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Establishment and dispersal of the fire ant decapitating fly *Pseudacteon tricuspis* in North Florida

Sanford D. Porter,[a,*] Luiz Alexandre Nogueira de Sá,[b] and Lloyd W. Morrison[a]

[a] *USDA-ARS, Center for Medical, Agricultural and Veterinary Entomology, P.O. Box 14565, Gainesville, FL 32604, USA*
[b] *Laboratório de Quarentena "Costa Lima," Embrapa Meio Ambiente, P.O. Box 69, 13.820-000, Jaguariúna, SP, Brazil*

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Abstract

The decapitating fly *Pseudacteon tricuspis* Borgmeier was released at eight sites in North Florida between the summer of 1997 and the fall of 1999 as a self-sustaining biocontrol agent of the red imported fire ant, *Solenopsis invicta* Buren. Several releases used parasitized fire ant workers while most involved adult flies released over disturbed ant mounds. Establishment and dispersal of fly populations were monitored by disturbing about 10 fire ant mounds at each site and then inspecting them closely for hovering flies over a period of about 30 min. Overwintering populations of flies were successfully established at 6 of 8 release sites. Over several years, fly populations at these sites increased to levels as high or higher than those normally seen in their South American homeland. By the fall of 1999, flies had expanded out 1–6 km from five release sites and occupied about 125 km^2. By the fall of 2000 the five initial release sites plus one new site had fused into one large area about 70 km in diameter. The flies had expanded out an additional 16–29 km and occupied about 3300 km^2. By the fall of 2001 the flies had expanded out an additional 10–30 km and occupied approximately 8100 km^2. Fly dispersal was not related to wind patterns in the Gainesville area. Based on the above rates of dispersal and an establishment rate of 66%, we estimate that a state the size of Florida would require 5–10 releases spaced over a 3-year period to cover the state in 6–9 years.

Keywords: Phoridae; *Pseudacteon tricuspis*; Formicidae; *Solenopsis invicta*; United States; Florida; Parasitoid; Classical biological control; Host preference; Establishment; Expansion; Wind drift

1. Introduction

The red imported fire ant, *Solenopsis invicta* Buren, was accidently introduced into the United States at the port of Mobile, Alabama in the 1930s. Over the next 60–70 years, the range of this pest has gradually expanded to occupy almost the entire southeastern United States (Callcott and Collins, 1996). New populations of this pest have recently been found in New Mexico, California, and even Brisbane, Australia. If eradication attempts in California are not successful, this pest will eventually spread up the West Coast of the United States (Korzukhin et al., 2001). The continent of Australia is similarly at risk. In the United States, *S. invicta* causes well over a billion US dollars of damage annually to crops, livestock, human health, and electrical equipment (Anon., 2001; Thompson and Jones, 1996), not including widespread environmental impacts on native organisms (Wojcik et al., 2001).

A number of effective chemical pesticides, principally baits, have been developed to control this pest in areas of high use like yards, playgrounds, and feed lots (Drees et al., 1996). However, the problems with chemical controls are that they are too costly to be used in most areas of the landscape and not sufficiently specific for environmentally sensitive areas. Additionally, chemical treatments generally must be used several times a year to maintain acceptable levels of control (Collins et al., 1992).

Possibilities for classical or self-sustaining biological control have been considered intermittently since the late 1950s (Allen and Silveira-Guido, 1974; Anon., 1965; Hays, 1958; Williams and Whitcomb, 1974). Over the

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[*] Corresponding author. Fax: 1-352-374-5818.
E-mail address: sdp@nersp.nerdc.ufl.edu (S.D. Porter).

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years, dozens of natural enemies have been reported in South America compared to only a few in the United States (Jouvenaz, 1983; Jouvenaz et al., 1977). Interest in these natural enemies waned because none of them seemed likely to kill large numbers of fire ant colonies. However, interest in self-sustaining biological control agents was rekindled in the early 1990s when researchers discovered that fire ant populations in the United States are 5–7 times higher than they are in their South American homelands (Porter et al., 1992, 1997b). A careful evaluation of many possible factors left escape from natural enemies as the most likely explanation for intercontinental population differences (Porter et al., 1997b). Researchers began to realize that fire ant biocontrol is more like weed biocontrol than biocontrol of crop pests in that fire ant enemies do not need to kill a colony directly to reduce fire ant populations (Feener and Brown, 1992). Enemies like pathogens and parasites simply need to stress fire ant colonies sufficiently so that the ecological balance is shifted in favor of native ants (Porter, 1998a). If this happens, fire ant colonies would be out-competed and population densities of this pest in the United States would drop to levels more like those normally found in South America where fire ants are not considered a major pest.

For most of the last decade, decapitating flies in the genus *Pseudacteon* have been the subject of intensive research efforts of scientists at our USDA-ARS laboratory in Gainesville, Florida (Porter, 1998a), and by colleagues at the University of Texas at Austin (Gilbert and Patrock, 2002) and cooperators in South America. Previous researchers reported that *Pseudacteon* flies were attracted to *Solenopsis* fire ants and appeared to oviposit on or in them (Borgmeier, 1921; Williams and Whitcomb, 1974). Subsequent research discovered the immature stages of *Pseudacteon* flies (Porter et al., 1995b) and a suite of specific behaviors that fire ants use to defend against attacks of these flies (Feener and Brown, 1992; Orr et al., 1995; Porter et al., 1995c). These defenses could only have evolved and been maintained if decapitating flies were having population level impacts on fire ant colonies or their production of sexual reproductives.

Of almost 20 possible species (Porter and Pesquero, 2001), we selected *Pseudacteon tricuspis* Borgmeier for release because studies showed that this fly was very host-specific (Gilbert and Morrison, 1997; Porter, 1998b; Porter and Alonso, 1999; Porter et al., 1995a) and because it was the first species to be successfully reared in the laboratory (Porter et al., 1997a). This species was also selected because it was one of 2–3 very common species in the regions around the cities of Jaguariúna and Rio Claro in the state of São Paulo, Brazil (Porter, 1998a) where the senior author did most of his field work (1994–1997).

Pseudacteon tricuspis was first released in the United States in Texas (Gilbert, 1996) beginning in 1995. Unfortunately, these initial attempts failed, probably because low numbers of flies were involved and because weather conditions were hot and dry. The first successful release occurred in North Florida in the late summer of 1997 (Porter et al., 1999). Additional releases have also been made with the assistance of cooperators in Arkansas (1998), Texas (1998–present), Alabama (1998–2001), South Carolina (1999–2001), Louisiana (1999–2001), Mississippi (2000), Oklahoma (1999–2000), Tennessee (1999), North Carolina (2000), and Georgia (2000). The fate of these releases will be discussed in subsequent papers. The objective of this paper is to document the release, establishment, and dispersal of the decapitating fly, *P. tricuspis* around Gainesville, Florida. We will also use data from this study to estimate the number of releases needed for these flies to occupy a state in a specified period of time.

2. Materials and methods

2.1. Flies released

The *P. tricuspis* flies released in this study originated from flies collected at the Laboratório de Quarentena "Costa Lima," Embrapa Meio Ambiente, Jaguariúna, State of São Paulo, Brazil during late May and early June 1996. Flies were collected while attacking *S. invicta* and *Solenopsis saevissima* F. Smith fire ants. These flies were the Brazilian form of *P. tricuspis* as illustrated by Porter and Pesquero (2001, Fig. 19a). They are very small flies, 1.0–1.8 mm in length—about the size of the fire ant heads from which they emerge. They were exported from Brazil under permits from the Ministerio Tecnologico, the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA), and the Ministério da Agricultura, Pecuária e Abastecimento (MAPA). They were imported into quarantine facilities in Gainesville, FL under a permit from USDA-APHIS with notification of the USFWS. We applied for field release after conducting an extensive evaluation of host specificity (Gilbert and Morrison, 1997; Porter, 1998b; Porter and Alonso, 1999; Porter et al., 1995a), writing an environmental assessment, and obtaining a USDA-ARS Finding of No Significant Impact (FONSI) on nontarget organisms. The flies were released under a permit from the Florida Department of Agriculture and with the acquiescence of USDA-APHIS. Voucher specimens of the flies were deposited in the Florida State Collection of Arthropods (FSCA), Gainesville, FL.

2.2. Release methods

Depending on the release site (Table 1), flies were either introduced into the field as adult flies or as immatures in parasitized fire ant workers. Release methods varied over time.

Table 1
Summary of field releases of the fire ant decapitating fly *P. tricuspis* around Gainesville, FL (1997–1999)

Site (#Releases)	Release period	Flies used	Mounds used (Gyny[a])	Method	Result
Kanapaha (5)	9–29 July and 16 September 1997	900	14 (poly)	Adult flies and parasitized ants	Failed
Dairy Farm (5)	1–15 September 1997	1200	19 (both)	Both, as above	Failed
Hogtown Cr. (8)	10 September–20 October 1997	1800	24 (mono)	Both, as above	Successful
CMAVE (many)	July 1997–October 1999	>6000	A few (poly)	Adult flies	Successful?
Morrill Farm (11)	29 April–3 June 1998	1600	45 (mono)	Parasitized ants	Failed?
Morrill Farm (11)	28 August–18 September 1998	1500	25 (mono)	Adult flies	Successful
Airport (9)	22 September–8 October 1998	1800	17 (mono)	Adult flies	Successful
Norfleet Farm (5)	26 October–7 December 1998	1100	16 (mono)	Adult flies	Successful
Sanders Farm (10)	25 October–9 November 1999	2800	46 (mono)	Adult flies	Successful

[a] Social form of fire ant colonies present: single-queen (monogyne) or multiple-queen (polygyne).

Initially, we simply released adult flies near disturbed fire ant mounds. Eventually, we developed a protocol where 25–40 adult flies were allowed to fly out of a wide-mouthed container to a newly disturbed fire ant mound 20–30 cm away. In order to keep ants active on the surface and available for fly attacks, fire ant mounds were disturbed every 3–10 min for up to 2 h. Progressive efforts at colony disturbance usually resulted in leveling the earthen mounds that fire ants build and we often dug 10–15 cm below the surface. When weather conditions were hot and dry, shading the mounds with several styrofoam plates on wire flags helped keep the ants active as did sprinkling several liters of water over the mound an hour or so before the release. We also found that macerating several pinches of ants between our fingers just prior to releasing the flies helped stimulate attacks (Vander Meer and Porter, 2001).

At several sites, we released immature flies in parasitized workers. This was done by shoveling dirt with 5–15 g of ants and brood from a mound into a bucket. These workers were then separated from the soil in the laboratory by drip flotation (Banks et al., 1981). Workers were separated from brood using sorting sheets and sieved (Porter and Tschinkel, 1985) to remove excess large and small workers not normally parasitized by *P. tricuspis* (Morrison et al., 1999b). We used workers that passed through a #16 sieve (US Standard), but were retained by a #20 sieve. Groups of 0.8 g of sieved ants (400–500 individuals) from a single colony together with 1 g of brood were placed in attack trays in the lab where flies were allowed to parasitize the ants for 2 days. These ants were returned to their mother colonies 3–4 days after they were collected.

2.3. Release sites

Locations of release sites are indicated in Fig. 3. Dates and methods of releasing flies are summarized in Table 1. The first field release of *P. tricuspis* in Florida was conducted at Kanapaha Botanical Gardens (Fig. 3, site A) in July 1997 (Table 1). Approximately 50 participants at a media event were each allowed to release 4–5 flies in the air or near a fire ant mound. On subsequent days, we released about 450 additional flies near disturbed mounds. Ants from several colonies were also brought into the lab where ovipositing flies were allowed to attack them for several days before they were returned to their mother colony. All told, about 700 flies were released at this site in July and another 200 in mid September. The second series of releases was conducted at the Hague Dairy Farm (B). Half of the mounds used were monogyne colonies around the edge of a small pond and the other half were polygyne colonies about 200 m away along a pasture edge. Several hundred flies were also released over field colonies. The third site was in a power line right-of-way next to Hogtown Creek (C). This site was a low wet triangle of about 0.3 ha bordered by trees on two sides and by a road embankment on the third. We released about 800 adult flies at this site over mounds and another 1000 flies were used to parasitize workers brought into the lab. The fourth release area was around our USDA laboratory on the University of Florida campus (D). This was an informal release site. A few adult flies were released over disturbed mounds, but most (>5000) were simply released out the back door of the lab when we had too many flies to use in our rearing operations (July 1997–October 1999). The fifth release site was on the Morrill Farm (E) near LaCrosse. This site was a 16-ha cow pasture. The pasture contained a mixture of trees, bushes, and several ponds. Releases at this site were conducted in the spring of 1998 and then again in the late summer. The sixth site was just north of the Gainesville Regional Airport (F). It was a narrow site along a 200-m strip of abandoned paved road. Either side of the road was closely bordered by a swampy forest. The seventh site was on the Norfleet Farm (G) near Newberry. This site was in an old abandoned phosphate pit, part of which was used to graze cattle and the other part had a mixture of trees and bushes. The final site was at Sanders Farm (H). This site consisted of a 4-ha pasture bordered by trees and several houses.

2.4. Monitoring fly establishment and dispersal

The presence of *Pseudacteon* flies in the field was determined by punching depressions (∼15–20 cm diameter) in fire ant mounds with a hand or a small shovel. Flies were detected by closely inspecting areas around disturbed ants for hovering flies (Fig. 1). Flies were easily aspirated with an Allen-type double chamber aspirator and checked with a hand lens if there was any doubt about their identity. A single person usually monitored 8–10 mounds, visiting each mound every 5–10 min over a period of up to 30 min. After each observation, the ants were stirred up to keep them active. Several pinches of ants in each mound were usually macerated between the fingers to release pheromones that attract the flies. Monitoring for flies was generally done between 11:30 am and 4:30 pm on days with air temperatures greater than 20 °C when adult flies are active (unpublished data and Morrison et al., 1999a). Sun shades (Fig. 1) were placed over mounds on hot sunny days so that the ants could remain active on the surface during the monitoring period.

Pseudacteon tricuspis flies prefer medium to medium-large fire ants (Morrison et al., 1999b), but polygyne or multiple-queen fire ant colonies have substantially fewer large workers than monogyne colonies (Greenberg et al., 1985). In order to determine if flies were less abundant in areas with polygyne fire ants, we scored observation sites as polygyne (P), mostly polygyne (P/M), monogyne (M), or mostly monogyne (M/P) based primarily on the size and color of workers in fire ant mounds inspected for flies.

Fig. 1. Lloyd Davis searching for *Pseudacteon* flies hovering over a fire ant mound. Note that part of the mound is shaded by a styrofoam plate on a wire flag and that flies are being collected with a double-chamber Allen-type aspirator.

3. Results

Even after more than 60 years without *Pseudacteon* parasitoids, the imported fire ants around Gainesville still recognized these flies as enemies. Colonies under attack by several flies often showed greatly reduced activity. This behavior was often the first clue that flies were present. Workers in colonies under heavy attack also froze motionless in tight clusters just like fire ants in South America do.

3.1. Fate of releases

Results of our fly releases are summarized in Table 1. The first release at Kanapaha Gardens was apparently not successful as no field-reared flies were recovered during repeated observations over the next 9 months. We were more successful with the second release at the Dairy Farm where we found some field-reared flies, about 24 total, 50–60 days after the first release, but none thereafter.

Field-reared flies were collected from the Hogtown Creek site 44 days after the initial release (Table 1). Flies were recovered every month from this site for the next year (Fig. 2). During a 3-month drought in the spring of 1998, fly numbers were very low, but numbers increased beginning late May and June when the summer rains began. Thereafter, fly numbers gradually increased until the fall of 2001 when they jumped from several dozen per 10 mounds to over a hundred.

We did not monitor for establishment around the CMAVE laboratory until the middle of May and early June 1999. At that time a few flies were found at several locations around the laboratory. No additional flies were found on three sample dates from July through

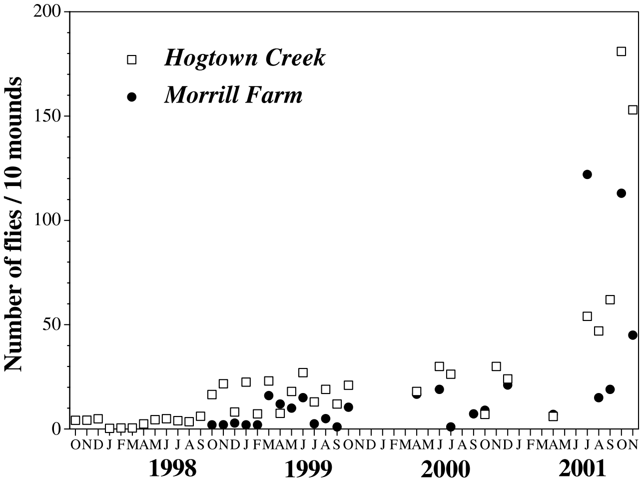

Fig. 2. Fly abundance at the Hogtown Creek and Morrill Farm release sites plotted against time. Points plotted from October 1997 to October 1999 are monthly averages of 1–4 sample dates. More recent points were not averaged.

September. However, in the middle of November, we began finding flies at CMAVE and surrounding sites. The pattern of distribution at that time indicated that releases from our laboratory were likely successful; however, we still could not exclude the possibility that these flies came from the Hogtown Creek site 5–8 km to the west.

The first releases at Morrill Farm appeared to fail or, at best, do very poorly (Table 1). We recovered only three flies near the end of June 1998 and one the middle of July, but no flies were found in August. The apparent failure of this effort caused us to switch back from releasing parasitized ants to releasing adult flies over disturbed mounds. However, it is just as likely that severe drought conditions from April through the end of June and frequent maximum temperatures in excess of 35 °C were responsible for the dearth of flies. The second release effort at Morrill Farm was much more successful. A single fly was recovered in the middle of October 1998 and thereafter flies were found almost every sample period for the next year (Fig. 2). As with Hogtown Creek, fly numbers gradually increased until the fall of 2001 when numbers jumped from several dozen flies per sample to over a hundred.

The Airport release site was also successful. A field-reared fly was found on 1 November 1998, 40 days after the first flies were released. Flies were recovered from this site every month for the next year, after which regular monitoring was discontinued.

Flies from the Norfleet Farm release were recovered on six occasions from February to October 1999. No flies were found on eight occasions during the same period including a 3-month dearth from late April to late July. However, 14 flies were found on 6 of 10 mounds in October 1999, a year after they were released.

Large numbers of flies were found at Sanders Farm in early January and again in late February 2000 indicating that the release was likely successful. However, by late spring 2000, the advancing wave fronts of flies from Hogtown Creek and Morrill Farm had probably reached this site.

After the first or second year, fly populations at the six release sites (Fig. 2) were as high or higher than those normally seen by the authors in Brazil or Argentina.

3.2. Dispersal

We checked for dispersal of flies out of the Hogtown Creek site in May 1998 (four sites) and October 1998 (one site) and found no flies along roads 0.1–1.4 km away even though flies were active and common at the release site. In June 1999, we found several flies at a site about 5 km southwest of the Hogtown Creek site, but again no flies where found at mounds a few hundred yards away from the site at Hogtown Creek. Flies were also found at Morrill Farm in June 1999. We found them at 11 of 13 sites up to 0.5 km away, but not at four sites beyond this.

In November and December 1999, we found flies had expanded out 3–4 km from our release site at Morrill Farm, 1–2 km out from our release site at the airport, and 1 km out from the release site at Norfleet Farm

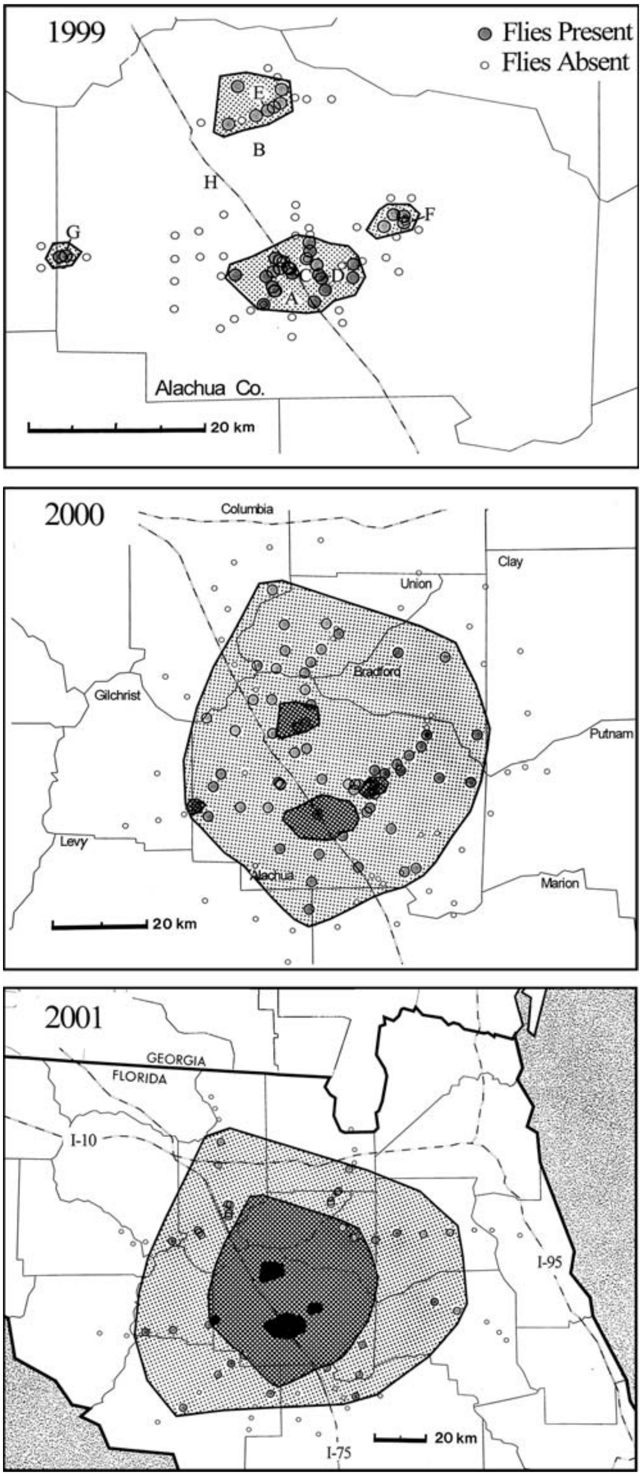

Fig. 3. Dispersal of the decapitating fly *P. tricuspis* (1999–2001) from release sites in Alachua County, FL. (A) Kanapaha Gardens, (B) Dairy Farm, (C) Hogtown Creek, (D) CMAVE, (E) Morrill Farm, (F) Airport, (G) Norfleet Farm, and (H) Sanders Farm.

(Fig. 3). We found flies 6, 3.5, and 2 km to the south, west, and north of the Hogtown Creek release site, respectively. We found flies 4, 4.2, and 3.5 km to the north, east and south of our laboratory. Flies were also found at four sites between the Hogtown Creek site and our laboratory. This pattern (Fig. 3) suggests that flies from both sites (3.5 km apart) had fused to form a large ellipse; however, as mentioned previously, it is possible that the flies came from the Hogtown Creek site. Within the areas enclosing positive sites, 86% of sites (32/37) contained flies; outside these areas we had 31 negative sites. Taken together the flies occupied about 125 km^2.

By the fall of 2000, flies had expanded out an average of an additional 19 km (range 16–29) (Fig. 3) and the four distributions from the previous year had all fused. Flies appeared to expand out of all but perhaps the Norfleet site. Dispersal out of the Norfleet site is uncertain because no westward movement was detected and movement in other directions would have been confounded with dispersal out of the other sites. Within the area enclosing positive sites, 80% of sites (63/79) contained flies; outside this area we found 32 negative sites. The flies had expanded to occupy 3300 km^2 by the fall of 2000. The number of flies found at sample sites decreased as the distance from release sites increased (Fig. 4).

The rate of outward dispersal increased again during 2001; the flies expanded outward an average of an additional 23 km (range 10–30) so that they occupied over 8100 km^2. The dispersal rate to the south was less than that to the north, east and west. Within the area enclosing positive sites, 86% of sites (36/42) contained flies; while outside these areas we had 25 negative sites.

The average air temperature during our samples was 27 ± 3°C (±SD) and the average relative humidity was 48 ± 13%. The average time until we found the first fly was 13 ± 8 min. About half of our sample sites with flies appeared to have polygyne (P) or mostly polygyne (P/M) fire ants and half had monogyne (M) or mostly monogyne (M/P) fire ants, but there was no significant difference in the number of flies observed among these sites (ANOVA, $P = 0.397$). We found the native fire ant *Solenopsis geminata* (Fabricius) at six sites where we found *P. tricuspis* attacking imported fire ants, but, as predicted (Porter and Alonso, 1999), none of the introduced flies were seen attacking the native fire ants.

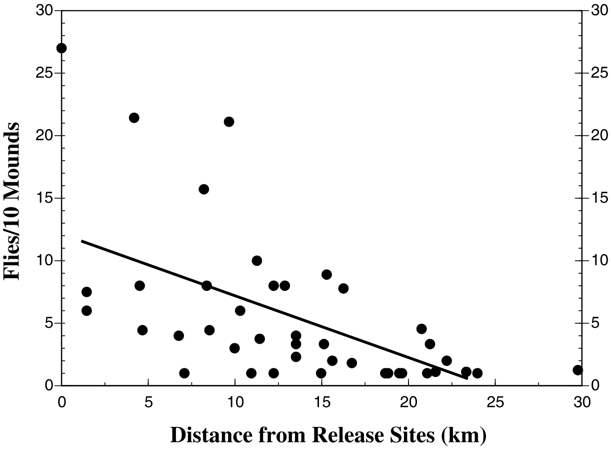

Fig. 4. Fly abundance as a function of distance from nearest release site, fall 2000. A linear regression is plotted ($y = 12.3 - 0.507x$, $R^2 = 0.329$, $P < 0.01$) because polynomial regressions were not significantly better (>0.05).

4. Discussion

4.1. Establishment

This paper documents the first successful release and establishment of a classical biological control agent against a pest ant. In fact, it is the first classical biocontrol agent released against any social insect pest that has established and then expanded rapidly across the landscape. Researchers in New Zealand were able to successfully introduce an ichneumonid parasitoid against introduced *Vespula* wasps, but after about 15 years this biocontrol agent is still restricted to several isolated release sites where it is expanding slowly (Barlow et al., 1998). Unfortunately, there has never been a case where a social insect pest has been successfully controlled with a self-sustaining biocontrol agent. This lack of success is partly due to lack of effort. With the exception of wasps in New Zealand and fire ants in the United States, very few attempts have been made to manage social insect pests with classical or self-sustaining biological control agents (Orr et al., 2001). This lack of effort is probably due to ignorance about natural enemies of social insect pests, the complexity of social insect biology, and limited funding for research that is not likely to produce economic profits. Nevertheless, the potential value of using classical biocontrol agents against social insects is clearly demonstrated by the impacts of tracheal mites and several kinds of diseases on honey bee populations (Morse and Nowogrodzki, 1990).

4.2. Dispersal

Dispersal out of our release sites accelerated over time (Fig. 3) so that by the third year flies were expanding out at a rate of about 23 km/year. Assuming 6–8 generations of flies per year (SDP—unpublished data), this means that the best dispersers in each generation of flies are traveling 3–4 km. Most flies probably do not disperse more than several hundred meters (Morrison et al., 1999a) in their short 1–3 day life spans (Porter, 1998a), but at least a few female flies are evidently able to travel much further. The increasing rates of dispersal may be due to rare dispersal events becoming more common with increasing numbers of flies or it is possible that rapidly dispersing flies are being selected for because they are able colonize new habitat more frequently.

The fact that 80–85% of sample sites within the wave front were positive demonstrated that the expanding wave front of flies occupied a high percentage of available sites. It also suggests that we were usually successful in finding flies when they were present; in other words, the frequency of false negatives was probably relatively low.

Decapitating flies were as common at polygyne sites as at monogyne sites. Perhaps the higher densities of fire ant workers normally found in polygyne areas (2–3 times, Macom and Porter, 1996; Porter, 1992) counterbalanced the lower frequencies of larger workers (Greenberg et al., 1985) that this fly needs to produce females (Morrison et al., 1999b). However, it is possible that more accurate assessments of average worker sizes at observation sites and actual censuses of established fly populations over longer periods of time would result in a negative correlation between these variables.

The relatively uniform dispersal patterns of *P. tricuspis* (Fig. 3) do not correlate well with the strongly bidirectional wind pattern in the Gainesville area during hours of fly activity (Fig. 5). Basically, the flies do not appear primarily to disperse either by drifting with the wind or by flying up wind tracking fire ant scents. Perhaps this is because they fly close to the ground where the wind is greatly reduced. Morrison et al. (2000) found no correlation between wind and the activity of native *Pseudacteon* flies in Texas although flies did arrive a few minutes sooner when winds were above 1.9 m/s at one of two sites. Slow dispersal to the south in 2001 may be due to the high prevalence of polygyne fire ant colonies in this region (Porter, 1992); however, as mentioned above, we did not detect lower populations of flies at sites with polygyne fire ants. Slow dispersal to the south could also be a quirk of the habitat or the sampling effort because this effect was not seen the year before.

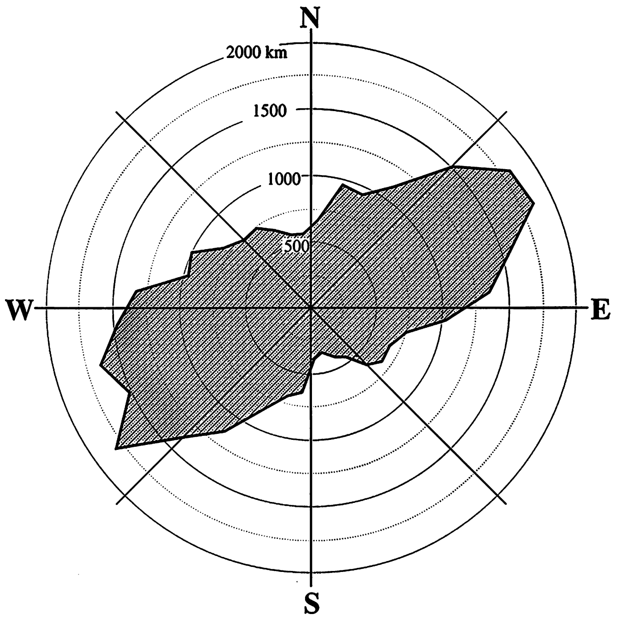

Fig. 5. Mean annual wind drift pattern at Gainesville Regional Airport (1999–2001) during hours of fly activity (800–1800 h, air temperature ≥ 21 °C; data were calculated by multiplying mean wind speed for each of 36 compass directions by the total number of hours that wind blew toward each direction). We used hourly data retrieved from NOAA's National Climatic Data Center (Edited Local Climatological Data text file: http://lwf.ncdc.noaa.gov; search for Gainesville, FL).

In the only other study of dispersal in *Pseudacteon*, Morrison et al. (1999a) found that native *Pseudacteon* species in Texas dispersed up to 650 m away from their nearest host *S. geminata* colony. Little is known of dispersal in other families of Phoridae (Disney, 1994) other than that they are often components of the aerial plankton caught in nets or on ships thousands of kilometers from land (Bowden and Johnson, 1976; Yoshimoto et al., 1962). The Phoridae are a very diverse family, however, and they are likely to be characterized by much variation in dispersal strategies and ability.

The dispersal ability of established *P. tricuspis* flies (23 km/year) is in the high range of rates reported for small parasitoids. Goldson et al. (1999) cited dispersal rates of 1–2 km/year for several hymenopteran parasitoids, 6 km/year for another, and tens of kilometers per year for yet another. Munro (1998) reported 13–24 km/year for an ichneumonid wasp parasitoid and 8–15 km/year for a tachinid fly parasitoid. Frank et al. (1996) reported a dispersal rate of 64 km/year for a large tachinid parasitoid of mole crickets. In contrast to the rates above, dispersal rates of some biocontrol agents released against exotic plants can be only a few hundred meters per year or less (Center et al., 2000; McClay and De Clerck-Floate, 1999) as can at least one parasitoid (Goldson et al., 1999).

4.3. Predicting dispersal rates

Determining dispersal rates from releases of *P. tricuspis* is important because it allows us to predict how many releases would be necessary to cover a given region in a specified amount of time. It also allows us to choose release sites that are spaced at sufficient intervals to fill a region with as few releases as possible. As described, dispersal rates varied among sites. During the first year, the Hogtown site showed no indication of dispersal even a few dozen meters away from the release site. Similarly, flies at the Norfleet site were only found 1 km from the release area. In contrast, flies were found 2 km out after a year at the Airport site and 4 km out after only about a year at the Morrill Farm site. Taken together we feel that 1.5 km would be a conservative estimate for dispersal at the end of the first year. In the second year, the Norfleet site did not expand, but the Hogtown site expanded out an additional 16 km. The Morrill Farm and Airport sites expanded out an additional 26 and 23 km, respectively. Consequently, we feel that 15 km would be a slightly conservative estimate for the added expansion in the second year. By the third year, all the sites had fused. A conservative estimate for the average expansion rate in the third year would be 20 km.

Assuming dispersal rates in future years are similar to the third year, we can predict how many successful releases it will take to fill the state of Florida in a given period of time (Fig. 6). One successful release per year for 3 years (3 total) would cover the state in just under 9 years. Two successful releases per year for 3 years (6 total) would cover Florida in about 7 years. Finally, four successful releases per year for each of three years (12 total) would fill Florida in just over 5 years. In other words, doubling the release effort from 2 to 4 per year only shortened the coverage time by 1.5 years (22%). These estimates, of course, do not take in to account the geographic shape of Florida. A few extra releases or another year or two would probably be needed to distribute the flies throughout the panhandle and out across the Keys. On the other hand, the third year of releases could probably be dropped with the 4/year scenario because they would account for less than 12% of the area covered after 5 years.

Additional releases would also need to be made to replace those that failed. We had a 66% success rate (Table 1), although it appeared to improve with later releases. All things considered, a state the size of Florida could probably be covered with flies in 6–9 years with 5–10 releases. Considering all southeastern states together and adding in a cushion for failed releases, we estimate that 90–140 releases would be necessary to complete the task in 6–9 years (provided cooler temperatures in more northern regions do not result in slower dispersal rates). Additional releases may also be needed for the Caribbean and perhaps California and Brisbane, Australia if eradication attempts in these two areas are not successful. We assume that similar release efforts would also be necessary for each additional species or biotype of fly imported.

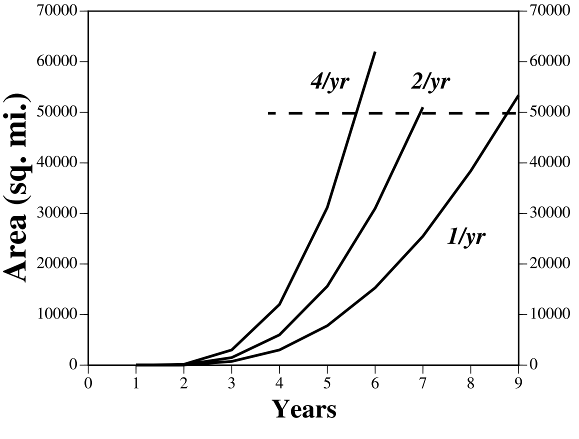

Fig. 6. Projections of dispersal scenarios from multiple releases of *P. tricuspis* flies. The graph assumes 1, 2, or 4 successful releases for each of 3 years and dispersal rates of 1.5 km the first year, 15 km the second year, and 20 km each year thereafter. The heavy dashed line indicates the total land area of Florida. For comparison, the approximate areas (km^2) occupied by fire ants in other southeastern states are as follows: Texas—400,000, Oklahoma—25,000, Arkansas—60,000, Louisiana—110,000, Mississippi—120,000, Alabama—130,000, Tennessee—20,000, Georgia—150,000, South Carolina—110,000, and North Carolina—35,000.

4.4. Future impacts on fire ant populations

Pseudacteon decapitating flies clearly impact fire ant populations because that is the only way fire ants could have evolved and continue to maintain specific defensive behaviors against this group of flies (Porter, 1998a). While the magnitude of this impact is still unknown, the impact of a single species of decapitating fly is likely to be small or moderate. Several additional species of flies and other natural enemies will almost certainly be necessary to obtain maximum impacts (Porter, 2000). It is clear from our data that fly populations require several years to reach maximum levels (Figs. 2 and 4). Additionally, if the flies are capable of tilting the ecological balance in favor of the native ants, then native ants are likely to need another year or two for their populations to build up in competition with the imported fire ants. In order to quantify the impacts of this fly, we have set up approximately 80 monitoring plots at increasing distances from the release sites. Fire ant populations at these plots are being estimated twice a year by mound counts, baits and pitfall traps. Flies moved into the first set of plots between spring and fall 2000. Over the next several years, we will monitor the impact of *P. tricuspis* on fire ant populations in these plots. The ultimate results of our release effort are still unknown, but it seems clear that self-sustaining biocontrol agents like *P. tricuspis* are the only hope we have for permanent control of imported fire ants in the rural landscape.

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