Post-release host-specificity testing of *Pseudacteon tricuspis*, a phorid parasitoid of *Solenopsis invicta* fire ants

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Abstract. Inherent in any biological control program is the risk of nontarget effects. *Pseudacteon tricuspis* Borgmeier, a parasitoid phorid fly, has been introduced to the United States from South America as a potential biocontrol agent of the red imported fire ant, *Solenopsis invicta* Buren. We conducted tests of host specificity on introduced populations of *P. tricuspis*, which are attracted to alarm pheromones released by their hosts during events such as mound disturbances and interspecific interactions. We monitored disturbed mounds of *S. invicta* and its close congener, *S. geminata* (F.), during the expansion of *P. tricuspis* across north Florida and after populations had been established for $\sim$3 years. We also tested host acceptance in established populations of *P. tricuspis* by offering trays containing *S. invicta*, *S. geminata*, and 14 additional ant species representing 12 different non-*Solenopsis* genera. Although *P. tricuspis* was commonly observed to hover over and attempt to oviposit on *S. invicta*, we never observed any parasitization attempts on any other ant species. As predicted by laboratory tests, released populations of *P. tricuspis* appear to be highly host specific and pose no obvious threat to nontarget species.

Key words: biological control, host specificity, nontarget effects, *Pseudacteon tricuspis*, *Solenopsis invicta*

Introduction

The greatest potential danger of a biological control program involves nontarget effects. There are many cases in which introduced biocontrol agents negatively impacted species other than the target pest (e.g., Howarth, 1991; Kauffman and Nechols, 1992; Simberloff and Stiling, 1996a, b; Follett and Duan, 2000; Louda et al., 2003 and references therein). Some of the most dramatic nontarget effects were caused by

the release of generalized vertebrate predators in the early days of biological control. Other types of biocontrol agents, however, have proven safer. For example, there are no published cases, to our knowledge, of sustained nontarget effects from parasitoids considered to be host-specific upon their release in the continental US.

Biocontrol efforts have been criticized because testing of host-specificity preceding introduction of alien species has often been perfunctory or non-existent (Civeyrel and Simberloff, 1996). Presumably, many released biocontrol agents have had little or no substantial impacts on nontarget species. Yet evidence for nontarget effects is scarce in most cases because post-release monitoring of nontarget species has been minimal (Simberloff and Stiling, 1996a; Stiling and Simberloff, 2000). Even if potential biocontrol agents are tested extensively in quarantine before release in the field, another danger exists: The behavior of an alien species may differ in the quarantine facility compared to the field (i.e., a cage effect), or the species may adapt or evolve to affect nontarget organisms (Hopper et al., 1993; Secord and Karieva, 1996).

An example of a biological control agent that has been tested extensively for host-specificity prior to release are phorid flies in the genus *Pseudacteon*, which are parasitoids of *Solenopsis* fire ants (Porter, 1998a; Morrison, 2000a). Host-specificity testing has been conducted on several *Pseudacteon* species in the field in South America (Porter et al., 1995; Porter, 1998b) and in quarantine facilities in the United States (Gilbert and Morrison, 1997; Morrison and Gilbert, 1999; Porter and Alonso, 1999; Porter, 2000). The South American *Pseudacteon* species tested revealed no tendencies to attack ant genera other than *Solenopsis*, and limited tendencies (depending upon the *Pseudacteon* species) to attack species outside the *saevissima* complex.

Host location behavior in parasitoids, however, often involves a hierarchy of physical and chemical stimuli (Vinson, 1976; Weseloh, 1981), and behavior in small attack trays in the lab may not accurately predict host–parasitoid interactions in the field. For example, *Pseudacteon tricuspis* Borgmeier will frequently parasitize foraging *S. invicta* Buren workers in small attack boxes in the laboratory (Morrison, 2000b), although *P. tricuspis* is not attracted from a distance to *S. invicta* foraging activity in the field (Morrison and King, 2004). In nature this *Pseudacteon* species is attracted to activity related to the release of alarm pheromones, such as mound disturbances, interspecific interactions, and mating flights (Morrison and King, 2004). Thus it appears that any potential impacts of this species on the target host will not be mediated through foraging *per se*.

We conducted a set of field experiments to verify the host-specificity of released populations of *P. tricuspis* in north Florida during the expansion of this population, and after this species had been established for several years and gone through 12–15 generations in the field.

Methods

P. tricuspis was first successfully released and established in Gainesville, Alachua County, Florida in 1997. It has since been released at other sites in Alachua County as well as in 10 other southeastern states (Porter et al., 1999). *P. tricuspis* has dispersed at rates of up to 30 km per year and now inhabits most of northern Florida (Porter et al., 2004).

We tested the host-specificity of *P. tricuspis* in the field at two time intervals: (1) during the expansion of *P. tricuspis* from Alachua County across northern Florida, and (2) after *P. tricuspis* had been established in Alachua County for ~ 3 years. We focused on attraction to *S. invicta*, the target host, and *S. geminata* (F.), a close congener native to the southeastern United States. Most *S. geminata* colonies disturbed in the field were the orange–red variety (*rufa*), which is predominant in north central Florida, but some colonies (~15%) were the black variety (*nigra*; see Trager, 1991). Other closely related native *Solenopsis* species known to be parasitized by *Pseudacteon* species (e.g., *S. xyloni* McCook) are not known to occur in north Florida.

P. tricuspis flies are attracted to disturbed *S. invicta* mounds, apparently locating their hosts through chemoreception of alarm pheromones (Morrison and King, 2004). Such disturbances may occur naturally due to trampling by large animals (e.g., cattle), digging by small animals (e.g., armadillos), or machinery (e.g., mowers). We located sites where both *S. invicta* and *S. geminata* were present, and disturbed 5–10 mounds of each with a small shovel (as in Porter et al., 2004). Usually all mounds (of both species) at a site were within 100 m of each other. We examined the mounds for the presence of *P. tricuspis* flies for 30 min. Phorid parasitoids that are attracted to mound disturbances usually appear within 20–30 min (often within the first 5 min; *personal observations*). With increasing time after a disturbance, fewer workers are present on the surface and the disturbance becomes progressively less attractive to *P. tricuspis*. We examined six sites in this manner during the expansion of *P. tricuspis* across north Florida (November 2000–October 2001), and six sites after *P. tricuspis* had been established for ~ 3 years (September–October 2003).

Because mound densities and the number of workers/mound were usually lower for *S. geminata* than for *S. invicta*, we also conducted a series of host-specificity trials by setting out equivalent biomasses of ants in trays. We selected sites where *P. tricuspis* was relatively abundant, and set out four trays each of *S. invicta* and *S. geminata* (*rufa* variety). Each tray was 40 cm × 26 cm × 8 cm (length × width × depth) and contained 2 g of worker ants, each from a different colony. Trays were placed along a transect ∼1 m apart in an alternate arrangement (i.e., no adjacent trays contained the same ant species). We observed all eight trays for 20 min, recording the number of *P. tricuspis* hovering over each tray at 5 min intervals. After 20 min had elapsed, we removed the *S. invicta* trays, leaving the *S. geminata* trays in place. At this point, *P. tricuspis* phorids were present in the area and had been actively attacking *S. invicta*, so we could be certain that the absence of oviposition attempts on *S. geminata* was not due to a dearth of flies or fly inactivity. We observed the four *S. geminata* trays for an additional 20 min, recording the number of *P. tricuspis* at 5 min intervals. This procedure was replicated at three sites in Alachua County during October 2003.

We also tested for attraction to ants in other genera. We used 14 different species of ants, in 12 unique genera from five subfamilies (Table 1). We set out six trays of *S. invicta* (1.5 g of workers and 1.5 g of brood in each tray). Again, each tray contained ants from a different colony. We recorded the number of *P. tricuspis* hovering over each tray at 5 min intervals for 20 min. We then removed the *S. invicta* trays and replaced them with the 14 trays of ants from other genera. Once again, at this point we could be certain that *P. tricuspis* phorids were present in the area and motivated to attack. The numbers and biomass of non-*Solenopsis* workers varied with the colony size and body size typical of each species. The trays with non-*Solenopsis* ants were observed for 20 min. This procedure was replicated at three different sites in Alachua County in October 2003.

Because *Pseudacteon* flight activity is limited by cold temperatures (Morrison et al., 1999), all trials were conducted on warm days ($\geq$24 °C). All observations were made between 12:00 and 16:00, when *P. tricuspis* is most active (Pesquero et al., 1996). Voucher specimens have been placed in the Florida State Collection of Arthropods in Gainesville, FL.

Results

During the *P. tricuspis* expansion phase, we monitored 47 *S. invicta* mounds and 22 *S. geminata* mounds at six different sites. (*S. geminata*

Table 1. Non-*Solenopsis* ant species used in field tests

Ponerinae
  Odontomachus brunneus (Patton)
Pseudomyrmecinae
  Pseudomyrmex pallidus (F. Smith)
Myrmecinae
  Pogonomyrmex badius (Latreille)
  Aphaenogaster miamiana Wheeler
  Aphaenogaster cf. *carolinensis* Wheeler
  Pheidole dentata Mayr
  Crematogaster pilosa Emery
  Crematogaster minutissima Mayr
  Cyphomyrmex rimosus (Spinola)
  Trachymyrmex septentrionalis (McCook)
Dolichoderinae
  Dorymyrmex bureni (Trager)
  Forelius pruinosus (Roger)
  Linepithema humile (Mayr)
Formicinae
  Camponotus floridanus (Buckley)

was not as common as *S. invicta* in the areas sampled along the expansion front.) *P. tricuspis* was observed at 13 (28%) of the *S. invicta* mounds, but never at any *S. geminata* mounds. This difference was significant ($\chi^2 = 7.498$, $p = 0.0062$, df = 1; chi-square test of homogeneity; Daniel, 1990).

After *P. tricuspis* had been established for ~ 3 years, we monitored 46 *S. invicta* mounds and 55 *S. geminata* mounds at six different sites. *P. tricuspis* was observed at 23 (50%) of the *S. invicta* mounds, and possibly at one of the *S. geminata* mounds ($\chi^2 = 32.1$, $p = 0.0001$, df = 1). One fly, apparently *P. tricuspis*, was observed hovering over a disturbed *S. geminata* mound for several seconds. No oviposition attempts were observed, however, and the fly left the mound before it could be collected and its identity verified.

In tests of attraction to *S. geminata* and *S. invicta* in trays, *P. tricuspis* was never observed hovering over any trays containing *S. geminata*, neither when trays were adjacent to *S. invicta* trays nor after *S. invicta* trays had been removed and only *S. geminata* remained. In contrast, male and female *P. tricuspis* flies were commonly observed hovering over trays with *S. invicta* and females frequently attempted to

Table 2. Number of *P. tricuspis* phorid flies and number of trays occupied by *P. tricuspis* in field tests offering ant workers in trays. All numbers are averaged over three sites

Ant species	Cumulative # of *P. tricuspis* (# of trays with *P. tricuspis*)			
	5 min	10 min	15 min	20 min
Experiment #1				
S. invicta offered simultaneously with *S. geminata* (0–20 min)				
S. invicta (four trays)	7.7 (2.0)	9.7 (3.0)	9.0 (2.7)	9.7 (2.7)
S. geminata (four trays)	0 (0)	0 (0)	0 (0)	0 (0)
S. geminata offered alone (20–40 min)				
S. geminata (four trays)	0 (0)	0 (0)	0 (0)	0 (0)
Experiment #2				
S. invicta offered alternately with non-*Solenopsis* ant genera				
S. invicta (six trays) (0–20 min)	6.3 (3.3)	11.0 (4.7)	16.0 (5.0)	17.6 (4.7)
non-*Solenopsis* genera (14 trays) (20–40 min)	0 (0)	0 (0)	0 (0)	0 (0)

oviposit (Table 2). At all three sites, *P. tricuspis* was observed at three of the four *S. invicta* trays at some point in the trials.

In the tests with non-*Solenopsis* ant genera, multiple *P. tricuspis* flies (males and females) were usually present at trays with *S. invicta* (Table 2). *P. tricuspis* was present at all six trays at some point in the trials at two sites, and present at five of six trays at the third site. In contrast, no *P. tricuspis*, nor any other parasitic phorid, was observed at any trays of non-*Solenopsis* ant genera. Variation in *P. tricuspis* abundance at *S. invicta* trays in the two sets of trials was likely due to daily variability in weather conditions.

Discussion

In previous host-specificity tests conducted in the field in Brazil, *P. tricuspis* was never observed attacking ant genera other than *Solenopsis*, or *Solenopsis* species outside the *saevissima* complex (Porter et al., 1995; Porter, 1998b). Pre-release tests conducted in quarantine facilities in the United States revealed a few (<10) apparent oviposition attempts by *P. tricuspis* on *S. geminata*, which is considered native to the United

States (Trager, 1991), compared to hundreds of confirmed ovipositions on *S. invicta* (Gilbert and Morrison, 1997; Porter and Alonso, 1999). All apparent ovipositions by *P. tricuspis* on *S. geminata* occurred after transferring a *P. tricuspis* female from a tray where it was parasitizing *S. invicta*. Although the chemical or physical cues associated with *S. geminata* rarely lead to parasitization attempts, *P. tricuspis* is capable of developing in *S. geminata* in the laboratory (Porter and Alonso, 1999).

Assuming 4–5 generations per year (SDP, unpublished data), our post-release tests of host acceptance in the field were conducted 12–15 generations after *P. tricuspis* colonized these sites. Yet *P. tricuspis* revealed the same high levels of host-specificity observed in pre-release tests in South America and in quarantine facilities. These results confirm the persistence of host preference in released populations of *P. tricuspis* in the United States. It is encouraging that *P. tricuspis* showed virtually no interest in parasitizing *S. geminata* or any other ant species. An introduced biocontrol agent with a low acceptance of nontarget species may still pose a threat to the native fauna if its population is sufficiently large (Lynch et al., 2002).

Surprisingly, we never observed any native phorid flies attempting to parasitize *S. geminata*, nor have we observed native phorids associated with *S. geminata* in north Florida on any other occasions. Yet *S. geminata* is host to a number of *Pseudacteon* species in other parts of its range, including Texas (Brown and Morrison, 1999; Morrison et al., 1999), the Bahamas, and the Caribbean (Disney, 1991). Both the orange–red variety (*rufa*), which is predominant in Texas, and the black variety (*nigra*), which is predominant in the Bahamas and Caribbean, are present in Florida.

P. tricuspis was present at a relatively higher proportion of *S. invicta* mounds ~3 years after colonization compared to the initial expansion phase (50 vs. 28%, respectively). The explanation for this difference is most likely that *P. tricuspis* populations were relatively low along the colonization front during the expansion phase, but increased in abundance after they had been established for several years at a site (Porter et al., 2004).

During the tests comparing host acceptance of *S. invicta* vs. *S. geminata*, one *S. invicta* tray (from one colony) never attracted *P. tricuspis*, although the other three *S. invicta* trays (from three other colonies) did. Some *S. invicta* colonies appear to be more attractive to *P. tricuspis* than others (Morrison and King, 2004); one possible mechanism is variation in the chemical signals released by the ants.

Pseudacteon species that are parasitoids of *Solenopsis* fire ants appear to initially locate their hosts from a distance by olfaction, and then switch to visual cues at close distances (Gilbert and Morrison, 1997; Orr et al., 1997; Porter, 1998a; Porter and Alonso, 1999). *P. tricuspis*, like other *Pseudacteon* species, prefers to parasitize workers within a certain size range (Morrison et al., 1997). Larger *Pseudacteon* species parasitize larger worker ants, and the size of the ant head capsule is positively correlated with the size of the developing phorid. Workers of some of the non-*Solenopsis* ants that we tested were clearly much larger or smaller than this size range, although the point of our tests was to gauge attraction rather than developmental ability.

Overall, our results indicate that after 3 years released populations of *P. tricuspis* appear to pose no threat to native *S. geminata* populations. Other native *Solenopsis* species in the size range attacked by *P. tricuspis*, such as *S. xyloni*, have not been tested, although *S. xyloni* has been virtually excluded wherever *S. invicta* is present (Wilson and Brown, 1958; Tschinkel, 1988; Porter et al., 1991; Trager, 1991). *P. tricuspis* is known to parasitize the invasive *S. richteri* Forel and *S. invicta* ×*S. richteri* hybrids (Porter et al., 1997), and other South American *Solenopsis* species in the *saevissima* complex (Folgarait et al., 2002).

P. tricuspis has never been observed to be attracted to any other ant genera and, even if attracted, would probably not be able to complete development in most ant species. This is due to the highly coevolved mechanisms of egg insertion into the live worker ant and development in the ant head capsule (Porter, 1998a; Morrison, 2000a). It would be difficult to imagine that *Pseudacteon* phorids would be able to switch to some novel non-ant host.

Finally, even though released *P. tricuspis* populations may reach relatively high abundances in the United States (Morrison and Porter, 2005a), after 3 years there are no indications that this species is responsible for any deleterious effects (direct or indirect) on any non-target organisms. Adult *Pseudacteon* are small and cryptic, with short adult life spans (Porter, 1998a; Morrison, 2000a). In fact, the only time parasitoid *Pseudacteon* species have been observed in the field is in the presence of their host ants.

A recent multi-year field experiment in north Florida was unable to document any measurable impact of introduced *P. tricuspis* parasitoids on host *S. invicta* populations (Morrison and Porter, 2005b). It is possible that phorid fly parasitoids are not major factors regulating fire ant populations. Alternatively, introduced *Pseudacteon* species may

require many years, or multiple phorid species may need to be introduced, before a measurable effect becomes apparent.

Acknowledgements

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