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Lloyd W. Morrison
Missouri State University

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Review Article

Biological Control of *Solenopsis* Fire Ants by *Pseudacteon* Parasitoids: Theory and Practice

Lloyd W. Morrison

Department of Biology, Missouri State University, 901 S. National Avenue, Springfield, MO 65897, USA

Correspondence should be addressed to Lloyd W. Morrison, lloydmorrison@missouristate.edu

Received 25 August 2011; Accepted 20 October 2011

Academic Editor: Jean Paul Lachaud

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Pseudacteon parasitoids are potential biocontrol agents of invasive *Solenopsis* fire ants. *Pseudacteon* species that parasitize the invasive *S. invicta* Buren and *S. richteri* Forel have been introduced to, and naturally dispersed across, the southeastern USA, although there is no evidence yet that *Solenopsis* host ant populations have decreased. The ability of introduced *Pseudacteon* species to regulate *Solenopsis* populations will depend upon the relative importance of top-down effects in the recipient communities. In this paper, I examine the characteristics of the *Pseudacteon/Solenopsis* parasitoid/host system and evaluate the extent to which research findings are consistent with top-down control. Laboratory and field experiments evaluating *Solenopsis* population regulation have been equivocal, and overall the available evidence provides little support for strong top-down effects in this system. Competitive exclusion may occur among introduced *Pseudacteon* species, and future efforts at biological control are likely to be more efficacious if they focus on other types of natural enemies.

1. Introduction

Many species of *Pseudacteon* (Diptera: Phoridae) are parasitoids of *Solenopsis* (Hymenoptera: Formicidae) fire ants. Several species of *Solenopsis* fire ants are invasive pests and others have the potential to be [1]. High densities of the invasive *S. invicta* Buren in North America are usually attributed to an escape from natural enemies [2]. Much recent research has focused on the potential use of *Pseudacteon* parasitoids as classical biological control agents to regulate *Solenopsis* fire ant populations, particularly *S. invicta* and *S. richteri* Forel in North America. Two South American *Pseudacteon* species—*P. tricuspidatus* Borgmeier and *P. curvatus* Borgmeier—have been released at multiple locations and dispersed naturally across the southeastern USA. It is estimated that *P. tricuspidatus* now occurs in 65%, while *P. curvatus* may occur in as much as 90% of the invasive *S. invicta/S. richteri* range [3]. Two other species—*P. litoralis* Borgmeier and *P. obtusatus* Borgmeier—have been established in localized areas, *P. cul-tellatus* Borgmeier has been recently released in Florida, and releases of additional species are planned [3, 4]. In addition to the direct effect of mortality, *Pseudacteon* phorids may have indirect effects on their *Solenopsis* hosts, affecting their

behavior and potentially putting the host species at a relative disadvantage with competing ants [5].

There have been many studies conducted on various aspects of the *Pseudacteon/Solenopsis* parasitoid/host system, and the literature is in need of an objective, critical review. There is great interest in whether the introduction of *Pseudacteon* phorids can regulate invasive fire ant populations, and if so, to what degree. I conducted original research on this system for a decade, but have more recently pursued other avenues of study. The success or failure (perceived or actual) of this biological control program has no bearing on my obtaining funding, promotion, or tenure. Thus, I am in a good position to conduct a knowledgeable, yet detached review. I do not attempt to review all the *Pseudacteon/Solenopsis* literature, but focus on the potential of introduced *Pseudacteon* parasitoids from South America to regulate population densities of host *Solenopsis* ants in their invasive range in North America, through both direct and indirect effects.

2. The Species

2.1. The Host. The genus *Solenopsis* contains about 185 described species worldwide; the ~20 *Solenopsis* species known

as “fire ants” are all native to the new world [1]. Three of these fire ants are invasive pests: *S. invicta*, the most notorious, is native to South America but has invaded North America, the Caribbean, Australia, Taiwan, and China [6]. *S. richteri*, also native to South America, has invaded the southeastern USA, where it has hybridized with *S. invicta* [7]. *S. geminata* (Fabricius), whose natural range spans southern North America to northern South America, has been found at numerous low latitude sites around the globe [7]. The vast majority of *Solenopsis* fire ant research has focused on these three species. All three are characterized by polymorphic workers, which live between 2 and 8 months, depending on worker size and temperature [8]. The massive fire ant literature has been summarized by Taber [7] and synthesized by Tschinkel [1].

One important aspect of *Solenopsis* biology that is relevant here is the seasonal cycle of population abundance. In the southeastern USA, *S. invicta* reaches peak abundances in midwinter, and the lowest worker numbers occurring in midsummer are only about half that of winter highs [9]. *S. invicta* above ground foraging activity is highest in summer, however, and lowest in winter when soil temperatures are too cold to forage [10, 11]. Thus, the availability of hosts to *Pseudacteon* parasitoids is greatest in the summer months, even though *S. invicta* absolute densities are near their lowest.

Beyond the seasonal oscillations in abundance, *Solenopsis* population size may vary with other factors. The *Solenopsis* species in question are disturbed habitat specialists [1, 12]. Disturbances come in all degrees, however, and across a broad scale either too much or too little disturbance may result in lower fire ant abundances [13]. Disturbance regimes undoubtedly vary temporally and result in variability in *Solenopsis* populations. Climatic events (i.e., droughts, floods, and unusually cold weather) may also affect *Solenopsis* abundances [14, 15]. Fluctuations in abundance due to a variable disturbance regime or such climatic events could either amplify or dampen the inherent seasonal oscillations.

Finally, *Solenopsis* fire ants have the propensity to rapidly increase in abundance. After removing all *S. invicta* from experimental plots in Florida, for example, *S. invicta* recolonized the plots and in only two years reached abundances similar to control plots [16]. It is against this background of wide and potentially variable fluctuations in host population size, in addition to a strong potential for colony growth, that the regulatory effect of *Pseudacteon* parasitoids must be evaluated.

2.2. The Parasitoid. Although a number of taxonomic issues remained unresolved, over 20 *Pseudacteon* species are known to parasitize *Solenopsis saevissima* complex fire ants in South America [17]. Similarly, more than 20 *Pseudacteon* species parasitize *Solenopsis geminata* complex fire ants from North America to northern South America [18]. The basic biology and natural history of *Pseudacteon* phorids that parasitize *Solenopsis* fire ants have been summarized by Porter [19] and Morrison [20]. The life cycle of *Pseudacteon*, in brief, is as follows. A female *Pseudacteon* hovers near *Solenopsis* worker ants and inserts eggs into the thorax of hosts in aerial attacks with a specialized ovipositor. Three larval instars—the

second of which migrates to the head—precede pupation. At pupariation, the worker is killed by the parasitoid consuming all the tissue inside the head capsule, which is then used as a pupal case. Development from egg to adult takes from 5 to 12 weeks, depending upon temperature and the *Pseudacteon* species. *Pseudacteon* are solitary parasitoids, with only one larva able to complete development in each host. Each female *Pseudacteon*, however, may produce >200 eggs [21].

3. Theory

Whether or not *Pseudacteon* parasitoids control or regulate population densities of *Solenopsis* fire ants can be thought of as a function of the relative importance of top-down versus bottom-up effects in the communities in question. In food web terminology, bottom-up effects occur when the abundance of a resource affects the population of the consumer of that resource. The higher the abundance of resources at lower trophic levels, the higher the abundance or diversity that can be obtained at higher trophic levels. Top-down effects, on the other hand, occur when the population density of a consumer affects the abundance of its resource. Top-down control refers to the situation where the abundance or diversity of lower trophic levels is dependent on effects from consumers at higher trophic levels [22]. There has been much discussion in the literature over the relative importance of top-down versus bottom-up effects in arthropod communities, including the seasonal and spatial variability in such effects [23–29].

In a community with strong top-down effects, *Solenopsis* populations would be regulated by *Pseudacteon* parasitoids (or other predators or parasites). In contrast, in a community with strong bottom-up effects, *Solenopsis* populations would ultimately be regulated by the food resources available to them, and simply support *Pseudacteon* populations but not be controlled by them. Larger *Solenopsis* populations could support larger *Pseudacteon* populations. Obviously, biological control of host ants requires a system with relatively strong (and consistent) top-down effects.

Interspecific competition has traditionally been viewed as the primary mechanism organizing ant communities and limiting ant populations [30]. It has been suggested, however, that top-down processes such as parasitism may also play an important role in some ant communities [31]. Here, I make no attempt to evaluate the importance of parasitoids to ant communities in general, but rather to determine which characteristics of the *Pseudacteon/Solenopsis* parasitoid/host system are consistent with top-down control. I refer to the prevalence of such top-down effects as “strong control,” in reference to the goal of regulating invasive *Solenopsis* populations.

The relative importance of top-down effects can be illustrated by comparing two scenarios: in the first scenario—“strong control”—top-down effects prevail. This scenario is characterized by (1) a diversity of *Pseudacteon* species that exert a broad range of parasitism pressure on host *Solenopsis* ants, (2) consistently high abundance and activity of *Pseudacteon*, (3) high rates of mortality resulting from parasitism, (4) a lack of refuge for, or ability to behaviorally adapt in,

host ants, and (5) shifting of the outcome of interspecific interactions with competing ants. The second scenario, which I term “weak control”, is characterized by (1) low diversities of *Pseudacteon* species, (2) low or fluctuating abundance or activity of *Pseudacteon*, (3) low rates of mortality resulting from parasitism, (4) the presence of a refuge or the ability to behaviorally adapt by host ants, and (5) little or no effect on the outcome of interspecific interactions with competing ants.

These two scenarios more appropriately represent the ends of a continuum rather than two mutually exclusive states (or because multiple characteristics are involved, the margins of a multidimensional space). Moreover, the characteristics of each scenario are largely independent of each other. Evaluation of recent research results relative to these scenarios allows for a greater understanding of the degree to which *Pseudacteon* parasitoids may control or regulate population densities of *Solenopsis* fire ants.

Given the high background population fluctuations of host *Solenopsis*, the potential effects of *Pseudacteon* as described in the two scenarios above are illustrated as a conceptual model in Figure 1. In the strong control scenario (Figure 1(a)), broad parasitism pressure (direct and indirect) depresses fire ant populations consistently over time, resulting in peaks and troughs of fire ant population cycles that are lower than without the parasitoids. The mean *Solenopsis* abundance over time is also lower.

In the weak control scenario (Figure 1(b)), parasitism pressure is weak and may only affect host ant populations seasonally, or is otherwise greatly limited in intensity. *Pseudacteon* populations also fluctuate, reaching their highest abundances and thus exerting peak parasitism pressure in the fall, due to greater host availability in the summer (because of higher above-ground foraging activity by the ants). Because of low rates of mortality due to parasitism and the ability of ants to adapt behaviorally and lessen the indirect effects, colony fitness is only slightly affected, and this decrease comes at a time when overall colony size is peaking. Because of the overall cyclical nature of *Solenopsis* abundance and the added stochastic effects of disturbance and climate (depicted in this figure as irregular seasonal oscillations), the impacts of *Pseudacteon* may be relatively small. Over the long term, such effects may be washed out by the greater population variability due to other factors. Under optimum disturbance intensity and climatic conditions, host ants may regain previous population peaks. In this scenario, the long-term average *Solenopsis* abundance or range of fluctuations may change relatively little due to *Pseudacteon*.

4. The Evidence

4.1. Diversity of *Pseudacteon* Species. In most locations that have been studied, multiple *Pseudacteon* species have been found. This is true for *Solenopsis saevissima* complex fire ants in South America and *Solenopsis geminata* complex fire ants in North America [17, 32–35]. Host ants are partitioned among *Pseudacteon* species along several axes, including size of worker [36–38], host location preferences [33, 39], and time of day [35–40]. Thus multiple *Pseudacteon* species

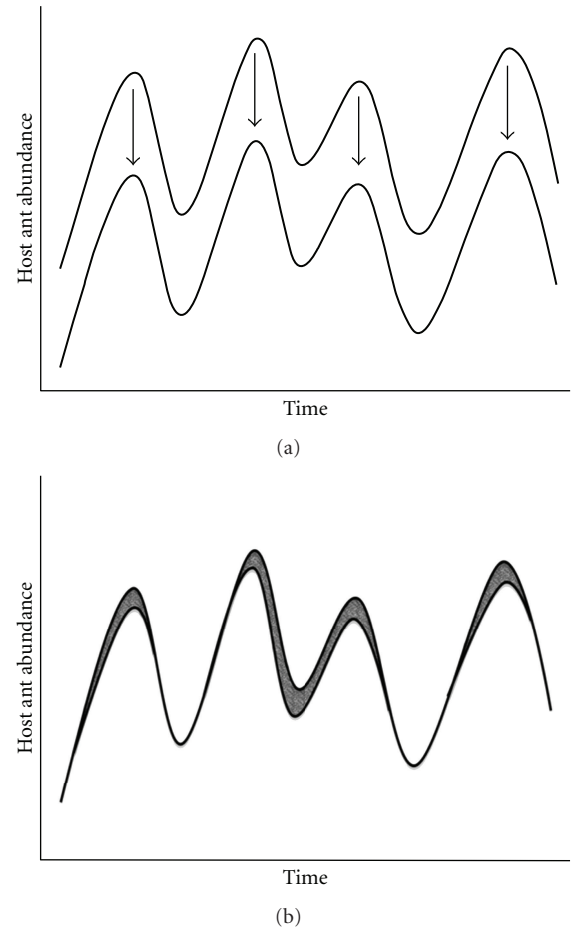


FIGURE 1: Two hypothetical scenarios of the potential effects of introduced *Pseudacteon* parasitoids on *Solenopsis* fire ant populations. (a) Strong control: parasitism pressure depresses fire ant populations consistently over time, resulting in peaks and troughs of fire ant population cycles that are lower than without the parasitoids. (b) Weak control: parasitism pressure primarily affects host ant populations seasonally, or to an otherwise relatively small extent, and ants rebound under optimum growth conditions. (Shaded areas indicate the amount of decrease due to the parasitoids.)

attack a greater size range of workers, engaged in a wider diversity of activities, over a longer period of time than a single *Pseudacteon* species would.

Although multiple *Pseudacteon* species may cooccur at a site, most species are usually relatively rare. This is also true both in North America [5, 34] and South America [32, 33, 35, 41–43]. The niche segregation observed is likely the result of competition among *Pseudacteon* species for hosts. There is now evidence that introduced South American *Pseudacteon* species are competitively displacing each other in North America [4, 44, 45], and a reanalysis of abundance data from South America suggests competitive exclusion exists there as well [44].

4.2. Abundance and Activity of *Pseudacteon* Species. Adult *Pseudacteon* live for only a few days [46], and reveal relatively great variability in abundance over time [34, 41, 47–49]. In

tropical and subtropical climates, *Pseudacteon* species are active year round, although relative abundance varies seasonally [32, 35, 41, 49]. *Pseudacteon* species are active from dawn to dusk, but diel variation exists among species [35]. In more temperate zones, flight activity of *Pseudacteon* is limited by cool air temperatures and adults may not be active in the winter months [34].

Introduced *P. tricuspidis* populations in the southeastern USA reveal cyclical patterns of seasonal abundance, with peaks in the fall and troughs in the spring [48, 50, 51]. *Solenopsis* above ground foraging activity, and thus host availability is highest in summer. Thus *P. tricuspidis* densities track host ant availability (with some lag time to be expected based on the 5–12-week-long development cycle) and greater availability of hosts (i.e., resources) is correlated with higher parasitoid (i.e., consumer) populations. Abundance patterns of *P. curvatus*, however, may differ, at least in some areas [S. D. Porter, unpublished data].

4.3. Mortality due to Parasitism. Parasitism rates (i.e., the percentage of *Solenopsis* workers in a colony infected with a *Pseudacteon* egg or larva at a given point in time) have been reported to be very low in a number of studies. In Texas, *S. geminata*—hosts of native North American *Pseudacteon* species—had parasitism rates of <3% [36]. Parasitism rates of *Solenopsis invicta* in its native range in Argentina by native South American *Pseudacteon* species were similarly <3% [35]. Parasitism rates of *Solenopsis invicta* in its exotic range in Florida from introduced *Pseudacteon* are generally ≤2% [48, 52, S. D. Porter, unpublished data]. These observed rates are an order of magnitude below the lowest parasitism rates associated with successful biological control programs (>30%) [53, 54]. These rates for successful biocontrol for other types of parasites, however, are based on the direct effect of mortality only.

Workers that are parasitized by *Pseudacteon* are not a random assortment from the colony, but rather represent primarily older ants with a shorter life expectancy. Fire ants exhibit a division of labor, in which the particular task engaged in by a worker depends on the age and size of that worker. In general, younger workers engage in relatively safe activities within the central colony, whereas older workers are found near the periphery of the nest, and the oldest workers engage in the most dangerous activity: foraging [55]. Mortality rates of foragers may be as high as 5% *per day* [1]. Because of the high mortality rates associated with foraging activities in ants in general, foragers have been described as a “disposable caste” [56].

Pseudacteon phorids attack host workers involved in foraging, interspecific interactions, and colony defense—all relatively dangerous activities. Thus most of the workers parasitized are engaged in high-risk activities and near the end of their natural lives, and colony fitness is affected to a lesser degree than if workers were parasitized at random with respect to age.

4.4. Host Ant Refuges and Behavioral Adaptations. A primary focus for research into the indirect effects of *Pseudacteon* has

been the reduction of foraging in host ants in the presence of these parasitoids. A number of studies involving different *Pseudacteon/Solenopsis* combinations in both North and South America have revealed that in the presence of these parasitoids, worker behavior changed and foraging at rich food resources dramatically diminished [5, 57–61]. The size of foraging *Solenopsis* workers has also been observed to decrease in the presence of *Pseudacteon* [52–64]. These studies, however, have almost exclusively focused on short-term effects of phorids at rich food resources, characterized by the recruitment of many workers in the absence of any shelter or refuge for the host workers and during ideal conditions for *Pseudacteon* flight activity.

Yet foraging in these *Solenopsis* species occurs under a great variety of conditions. In other words, these ants are characterized by a relatively broad foraging niche (*sensu*, [65]). They may forage by day or night [5, 66], as long as the soil temperature is at least 15°C [10, 11]. *Solenopsis* fire ants are omnivorous, with a very catholic diet [67, 68]. They excavate elaborate underground tunnel systems [69], and some unknown proportion of their food may be derived from underground sources (i.e., plant roots or root homopterans) [67]. The range of food items and types varies greatly; they may retrieve small items individually, but many workers may recruit to larger or long-lasting resources.

In contrast, *Pseudacteon* flies are not active after dark. Their aerial mode of attack makes it impossible to attack workers in underground tunnels (worker ants will quickly kill *Pseudacteon* flies if they can catch them). Additionally, *Pseudacteon* are unlikely to affect foraging of items that can be retrieved individually, although this has not been carefully studied. Some *Pseudacteon* species may not even affect foraging of relatively rich food resources if these are uncontested. Introduced *P. tricuspidis* in North America, for example, were not attracted to workers foraging at such resources, unless involved in interspecific interactions with other ants [39]. *P. tricuspidis* is attracted to the alarm pheromones and venom alkaloids that are typically released in such interactions [70, 71].

Pseudacteon native to North America are not active when air temperatures drop below 20°C [34], although some species in South America are active down to 14°C [41]. Thus there may be a narrow temperature zone in which it is warm enough for above-ground *Solenopsis* foraging, but not for *Pseudacteon* activity, although this appears to vary geographically and by species. Thus, *Pseudacteon* phorids will affect some unknown fraction of the overall broad spatiotemporal foraging niche of *Solenopsis*.

Furthermore, although the reduction in food obtained from such rich food resources may appear very large in the short term, in the longer term *Solenopsis* ants may be able to adapt behaviorally and still obtain much of the resource in question, if not removed by competitors. Field studies have shown that although forager numbers may decrease, *Solenopsis* workers do not usually completely abandon food resources in the presence of *Pseudacteon*, but some workers remain behind to guard the resource [34, 47, 59]. Foraging has even been observed to rebound to earlier levels after a depression by *Pseudacteon* [33]. Workers have been observed tunneling

beneath a rich food source and covering it with dirt and debris [5, 47].

Although most laboratory studies have constrained foraging to occur only in the presence of *Pseudacteon*, the design of one laboratory study allowed a colony of *S. invicta* to forage simultaneously in one arena with *P. tricuspis* and in a second arena without the parasitoid. Although less food was retrieved from the arena with *P. tricuspis*, the sum of food obtained from both foraging arenas was not different from that obtained in control trials without parasitoids [61]. Thus the colonies were able to compensate for decreased food retrieval caused by *P. tricuspis* harassment by simultaneously increasing food consumption when food was available elsewhere.

4.5. Effects on Interspecific Interactions. *Pseudacteon* species were never expected to have large direct effects of mortality on *Solenopsis* ants, and the expectation of this parasitoid's ability to regulate host ant populations was based primarily on the indirect effect on host behavior. These short-term behavioral effects would mean relatively little to colony fitness if they merely represented a delay in obtaining food resources. If, however, other ant species are able to secure a competitive advantage due to *Solenopsis*' parasitoid evasion behavior and are able to obtain relatively more food resources, then *Pseudacteon* could play an important role in mediating overall ant community dynamics and species abundance relationships.

Orr et al. [60], working in South America, observed *S. invicta* to lose food resources to competing ants in the presence of *Pseudacteon* phorids. Other studies, however, have found that host *Solenopsis* workers under *Pseudacteon* attack often did not lose control of the resource to competing ants. Studies of *Pseudacteon* parasitoids specific to *S. geminata* in Texas revealed that the presence of the parasitoids had no effect on the outcome of interspecific interactions involving *S. geminata* [5, 47]. A comparative study in Brazil revealed that *S. invicta*-specific *Pseudacteon* had no effect on the outcome of interspecific competition between *S. invicta* and other ants at two of three sites [72]. Thus, based on the available evidence, the ability of parasitoids to affect the outcome of interference competition among ant species appears to be too weak to be scientifically documented in many communities.

5. Long-Term Experiments

5.1. Laboratory Experiments. It has proven difficult to provide evidence for the success (or failure) of introduced *Pseudacteon* species in regulating host *Solenopsis* ants at the population level. Most evidence for a *Pseudacteon* effect, as discussed above, comes from short-term behavioral studies (minutes to hours in duration). In a relatively long-term lab study (28 days) incorporating both *Pseudacteon* phorids and a competing ant, *Forelius pruinosus* (Roger), Mottern et al. [73] reported a reduction in foraging in *S. invicta* due to *Pseudacteon* harassment, but no change in the colony growth rate of *S. invicta*. It is possible that the duration of this experiment was too short, or the method used to measure colony growth (i.e., photographing brood piles) was not precise

enough. The most likely explanation, however, is that ants were allowed to forage beyond the period that *Pseudacteon* attacked, and *Solenopsis* was able to compensate by increasing food retrieval when *Pseudacteon* were not active. Mottern et al. [73] state that such conditions would be "representative of those found in nature." No change in the growth rate of the competing ant was observed either, although this was not surprising because *F. pruinosus* never entered the communal foraging chamber.

In a longer lab study (50 days), Mehdiabadi and Gilbert [74] documented that the reduction of foraging in *S. invicta* due to *Pseudacteon* harassment did, as expected, eventually result in reduced colony fitness. In that study, the presence of *P. tricuspis* reduced the abundance of middle-sized workers, but not small- or large-sized workers. Worker ants, however, were always constrained to forage in small trays for limited periods in the presence of *P. tricuspis*, without any refuge or potential to adapt their foraging behavior. It is noteworthy that a combination of *P. tricuspis* phorids and a competing ant—this time *Forelius mccooki* (McCook)—had no greater effect on colony fitness than the competing ant alone [74]. As in the Mottern et al. [73] study, no increase was observed in the reproductive output of the competing ant [75]. (Interestingly, Mottern et al. [73] criticized the statistical analysis of Mehdiabadi and Gilbert [74], claiming that no significant differences existed for any of their treatments!)

Thus, the ambiguous results of these laboratory experiments provide little empirical support for the idea that *Pseudacteon* phorids could mediate competitive interactions that would ultimately lead to a decrease in *Solenopsis* populations, while allowing for a relative increase in competing ant populations. The general problem with such laboratory experiments is that the design can greatly influence the outcome. Given the complexity of fire ant foraging and the multitude of interactions with other species, any community-level laboratory experiment is destined to be an oversimplification of the natural world with limited inference.

5.2. Field Experiments. Field experiments, while more realistic, have their own limitations, in this case primarily logistical. Fire ant populations are undoubtedly affected by many factors, and while many of these variables can be controlled for in the laboratory, attempting to isolate the effect of one factor in the context of a broad field experiment is very difficult. Moreover, introduced *Pseudacteon* species spread naturally at a rapid rate; *P. tricuspis* dispersed at rates of up to 30 km/year for the first few years after establishment in north Florida [76], and at rates of up to 57 km/year over the following four years [77]. After three and a half years, *P. curvatus* had dispersed even farther in Florida than *P. tricuspis* did over the same period after initial release [78]. In Texas, small satellite populations of *P. tricuspis* have been found tens of km beyond the main expansion front; this jump dispersal was probably assisted by the prevailing winds [79].

Thus it is difficult to have true control sites that are not colonized within the time course of an experiment. Control sites would have to be placed so far away that there could be systematic differences in environmental variables between the treatment and control sites. This is almost a moot point,

as by now the vast majority of the invasive range of *Solenopsis* in the southeastern USA is estimated to have been colonized by at least one introduced *Pseudacteon* species [3]. Because of the tiny size of *Pseudacteon*, it is impractical to attempt to construct enclosures or exclosures, as these would include or exclude almost all other species (except microscopic ones).

The only published field experiment—including control plots (albeit 2 counties away) and spanning relatively large spatiotemporal dimensions—failed to find any measurable effect of introduced *P. tricuspidis* on *S. invicta* in Florida [50]. The study was ended after 3 years when *P. tricuspidis* dispersed to control plots. Relatively large variabilities were observed in fire ant activity and abundance, however, in both treatment and control plots. Thus the effects of this parasitoid would have had to be relatively large (perhaps reducing host ants by as much as 30%) to be detectable [50].

Studies are underway to gauge impact by comparing fire ant abundances before and after the introduction of *Pseudacteon*, in the absence of any control sites [3]. Such comparisons could be misleading, however, and should be interpreted with extreme caution. Fire ant abundances can and do change in response to many factors. *S. invicta* abundance, for example, was found to decrease by almost an order of magnitude over 12 years at a Central Texas site [80]. *Pseudacteon* species had not become established in Central Texas at the time, although other natural enemies of fire ants were present [80]. Additionally, numerous pathogens of *Solenopsis* fire ants are now known to be present in North America, and many have relatively high infection rates [52, 81, 82]. Finally, broad scale trends (i.e., climate cycles or directional change) may affect fire ant abundances independently of parasitoids.

6. Synthesis

6.1. Summary of the Evidence in Relation to Theory. Multiple *Pseudacteon* species frequently cooccur, although usually only one or a few species are very abundant. Overall, the *Pseudacteon* assemblage present at a given location may reach relatively high abundances at times, although populations fluctuate, and in the case of the introduced *P. tricuspidis* in Florida, in synchrony with host availability. Parasitism rates are usually very low, and most workers parasitized are probably near the end of their natural lives, so this direct effect of parasitism may be almost negligible. Host ants may engage in much of their foraging in the absence of *Pseudacteon* flies and have the ability to adapt their behavior in the presence of this parasitoid, so that in the long term, the overall reduction in resource retrieval is likely much less than that suggested in short-term observations. Finally, *Solenopsis* species often do not lose control of rich food resources to competing ants in the presence of *Pseudacteon*.

Thus the available evidence suggests that any impacts of *Pseudacteon* phorids on host ant populations are generally small, especially when measured over the relatively large population variability of *Solenopsis* fire ants. Moreover, given the ability of *Solenopsis* to rapidly increase in population size under ideal conditions, any depression in *Solenopsis* populations by *Pseudacteon* phorids could be ephemeral if parasitism pressure is not consistent. Thus, the effects are probably

much closer to the “weak control” scenario described above, although such effects could vary geographically and temporally. Experimental assessments of the impact of introduced *Pseudacteon* species have been few, and the results equivocal, although certainly no large impacts have been documented with any scientific rigor. Unfortunately, due to the constraints described above, we may never have a reliable, precise estimate for the effect of *Pseudacteon* parasitoids on *Solenopsis* fire ant populations in nature.

Thus the available evidence provides little support for strong top-down effects in this system. The accumulated data reveal that introduced *P. tricuspidis* in North America are positively correlated with *S. invicta* availability, both temporally [48, 50, 51] and spatially [51]. These findings are not inconsistent with the hypothesis that larger *Solenopsis* fire ant populations simply support higher abundances of *Pseudacteon* parasitoids, and that *Solenopsis* populations are primarily regulated by other factors.

6.2. Host Specificity and Knowledge Gaps. Although *Pseudacteon* phorids may have relatively small effects on fire ant populations, they possess two very desirable qualities of a biocontrol agent. They have been documented to be highly host specific, in a battery of tests conducted: (1) in the field in South America [83, 84], (2) in the lab prior to the release of South American *Pseudacteon* species to North America [85–88], and (3) in the field in North America after the establishment of introduced populations [89, 90]. Thus, *Pseudacteon* phorids appear to be safe (i.e., no documented adverse effects on any other species), which is the most important quality of any biocontrol agent. Additionally, once established, *Pseudacteon* species will persist as a permanent component of communities in which host *Solenopsis* are found, and naturally disperse to others.

Several aspects of *Pseudacteon*/*Solenopsis* interactions need more study. Some *Pseudacteon* are attracted to mound disturbances [33, 39], although the potential effects of *Pseudacteon* on mound disturbances are less clear than those of interruption of foraging. The presence of *Pseudacteon* may delay the mound rebuilding process, but only for a matter of hours, until *Pseudacteon* activity ceases with darkness. The mound is important in regulating brood temperature and thus development [91], and movement of brood out of the mound due to disturbance and delayed reconstruction could adversely impact colony fitness, although such an effect seems ephemeral and thus relatively small. The frequency of natural mound disturbance events is an important variable in assessing this impact, and this disturbance regime no doubt varies geographically.

Morrison and King [39] found that numerous *P. tricuspidis* flies were attracted to *S. invicta* mound disturbances when nonnestmate *S. invicta* were added, resulting in interspecific interactions, but on average fewer than one parasitoid was attracted in the absence of such interactions. Thus, most mound disturbances in the absence of interspecific interactions would probably be little affected by *P. tricuspidis*, although other *Pseudacteon* species may differ in this aspect of their behavior. *Pseudacteon* are also attracted to *Solenopsis* mating flights [92]. Although *Solenopsis* reproductives are

not suitable hosts [19], workers are very active on the mound surface before the reproductives take flight [93], and the presence of *Pseudacteon* could dampen this activity, potentially disrupting the mating flight. Large numbers of workers may be vulnerable to parasitism during mating flights or mound reconstruction, and such workers may be younger than workers engaged in foraging, thus representing a potential greater loss to overall colony fitness. Finally, *Pseudacteon* are carriers of pathogens that infect *Solenopsis* [94], although actual vectoring of diseases among colonies has not been demonstrated.

6.3. Implications and the Bigger Picture. Efforts are underway to introduce additional South American *Pseudacteon* species to North America. The question is how many additional species should be introduced? Because of the relatively high degree of niche partitioning observed in *Pseudacteon* species in South America, and the coexistence of multiple species at a site, the traditional wisdom has been that multiple *Pseudacteon* species will coexist at North American release sites, and that more *Pseudacteon* species will exert greater parasitism pressure on host *Solenopsis* ants. The species abundance patterns of *Pseudacteon* in both North and South America, and the recent, relatively unexpected finding of competitive exclusion among introduced *Pseudacteon* species, however, suggest only one or two introduced species may be abundant at any given location. Thus the introduction of additional *Pseudacteon* species may simply reduce the abundance of already-established species, without substantially increasing the density of the overall *Pseudacteon* assemblage.

An argument can be made that multiple *Pseudacteon* species are necessary because of the diversity in invasive *Solenopsis* populations in North America. Both *S. invicta* and *S. richteri* (and a hybrid) are present, and colonies may be either polygyne (i.e., multiple queen) or monogyne (i.e., single queen) [1]. There have been attempts to “match” or find the best combination of South American *Pseudacteon* species or biotypes with North American *Solenopsis* populations [95]. Ultimately, given the speed of dispersal of this parasitoid, after introductions of multiple *Pseudacteon* species to multiple locations in the *Solenopsis* invasive range, the flies may eventually sort themselves out. Not all *Pseudacteon* species may disperse at the same rate as *P. tricuspidis* and *P. curvatus*, however. *P. litoralis* has spread much more slowly from a single release site in Alabama [4]. Although *Pseudacteon* species appear to have no detrimental effects, the time and effort involved in evaluating, rearing, and releasing these flies might be better spent evaluating other types of natural enemies. At this point, it seems likely that the marginal contribution of each additional *Pseudacteon* species released will be diminished as more species are added.

In South America, a diversity of parasites, pathogens, predators, and competitors affect *S. invicta* [1, 96]. Thus, introduction of a single type of natural enemy is unlikely to result in outsized reductions of invasive *Solenopsis* populations. It is more likely that regulation is incremental, and that each type of introduced natural enemy may have a relatively small effect, yet one that is cumulative so that overall

control becomes greater with the addition of more types of natural enemies. Thus, the continued search, evaluation, and introduction of other safe (i.e., host-specific) natural enemies of *Solenopsis* fire ants may eventually lead to measurable levels of fire ant population regulation.

Given the general lack of evidence for strong top-down control in this system, it is possible that other ants represent the greatest natural enemies of *Solenopsis*. The South American ant fauna contains more species that are strong competitors of *S. invicta* than does the North American fauna [72, 97, 98]. Many of these ant species would have their own deleterious impacts to recipient biotas, perhaps even greater than *Solenopsis* fire ants, and introductions of such natural enemies are not seriously contemplated. If competition from other ants is the primary reason that *S. invicta* is less abundant in South America, it follows that introductions of all possible other types of natural enemies will not result in a decrease of North American *S. invicta* or *S. richteri* populations to South American levels.

The conventional wisdom of *Pseudacteon* biological control is that the presence of these parasitoids may shift the competitive balance away from *Solenopsis* fire ants to native ant species, allowing for a relative increase in abundance of the native species at the expense of the invasive *Solenopsis*. Recent work on the effects of disturbance, however, challenges the conventional wisdom that *Solenopsis* fire ants are strong competitors that have displaced native ants primarily due to a competitive asymmetry. King and Tschinkel [99] obtained experimental evidence suggesting that native ants are first displaced as a result of habitat disturbance, and then *Solenopsis* fire ants—which are disturbed habitat specialists—move into the disturbed areas. Experimentally removing *S. invicta* from disturbed areas did not result in an increase of native species [100]. In this study, conducted in forest habitat in Florida, “disturbance” resulted in the simplification of habitat structure to a type that was more similar to the habitat where *S. invicta* is native (i.e., open areas with high insolation). Thus, at least in some areas, disrupting the behavior of *Solenopsis* fire ants or even reducing their abundances may have limited effects on native ant diversity, in the absence of restoring disturbed or simplified habitats.

Habitat type or disturbance alone, however, cannot adequately explain the high abundances of invasive *Solenopsis* fire ants in North America. *Solenopsis* species were found to be more abundant at the same type of disturbed (i.e., roadside) sites in North America relative to South America [2]. Thus the abundance of *Solenopsis* fire ants in an area is likely the result of a number of factors (and interactions of factors), including habitat type, degree of habitat disturbance, and the presence of natural enemies. Ultimately, efforts to reduce invasive fire ant densities would probably benefit by taking a broad perspective and include attempts at habitat restoration in addition to the introduction of an array of natural enemies.

Acknowledgment

Sanford Porter made helpful comments on the paper.

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