorid flies. Field assays for host selection demonstrated the preference of the *Pseudacteon* fly communities for the local fire ant species (89). Laboratory no-choice and pair-wise choice bioassays demonstrated that the Las Flores (Argentina) biotype of *P. curvatus* obtained from *S. richteri* populations preferred *S. richteri* and hybrid fire ants over *S. invicta*, and the strong preference for *S. richteri* was retained even after it was successfully reared for many generations on *S. invicta* (13, 42, 98). A similar pattern was found in laboratory tests demonstrating that *P. tricuspis* biotypes from *S. richteri* workers or *S. invicta* workers prefer their original host species (101). More recently, a multiple-choice bioassay with the three imported fire ant species/forms demonstrated that the Jaguariuna (Brazil) biotype of *P. tricuspis* originating from *S. invicta* populations showed greater preference for *S. invicta* and hybrid fire ants over *S. richteri* (50). The Formosa (Argentina) biotype of *P. curvatus* showed similar preference for *S. invicta* and hybrid fire ants over *S. richteri*, although the trend was not as strongly conclusive as for *P. tricuspis* (50). Hybrid workers are apparently as attractive as either *S. richteri* or *S. invicta* workers. Thus, the evident preference of phorid flies seems to be genetically determined.

## HOST-SIZE SELECTION

*Pseudacteon* species vary considerably in size and can be categorized into three size classes: large (*P. litoralis*), medium (*P. borgmeieri*, *P. nocens*, *P. obtusus*, *P. solenopsisidis*, *P. tricuspis*, and *P. wasmanni*), and small species (*P. cultellatus*, *P. curvatus*, *P. notocaudatus*, *P. nudicornis*, and *P. obtusitus*) (Table 3) (13, 86, 94, 142). They are highly selective in the size of fire ant workers to be parasitized. Each species of fly shows oviposition preference for a certain size range of host workers, and fly size positively correlates with head size of host ant attacked (18, 33, 40, 43, 45, 70, 71, 80). The small, medium, and large *Pseudacteon* species prefer workers that are smaller, equal to, and larger than

**Table 3** Thorax widths of *Pseudacteon* species and head widths of parasitized *Solenopsis* workers (mm ± standard deviation)

Species	Sex	Thorax width of fly	Head width of parasitized ant	Reference(s)
<b>Large</b>				
<i>Pseudacteon litoralis</i>	Female	0.57 ± 0.03	— ( <i>Solenopsis invicta</i> )	(86)
	Female	0.55 ± 0.05	1.02 ± 0.17 (polygyne <i>S. invicta</i> ) 1.11 ± 0.15 (monogyne <i>S. invicta</i> )	(70, 71)
	Female	0.55 ± 0.06	— ( <i>S. richteri</i> )	(13)
		0.57 ± 0.06	— ( <i>S. invicta</i> )	
		0.58 ± 0.04	— ( <i>S. interrupta</i> )	
Both	—	1.19 ± 0.08 ( <i>S. invicta</i> + <i>S. saevissima</i> )	(105)	
Both	—	1.13 ± 0.13 ( <i>S. invicta</i> + <i>S. saevissima</i> )	(80)	
<b>Medium</b>				
<i>P. affinis</i>	Female	—	0.97 ± 0.18 ( <i>S. saevissima</i> )	(90)
<i>P. borgmeieri</i>	Female	0.45 ± 0.04	— ( <i>S. saevissima</i> )	(86)
	Female	0.48 ± 0.06	— ( <i>S. richteri</i> )	(13)
<i>P. browni</i>	Female	0.45 ± 0.06	0.90 ± 0.20 (polygyne <i>S. geminata</i> ) 0.92 ± 0.16 (monogyne <i>S. geminata</i> )	(70, 71)
<i>P. calderensis</i>	Female	0.41- 0.51	— ( <i>S. interrupta</i> )	(11)
<i>P. disneyi</i>	Female	—	0.81 ± 0.10 ( <i>S. saevissima</i> )	(90)
<i>P. nocens</i>	Female	0.50 ± 0.06	— ( <i>S. invicta</i> )	(13)
	Female	0.42 ± 0.05	0.83 ± 0.11 ( <i>S. richteri</i> + <i>S. invicta</i> )	(45)
	Male	0.32 ± 0.04	0.63 ± 0.09 ( <i>S. richteri</i> + <i>S. invicta</i> )	(45)
<i>P. obtusus</i>	Female	0.52 ± 0.04	— ( <i>S. invicta</i> )	(13)
		0.49 ± 0.05	— ( <i>S. interrupta</i> )	
<i>P. solenopsidis</i>	Female	0.47 ± 0.04	— ( <i>S. invicta</i> )	(86)
	Female	0.50 ± 0.04	— ( <i>S. invicta</i> )	(13)
<i>P. tricuspis</i>	Female	0.49 ± 0.03	— ( <i>S. invicta</i> )	(86)
	Female	0.50 ± 0.04	0.93 ± 0.19 (polygyne <i>S. invicta</i> ) 0.92 ± 0.16 (monogyne <i>S. invicta</i> )	(70, 71)
		0.60 ± 0.06	— ( <i>S. richteri</i> )	
		0.53 ± 0.06 0.43 ± 0.07	— ( <i>S. invicta</i> ) — ( <i>S. interrupta</i> )	
	Both	—	1.16 ± 0.11 ( <i>S. invicta</i> + hybrid)	(109)
Both	—	0.95 ± 0.13 ( <i>S. invicta</i> + <i>S. saevissima</i> )	(80)	
<i>P. wasmanni</i>	Female	0.47 ± 0.04	( <i>S. saevissima</i> )	(86)
	Female	0.48 ± 0.03	0.77 ± 0.15 (polygyne <i>S. invicta</i> ) 0.90 ± 0.16 (monogyne <i>S. invicta</i> )	(70, 71)
<b>Small</b>				
<i>P. bifidus</i>	Female	0.36 ± 0.03	0.75 ± 0.15 (polygyne <i>S. geminata</i> ) 0.80 ± 0.08 (monogyne <i>S. geminata</i> )	(70, 71)
<i>P. cultellatus</i>	Female	0.36 ± 0.05	0.75 ( <i>S. richteri</i> ) 0.66 ( <i>S. invicta</i> )	(40)
	Female	0.31 ± 0.05	—	(13)
		0.33 ± 0.02	—	
	Female	—	0.84 ± 0.12 ( <i>S. saevissima</i> )	(90)
Male	0.33 ± 0.02	0.75 ( <i>S. richteri</i> ) 0.66 ( <i>S. invicta</i> )	(40)	

(Continued)

Table 3 (Continued)

Species	Sex	Thorax width of fly	Head width of parasitized ant	Reference(s)
<b>Small</b>				
<i>P. curvatus</i>	Female	0.33 ± 0.04	0.66 ± 0.11 (polygyne <i>S. invicta</i> ) 0.71 ± 0.11 (monogyne <i>S. invicta</i> )	(70, 71)
	Female	0.39 ± 0.04 0.36 ± 0.05 0.35 ± 0.03	— ( <i>S. richteri</i> ) — ( <i>S. invicta</i> ) — ( <i>S. interrupta</i> )	(13)
<i>P. notocaudatus</i>	Female	0.36 ± 0.04	— ( <i>S. interrupta</i> )	(13)
<i>P. nudicornis</i>	Female	0.34 ± 0.02	— ( <i>S. saevissima</i> )	(86)
	Female	0.35 ± 0.07 0.34 ± 0.03	— ( <i>S. invicta</i> ) — ( <i>S. interrupta</i> )	(13)
<i>P. obtusitus</i>	Female	0.35 ± 0.04	— ( <i>S. invicta</i> )	(86)
	Female	0.36 ± 0.04	— ( <i>S. invicta</i> )	(13)

Dash indicates that measurements are not available from references.

the colony average, respectively. This preferred size range is usually consistent across different ant species and within an ant species (71, 80). Specific host-size preference may be an important factor mediating coexistence of multiple *Pseudacteon* species that utilize the same host species (70, 86).

## HOST LOCATION AND PREFERENCE MECHANISMS

Like hymenopteran parasitic wasps, dipteran parasitic flies use a range of olfactory, visual, and acoustic cues to locate suitable hosts (36, 57, 65). Semiochemicals can be used as both long- and short-range cues in host location, and visual signals are generally used as short-range cues (61). These host- and habitat-derived cues can be detected and processed synergistically by ant parasitoids of the family Phoridae for host location (65, 75). A study on host location behavior of a parasitic fly, *Apocephalus paraponerae* Borgmeier, provided the first evidence that phorid parasitoids use olfactory cues to locate hosts (7). The alarm pheromones 4-methyl-3-heptanone and 4-methyl-3-heptanol that are released by disturbed or injured workers of the giant tropical ant *Paraponera clavata* Fabricius serve as chemical cues for host location, and the appropriate size of the injured worker serves as a visual cue for host acceptance (37, 65). The presence of species-specific cuticular chemicals appears to be a requirement to trigger oviposition behavior, and flies tend to parasitize ants with intact surface chemicals (62, 65). A combination of visual and chemical stimuli increases host recognition in phorid flies (65).

The olfactory cues may originate from ant workers during interspecific interactions. In the presence of interspecific competition, apparently more phorid flies are attracted to foraging ant workers (58, 84). Both recruitment and alarm pheromones can be used by phorid flies in host location. Because they provide reliable and stable cues for intraspecific communication, it is not surprising that these host pheromones are exploited by parasitoids as useful host-recognition cues.

Field (18, 75, 86, 95, 100) and laboratory (48, 50) studies demonstrated attraction of *Pseudacteon* flies to *Solenopsis* fire ant workers. Some *Pseudacteon* species prefer to attack *Solenopsis* workers at disturbed mounds, whereas others attack foraging workers more frequently (44, 85, 86, 135). Phorid flies are also attracted to colonies exhibiting aggressive interspecific interactions and to mating flights (66, 75). In addition to live workers, phorid flies are attracted to freshly killed or crushed workers, and even dead workers from midden piles (111). Attraction of phorid flies to fire ant workers was confirmed to be mediated by odors from workers (21, 22, 119, 124). Chemicals



released by disturbed fire ant workers, possibly fire ant alarm pheromone or other defensive compounds, were initially proposed as host-location cues for phorid flies (75, 124). The identification of 2-ethyl-3,6-dimethyl pyrazine as a component of the alarm pheromone of *S. invicta* accelerated investigation on the role of fire ant alarm pheromone in mediating interactions between fire ants and phorid flies (125). Fire ant alarm pheromone and structurally related pyrazines 2,3-dimethyl pyrazine, 2,3-diethyl-5-methyl pyrazine, and 2-ethyl-3(5, or 6)-methyl pyrazine are all behaviorally attractive to phorid flies, confirming the role of fire ant alarm pheromone in mediating attraction of phorid flies to fire ant workers (82, 117).

A single fire ant worker produces ~300 pg of alarm pheromone stored in mandibular glands (125). Although it is enough to elicit behavioral activity in fire ant workers, this amount of pheromone is far below the detection threshold by phorid flies (82). Phorid flies typically respond from long range to fire ants at the population level. Thus, it is conceivable that phorid flies may have evolved to respond to higher doses of the alarm pheromone compared to fire ant workers.

Disturbance causes fire ants to release many defensive compounds, including alarm pheromone and venom alkaloids (124, 126). Combining fire ant alarm pheromone and venom alkaloids additively attracts female and some male phorid flies, regardless of fly species (116). Fire ant alarm pheromone, which is highly volatile with low molecular weight, is likely the long-range attractant for parasitic phorid flies. It is plausible that phorid flies are attracted over long distances by fire ant alarm pheromone and then use less volatile venom alkaloids as short-range host-location cues and visual cues to recognize their hosts (24, 117). In fact, male phorid flies of some species may have evolved to use fire ant defensive secretions as mate-finding cues. In addition to alarm pheromone and venom alkaloids, other unidentified defensive compounds may be part of the suite of semiochemicals used by phorid flies to find their fire ant hosts.

*Pseudacteon* flies may have evolved similar host-finding mechanisms involving the use of alarm and defensive secretions of their ant hosts (116, 140). For instance, formic acid, which is the defensive secretion of host formicine ants in the genus *Lasius*, is used as a host-finding cue by *P. formicarum* Verrall (60). *P. brevicauda* Schmitz responds to 3-octanone and 3-nonanone, the alarm pheromones of its ant host, *Myrmica rubra* Linnaeus (140). However, formic acid and 3-octanone are shared by many ant species and may not be the only cues involved in host detection. Additional visual and chemical cues may play important roles.

Some *Pseudacteon* flies, such as *P. solenopsidis* and *P. obtusitus*, are rarely attracted to disturbed fire ant colonies and parasitize workers along foraging trails (86, 142). They are probably attracted to host worker recruitment pheromones or chemical signals associated with foraging activities. Other *Pseudacteon* flies, such as *P. nocens* and *P. obtusus*, are attracted to ant trails and to disturbed mounds (41, 45, 46, 135). Species richness and abundance of phorid flies are higher at disturbed mounds than on nearby foraging trails (46), suggesting that alarm pheromone is more effective than trail pheromone in attracting phorid flies. Different *Pseudacteon* species may have adapted to detect a variety of chemical signals utilized by fire ant hosts under different ecological circumstances for host location.

*Pseudacteon* flies respond to the *cis/trans* alkaloids and to the alkaloid mixture, but not to cuticular hydrocarbons (24). The *cis* alkaloid fraction is relatively more potent than the *trans* alkaloid fraction. Nine venom alkaloid components, including five *cis* alkaloids (*cis*-C11, *cis*-C13:1, *cis*-C13, *cis*-C15:1, and *cis*-C15), two *trans* alkaloids (*trans*-C11 and *trans*-C13:1), and two 2,6-dialkylpiperidine ( $\Delta^{1,6}$ -C15:1 and  $\Delta^{1,6}$ -C15), elicited significant antennal activity in *P. tricuspis* in coupled gas chromatography-electroantennogram detection analysis (24). Venoms of the native fire ants *S. geminata* and *S. xyloni* also contain large amounts of *cis*- and *trans*-C11 (5, 118) and may also attract phorid flies. Compositions of piperidine alkaloids in the venoms of different *Solenopsis* species are qualitatively and quantitatively different (4, 143). Differences in venom alkaloid

composition may provide reliable host-specific signals for phorid flies to discriminate fire ant species. The amount of the *trans* alkaloids in *S. invicta* workers is two orders of magnitude greater than that of the *cis* alkaloids (143). Therefore, the ratio of *cis* to *trans* alkaloids may be important for the attraction of phorid flies. Because phorid flies from South America have highly specific host preference for *S. saevissima* complex ants, the venom alkaloids of North American *S. geminata* and *S. xyloni* may not elicit a behavioral response in South America *Pseudacteon* flies. Similarly, the venom alkaloids of imported fire ants may not elicit a behavioral response in *Pseudacteon* flies from North America, as they show a strong preference for fire ants in the *S. geminata* complex. The *S. richteri* × *S. invicta* hybrids are as attractive as the two parental species to phorid flies (50, 98). The cues mediating the attraction are likely qualitative traits that are well conserved in the hybrid under genetic control.

Short-range visual cues may contribute to discrimination among ant genera because the flies have a large number of ommatidia. Nevertheless, visual cues probably do not contribute to discrimination among different fire ant species because workers are very similar even for a trained taxonomist. Visual cues are likely much more important for host preferences in relation to fire ant size rather than olfactory cues (28, 56).

### FIRE ANT REACTIONS TO PHORID FLY ATTACKS

When a phorid fly hovers (several millimeters above) in an attempt to oviposit (**Figure 1**), a worker ant can sense its presence possibly by a combination of olfactory, visual, and auditory cues, such as wing vibrations at close range. The ants assume a curled defensive posture to effectively avoid potential parasitism (33, 35, 108). Some ants respond aggressively and attempt to catch the attacking fly or dispense venom by vibrating their gasters (67, 108, 135). When attacked by phorid flies, fire ants exhibit a suite of specific defensive behaviors and postures (27, 108, 142). Generalized behavior and body postures in fire ants against phorid flies include (a) a typical immobilized so-called freezing behavior, (b) a stereotypical U, n, C, or toppled posture, and (c) rapidly retreating into exit holes or hiding inside any available crevices. The specific behavioral response depends on the species of *Pseudacteon*. These behaviors likely reduce oviposition attempts and are especially beneficial to fire ant fitness, considering that only a small proportion of oviposition attempts results in successful egg deposition by phorid flies. Therefore, phorid-specific defensive behaviors clearly evolved under substantial parasitism pressures.



**Figure 1**

Phorid fly (*Pseudacteon littoralis* in panels a and b, *Pseudacteon nocens* in panel c) attempting to attack a fire ant worker. Photos by S.D. Porter, USDA-ARS; panel a adapted with permission from Reference 83, and panels b and c used with permission from S.D. Porter.

After being attacked, workers frequently appear stunned for a few seconds and often stilt up on their legs for up to a minute before running away or sometimes engage in gaster flagging behavior (67, 86, 108). The attacked worker attracts nestmates for tending for several minutes possibly via defensive chemicals (108, 142). Ant response to an attack may vary with phorid species. Phorid flies that initiate less reaction from hosts are able to attack more hosts (142).

Parasitized workers remain inside their nests and probably tend brood (27). Development of phorid immatures induces behavioral changes in parasitized ants consistent with host manipulation to benefit survival of the parasitoid. They leave the nest just 8–10 h prior to their decapitation so the fly maggots can pupate outside of the ant nest (51). Alternatively, decapitated heads with fly pupae have been shown to be deposited by nestmates in middens piles in laboratory observations (105, 109). However, the fate of parasitized workers under natural conditions before decapitation is still largely unknown (76).

## DIRECT IMPACTS

Parasitism rates in nature vary among fire ant colonies, among locations, and over seasons. High parasitism rates match the highest fly abundance, generally in spring or fall (12). Natural parasitism rates of *S. geminata* by North American phorid flies have been reported to be less than 3% (70). Overall parasitism rates of *S. invicta* colonies naturally attacked by phorid flies in native Argentina were 0.24%, and the maximum seasonal parasitism rate per colony could be as high as 2.81% (12). The maximum parasitism rates in introduced populations of *P. tricuspis* in Florida have ranged below 1% (76, 122). These observed rates are an order of magnitude below the parasitism rates for successful biocontrol programs (>30%) (69). It has been noted that parasitism rates of *S. invicta* workers in laboratory conditions can be as high as 20–30% in ants subjected to *P. tricuspis* attack (76). Even though the reported field parasitism rates are presumably underestimated, actual parasitism rates are still considerably low (76). Therefore, the direct effect of ant mortality due to phorid flies in the field is very low. Furthermore, host workers attacked by phorid flies are generally engaged in high-risk activities like foraging, interspecific interactions, and colony defense. Moreover, only half of *S. invicta* colonies were found to be infected with *P. tricuspis* larvae, leading to a very low direct impact (76). It can be argued that direct mortality is not the primary effect of phorid flies on fire ant populations.

## INDIRECT IMPACTS

Because the natural parasitism rates are very low, the primary effect of *Pseudacteon* flies on fire ants is probably indirect. This mainly involves disrupting worker ant foraging behavior at the colony level (63, 67, 94). Foraging capacity of fire ants for food decreases dramatically in the presence of phorid flies (34, 44, 63, 66, 81, 85, 86, 108). Therefore, a single fly can affect the foraging of hundreds of worker ants. A few flies are sufficient to stop foraging of an entire colony within a couple of minutes (108). The attack by phorid flies leads to cessation of most recruitment activity, abandoning of food resources, decreases in the number of foraging workers and the quantity of food intake, and a shift in worker size on foraging trails (25, 44, 63, 112, 114). Attacks by *P. curvatus* in its native South American range diminish large foraging workers of *S. invicta*, resulting in a greater proportion of small workers (26). This negatively impacts colony success because worker size polymorphism is important to task allocation (107). Releases of multiple fly species utilizing ant hosts with a wide range of sizes were expected to achieve more effective manipulation of *S. invicta* populations in North America (71).

Ant foraging activity usually remains suppressed (or strongly reduced) as long as the flies are active, which can be up to several hours (94). It takes about 30–90 min or even longer for ant

recruitment activity to rebound to prephorid presence numbers (44, 142). To minimize negative effects caused by attacking phorid flies, fire ant workers have developed alternative foraging strategies to compensate for decreased food retrieval (68, 69). Workers usually cover a rich food source with dirt and debris, renew their underground tunnel system, and feed from underneath the food source using tunnels, or they switch to nocturnal aboveground foraging to relieve parasitism pressure because phorid flies are exclusively diurnal (12, 66, 74, 114). These compensatory behaviors may explain why the reduced foraging rates did not translate into reduced colony growth (68).

Phorid flies potentially mediate competitive interactions between their host and competing ant species (32). Many early studies have verified that phorid flies reduce the competitive dominance of host ants; affect the outcome of their host's interspecific interactions with more dominant, codominant, or subordinate species; and perhaps shape the diversity and composition of ant communities (34, 69). The fact that the native fire ant *S. xyloni* has a competitive advantage and an increased ability to coexist with *S. invicta* when aided by phorid flies of *S. invicta* supports the adverse impact (113). The relative aggressive tendencies of an ant species, resource availability, and environmental conditions are critical factors in determining the competitive balance of fire ants against other competitive ants in the presence of phorid flies. For instance, field *S. invicta* colonies were observed to lose food resources to subordinate competing ants in the presence of phorid flies in South America (85). However, the relative importance of indirect effects of phorid flies on interspecific exploitative competition varies geographically (38). The presence of *S. geminata*-specific phorid flies had no effect on pure interference competition between *S. geminata* and other codominant species in North America (66, 68, 74). The low presence of phorid flies apparently affected the foraging rate of *S. invicta* but not the outcome of interspecific interactions between *S. invicta* and other codominant species in South America (10, 38). Although the fire ant colony under phorid attack is always at a competitive disadvantage, the foraging advantage of competing species did not translate into enhanced colony growth (64). The ability of phorid flies to shift the competitive advantage away from *S. invicta* to native ants has been questioned for evidence that fire ant workers under phorid attack often do not lose control of food resources to competing ants in many communities (66, 68, 69, 74). To date, a generalized inference regarding the overall effect of phorid flies on fire ants cannot be achieved from studies focused on short-term and behavioral effects of the flies on interspecific competitions. Large-scale and long-term field tests are required to evaluate the actual effect.

Interestingly, male phorid flies of two species (*P. obtusus* and *P. tricuspis*) arrive at disturbed mounds significantly sooner than females and display hovering behavior while looking for females (46, 94). This hovering behavior can also elicit defensive postures in workers and is capable of inhibiting fire ant foraging (34, 50, 68, 108). These males may pose a significant impact on field fire ant populations and contribute more than previously thought to the overall effect of phorid flies on fire ants in the field.

Additionally, *Pseudacteon* flies are known carriers of the fire ant microsporidian pathogen *Kneallhazia solenopsae*, but transmission among colonies has not been confirmed (83). Infection by *K. solenopsae* is apparently not detrimental to *Pseudacteon* development but capable of decreasing survival and fecundity in *S. invicta* and *S. richteri* queens (83). Indirect effect of phorid flies as pathogen vectors may provide important population-level impacts.

## POPULATION-LEVEL IMPACT

Phorid flies directly impact fire ant populations by parasitizing ant workers and indirectly do so by limiting fire ant foraging. Because phorid flies are unlikely to reduce fire ant populations by direct mortality, the indirect impacts on foraging and interference competition were expected

to be enough for substantial suppression of introduced *S. invicta* populations (77). An almost twofold decrease in colony protein consumption and a significant reduction in numbers of large-sized workers increase the expectation of population-level impacts by *Pseudacteon* parasitoids (63). These reductions appear to put the native ants at a competitive advantage for the location and dominance of available resources if the introduced phorid flies stress fire ant colonies severely. Theoretically, abundance of phorid flies should allow native ant species to better compete with *S. invicta* to turn over community dominance in the long term. So far, the real promise of population-level impact on *S. invicta* populations has not been realized perhaps because competing ants in North America are weaker competitors than their South American counterparts (85).

Abundance of *P. tricuspidis* released in north central Florida positively correlated to *S. invicta* density. Phorid populations were likely still increasing in the early stages of colonization (77). Because of wide background variability of *S. invicta* populations in the field (10–30%), however, no measurable impact of *P. tricuspidis* released in north central Florida on *S. invicta* populations was observed over the temporal and spatial scales measured (77). Wide seasonal fluctuations of *S. invicta* populations might have masked the impacts of *P. tricuspidis*. As many biotic and abiotic factors can impact fire ant abundances, it is very difficult or impossible to conduct experimental manipulations at the community level. Both laboratory and field experiments provide little support for the expectations that *Pseudacteon* phorid flies could mediate competitive interactions at the community level (69, 81).

In South America, *S. invicta* faces parasitism pressure from a variety of phorid species and competition pressure from diverse sibling species and other ant species. A single phorid species is unlikely to decrease *S. invicta* densities by reducing their competitive ability. A higher level of phorid parasitism pressure can be achieved in nature over a longer period by releasing a mix of complementary phorid species with differing niches or biotypes adapted to attack *S. invicta*. In Argentina, significantly more *P. cultellatus*, *P. litoralis*, *P. nocens*, and *P. tricuspidis* attack fire ant workers at disturbed mounds than along foraging trails, whereas the same number or more numbers of *P. curvatus*, *P. nudicornis*, and *P. obtusus* attack along foraging trails and at disturbed mounds (46, 86). Attacking ants on foraging trails likely has a greater effect on host behavioral modification than attacking them on nest mounds. Positive associations among different *Pseudacteon* species are common in their native ranges (46). In contrast, negative associations between *P. curvatus* and *P. tricuspidis* have been observed in their introduced range. Colonization by *P. curvatus* leads to a rapid and strong decline in the densities of *P. tricuspidis* despite their nonoverlapping use of workers (59). *P. curvatus* parasitizes more abundant minor fire ant workers than major workers utilized by *P. tricuspidis*, suggesting a greater availability of hosts for *P. curvatus*. Competitive displacement of *P. tricuspidis* by *P. curvatus* has been attributed to both direct and indirect competition (59). A sex-ratio shift in *P. tricuspidis* from strongly male biased to weakly female biased suggests a direct exploitive competition for smaller-sized workers. A more important indirect competitive effect appears to suppress reproductive opportunities of *P. tricuspidis* perhaps because *P. curvatus* occurs in much higher densities, driving a population-level competitive displacement.

Introduced phorid populations can take up to four years to reach maximum levels, and native ants require one or two more years for their populations to build up in competition with the imported fire ants (99). Long-term monitoring is needed to ascertain the full ecological consequences of phorid introductions. To date, six introduced phorid species have been expanding in the imported fire ant infested areas. Other natural enemies, such as pathogens, microsporidia, nematodes, and viruses from South America, will have greater impact on the imported fire ant populations throughout the southern United States than parasitic phorid flies (6, 83, 137). A

combination of these different types of natural enemies as self-sustaining biocontrol agents is expected to be capable of tilting the ecological balance in favor of the native ants (94).

## CONCLUSIONS AND PERSPECTIVES

In South America, *S. geminata* is broadly sympatric with *S. saevissima* complex fire ants (120). *Pseudacteon* flies have had millions of years to coevolve with their particular host species complexes. A switch of host complex has not occurred even under the strong selective advantages provided by competing *S. invicta* in North America. There are 22 known *Pseudacteon* species that are highly host specific to the *S. saevissima* complex of *Solenopsis*. *Pseudacteon* flies are commonly found at disturbed mounds and on ant foraging trails. They affect fire ants primarily by disrupting fire ant foraging and reducing their competitive advantages. Worker pheromones and species-specific defensive chemicals are utilized by the flies for host location and discrimination. Phorid flies may rely on visual cues for size preference. Understanding the host location mechanism can provide insight into dipteran parasitoid–host interactions and the potential efficacy of phorid flies as biocontrol agents.

*Pseudacteon* communities often consist of 5–10 species that partition their use of the common host resource along a number of environmental axes (41, 67, 86). The high species richness of phorid parasitoids and fire ant reactions to their presence suggest a long evolutionary history.

Phorid flies are likely adapted to their geographically unique ant hosts and to different climates (13, 14, 39). Genotype matching between phorid flies and fire ants is a key factor in the search for sustainable biological control agents for *S. invicta* introduced into the United States (15, 128). Climate matching between the native and introduced ranges for phorid flies is also an important consideration for choosing potential phorid species (15, 39). It is thought that *Pseudacteon* flies would do better in North America in areas with climates that best match their native ranges in South America. For instance, selecting phorid species with broad ranges, like *P. cultellatus*, *P. litoralis*, *P. nocens*, and *P. obtusus*, from arid areas of western Argentina may facilitate acclimatization to hot and arid areas in Texas (43, 46, 49).

Release from natural enemies and absence of highly competitive ant species contribute to the success of introduced fire ants (10, 110). Six species that can parasitize both imported fire ant species were selected for mass rearing and release (42). The first two released species, *P. tricuspis* and *P. curvatus*, have spread to most areas occupied by the imported fire ant populations in the southern United States. However, there is interspecific competition among sympatric fly species, which makes establishment of new species more difficult (59). Strategic releases of an additional *Pseudacteon* species in fly-free areas would fill gaps in the distribution of the first two species. Further, coexistence of multiple fly species would expand the breadth and magnitude of their impact on fire ant populations as they cover a greater size range of workers. Moreover, multiple fly species with different activity patterns would contract enemy time-free space during daylight for the fire ants. A multispecies biocontrol strategy can mirror the diversity and structure of phorid flies in the native range of *S. saevissima* complex fire ants.

Long-term monitoring efforts are required for evaluating the success of field releases of multiple fly species. Given that releases of these natural enemies will not eradicate fire ants, successful self-sustaining parasites and pathogens may ultimately reduce fire ant populations to levels closer to those in South America. However, the lack of a strongly competitive ant assemblage in the introduced range may limit the potential control exercised by biocontrol agents.

## DISCLOSURE STATEMENT

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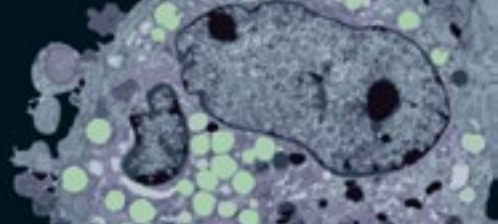
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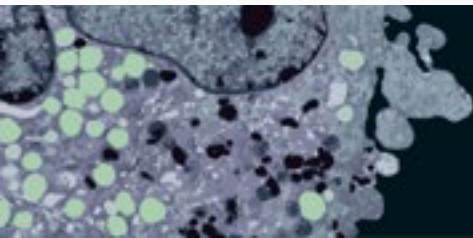
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