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Population spread of the introduced red imported fire ant parasitoid, *Pseudacteon tricuspis* Borgmeier (Diptera: Phoridae), in Louisiana

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Abstract

Predicting the spread of introduced species, such as natural enemies used in classical biological control programs, requires quantitative data on the rates of spread. Here, the pattern of spread of *Pseudacteon tricuspis* Borgmeier (Diptera: Phoridae), a parasitoid of the red imported fire ant (*Solenopsis invicta* Buren; Hymenoptera: Formicidae), was monitored at two widely separated release sites in Louisiana, USA. At both sites, *P. tricuspis* range expansion (measured as the mean radius of the range from four cardinal directions) was accelerating during the first four years post-release. This pattern contrasts with a linear pattern expected with simple diffusion. This suggests that population spread involved both a neighborhood diffusion and long-distance dispersal component. This is known as stratified or jump dispersal. Annual rates of spread were low in the first two years post-release (possibly owing to an Allee effect), increased rapidly in years 3–4, and slowed down or leveled off by years 5–6. Annual spread rates reached a peak of 15–25 km/yr, with the northward spread being about 40% greater than the spread in the other cardinal directions. High rates of spread in the latter years and directional bias in the spread of *P. tricuspis* may have been driven by prevailing winds and two northward-moving hurricanes. Spread of introduced species offers insight into factors affecting spread that is more difficult to evaluate for native species.
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1. Introduction

Classical biological control involving the introduction of natural enemies to suppress exotic pest species has been ongoing for more than a century (see Huffaker and Messenger, 1976; Coulson et al., 2000). Success of the biological control agent depends in part on its ability to establish, spread and eventually occupy the range of its host. For example, successful biological control of the chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae), in Japan was achieved by the introduction and rapid spread (approximately 60 km/yr) of the introduced parasitoid, *Torymus sinensis* Kamijo (Hymenoptera: Torymidae) (Moriya et al., 2002). Early models of the spread of animal and plant populations were based on the process of diffusion and predicted a simple linear rate of spread (Fisher, 1937; Skellam, 1951; reviewed by Hengeveld, 1989; Andow et al., 1990; Okubo and Levin, 2002; Hastings et al., 2005). However, empirical patterns of spread for many species are nonlinear, likely attributable to appreciable rates of long-distance dispersal (e.g., Hengeveld, 1989; Andow et al., 1993; Shigesada et al., 1995; Johnson et al., 2006; Muirhead et al., 2006). In these species, nascent populations appear well beyond the edge of an expanding range in what is known as stratified or "jump" dispersal (Hengeveld, 1989).

For many species, human transport processes, such as the movement of the Argentine ant (*Linepithema humile* (Mayr) by cars and trucks (Suarez et al., 2001), or the zebra mussel (*Dreissena polymorpha* (Pallas)) by boats (Buchan and Padilla, 1999) are thought responsible for jump dispersal. Ignoring this component of dispersal can lead to significant underestimates of range expansion of invasive

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pests and natural enemies introduced for their biological control.

The red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), is a ubiquitous and economically important pest in the southeastern United States (Lofgren, 1986). Much has been published about the introduction, spread, biology, economic and environmental impacts, and control of *S. invicta* in the United States (see Vinson, 1997; Tschinkel, 2006). Early efforts to eradicate *S. invicta* with chemical control were met with limited success (Taber, 2000; Tschinkel, 2006). Recently, more attention has focused on the potential for biological control of *S. invicta* by importing several specialist parasitoids in the genus *Pseudacteon* Coquillet (Diptera: Phoridae) from the indigenous range of *S. invicta* in South America.

Pseudacteon tricuspis Borgmeier was the first phorid fly species introduced to the United States for biological control of *S. invicta*. It was initially released in Texas in 1995 (Gilbert, 1996) and Florida in 1997 (Porter et al., 1999). In cooperation with the USDA-ARS, the first releases of *P. tricuspis* in Louisiana took place in September 1999 and May 2000. *Pseudacteon tricuspis* successfully established at each release site (Henne and Johnson, unpublished data).

Available information on dispersal and spread of *Pseudacteon* flies is limited to three studies. Using traps baited with *S. geminata* (Fabricius) workers, Morrison et al. (1999a) found that *Pseudacteon* parasitoids in Texas dispersed up to 650 m from the nearest *S. geminata* population. Porter et al. (2004) monitored the spread of *P. tricuspis* from multiple release sites in north-central Florida and found that the average rate of spread was 10–30 km/yr. With an additional two years of data, Pereira and Porter (2006) revised these latter estimates to 26–57 km/yr. These studies did not evaluate whether *Pseudacteon* spread fit the theoretical expectations of neighborhood diffusion or that of stratified dispersal (see Shigesada et al., 1995; Hastings et al., 2005). Data of this sort are useful in understanding animal movement behavior and is necessary to develop predictive models of species spread (Turchin, 1998). The aim of this paper is to describe and model the spread of two established *P. tricuspis* populations in Louisiana.

2. Materials and methods

2.1. Biology of Pseudacteon parasitoids

Parasitic flies of the genus *Pseudacteon* contribute to maintaining lower abundances of *S. invicta* in South America (Porter et al., 1992), and thus may be useful in the suppression of *S. invicta* populations in the United States. Although there are native species of *Pseudacteon* that attack native North American fire ants (*S. geminata* and *S. xyloni* McCook), they have never been observed to attack *S. invicta*. By reuniting *S. invicta* with several species of its native *Pseudacteon* parasitoids, it is hoped that the ant communities in the United States that are currently dominated by *S. invicta* may shift in favor of native ant species (Porter, 1998).

Phorid parasitoids locate their hosts by detecting ant semiochemicals (Porter, 1998; Morrison and King, 2004). For example, *P. tricuspis* is attracted to alarm pheromones emitted by *S. invicta* during mound disturbances, alate flights, and intra- and interspecific fighting (Williams et al., 1973; Pesquero et al., 1993; Morrison and King, 2004), and primarily attacks major workers (Morrison et al., 1999b). Female *Pseudacteon* inject a single egg into the host ants' thorax, the larva consumes the head contents and eventually pupariates inside the empty decapitated head capsule (Porter et al., 1995).

A considerable body of evidence suggests that parasitic phorid flies mediate competitive interactions between various ant species (e.g., Feener, 1981; Feener and Brown, 1992; Folgarait and Gilbert, 1999; Morrison, 1999, 2000; Orr et al., 1995, 2003). *Solenopsis* spp. workers will reduce or terminate foraging activity in response to attacks by *Pseudacteon* flies (Feener and Brown, 1992; Orr et al., 1995; Morrison, 1999). Mehdiabadi and Gilbert (2002) found that a single attacking *P. tricuspis* female per 200 foraging *S. invicta* workers decreased colony protein consumption almost twofold and significantly reduced numbers of large-sized workers 50 days later. These studies demonstrate the potential for *Pseudacteon* parasitoids to reduce *S. invicta* populations (but see Tschinkel, 2006).

2.2. Release sites

Initial *P. tricuspis* releases in Louisiana were conducted at the following locations: (1) 17 km northeast of Covington (St. Tammany Parish) (30° 36′ 35″N; 90° 01′ 19″W), 8–13 September 1999 (2165 flies released); (2) 9 km east of Norwood (East Feliciana Parish) (30° 59′ 05″N; 91° 00′ 46″W), 27 April-8 May 2000 (4714 flies released). These release sites were unmaintained pastures located approximately 100 km apart and had abundant *S. invicta* populations. Adult *P. tricuspis* were released at disturbed *S. invicta* mounds over a 6–12 day period, and approximately 400 flies were released daily at ten disturbed *S. invicta* mounds. Mounds were continuously disturbed for 2 h to maintain *S. invicta* activity and availability to oviposition by *P. tricuspis* (Porter et al., 2004).

2.3. Evaluating population expansion

Post-release surveys to determine the annual spread limits of *P. tricuspis* were conducted during the fall of each year (September to November) when abundances were highest (Henne and Johnson, unpublished data). Fly surveys were normally conducted between 1100 and 1700 h when ambient temperatures were warm enough for fly activity (>20 °C) (Morrison et al., 1999a). We monitored the spread of *P. tricuspis* along transects in four cardinal directions (i.e., north, south, east, and west) from the release point. Every year, we started our survey along each

transect, approximately 3 km outward from the previous year's range limit. Within a 100 m radius of that point, we located 10 *S. invicta* mounds in disturbed habitat (e.g., roadsides, pastures). Two of us (D.H. and S.J.) would vigorously disturb the mounds with spades (5–10 s) and count the number of *P. tricuspis* adults that arrived during the ensuing of 30 min. Normally, flies would appear within a few minutes of mound disturbance. The sampling location was also recorded with a Magellan™ GPS 315/320 (accurate to within 25 m) for later plotting on a computer mapping program (Maptech® Terrain Navigator Pro) or Google™ Earth.

If no flies were detected at the disturbed mounds within 30 min, we moved approximately 1 km (the exact distance depended on the presence of suitable *S. invicta* habitat) toward the release area. If flies were present, the researchers moved 1–2 km further away from the release area. The survey was continued in each direction until the limits of spread were established to within 1 km of their approximate locations. Annual surveys were conducted from 1999 (approx. 40 days post-release) to 2005 for the Covington release and from 2001–2006 for the Norwood release (approx. one year post-release).

2.4. Modeling *P. tricuspis* range expansion

2.4.1. Average radius of spread

The mean radius from a point of introduction is the simplest measure of a species' range and provides an estimate of the expansion rate when it is obtained at known time intervals (Hengeveld, 1989). The change in spread radius with time is expected to take on one of three forms: linear (constant rate of spread as predicted by early diffusion-based models), accelerating (rate of spread continually increases over time), or biphasic (initially slow rate of expansion followed by an abrupt transition to an accelerating expansion rate) (Shigesada et al., 1995; Turchin, 1998). The mean ± SE annual spread radius (based on four transects) for each expanding *P. tricuspis* population in Louisiana was computed. Linear (null model) and quadratic polynomials were fitted to the mean annual spread radius of both populations and compared using the extra sum-of-squares *F*-test in Prism® 4.03 (GraphPad Software, Inc., San Diego, CA). The linear and quadratic terms were deemed significant if the associated *p*-values were $\leqslant 0.05$.

2.4.2. Annual spread rates

Simple models of diffusion predict the spread rate of *P. tricuspis* to be constant over time (Shigesada et al., 1995; Turchin, 1998). If this is not the case, we can identify time periods for which the rate of spread is low (e.g., if an Allee effect is operating during the early stages of range expansion), or accelerating. Because both populations exhibited consistent directional bias in expansion rates (see Section 3), separate curves were generated for each transect. To more clearly depict the latent, accelerating and plateau phases of expansion over time, we plotted the relationship between annual spread rate (spread radius in year t minus the spread radius in year $t-1$) and year since release. A logistic model was fit to the Covington 2000–2005 north and west annual spread rates, and to the 2000–2004 south and east spread rates using Prism® 4.03. Because the Norwood population did not exhibit any measurable spread in the first two years (zero individuals in 2001 and two individuals among 74 mounds in 2002), there were too few data points to fit the logistic model to its annual spread rates. The logistic model used was a dose–response model, equivalent to a three-parameter logistic model (Motulsky and Christopoulos, 2003) and had the analytic form: $y = \text{Bottom} + [(\text{Top} - \text{Bottom})/1 + 10^{\text{LogEC}_{50-x}}]$. The parameters, bottom (constrained > 0) is the y-value at the bottom plateau, top is the y-value at the top plateau, and LogEC_{50} is the x-value halfway between bottom and top.

2.4.3. Decline of *P. tricuspis* abundances away from release points

One expectation of simple spatial spread models is that the density of the organism should decay at an approximately exponential rate with distance from the release point (Turchin, 1998; Okubo and Levin, 2002). When abundances are ln-transformed, the relationship is expected to be linear. Data from *P. tricuspis* transect surveys were transformed [$\ln(n+1)$], where n is the total number of flies observed at 10 *S. invicta* mounds. Linear regression was performed using Prism® 4.03.

3. Results

3.1. *Pseudacteon tricuspis* range expansion

Both the Covington and Norwood *P. tricuspis* releases resulted in expanding populations (Table 1). By the fall of 2005, the leading edges of the westward expanding Covington and eastward expanding Norwood populations were approximately 8 km apart. Based on expansion rates at that time (see below), these populations were projected to merge in 2006. Thus, the Covington survey was terminated after the 2005 survey. The Norwood population was surveyed through 2006, but the presumed merger prevented us from determining its eastern expansion limit.

For both populations, the average annual radius of spread increased nonlinearly with year since release (Fig. 1). Adding a quadratic term to the linear models significantly improved the fit [Covington $df = 1,3$ ($F = 164$, $p = 0.001$) $y = 3x^2 - 12000x + 1.2e^{0.007}$ ($R^2 = 1.0$, $n = 6$); Norwood $df = 1,3$ ($F = 85$, $p = 0.003$), $y = 4.2x^2 - 17000x + 1.7e^{0.007}$ ($R^2 = 0.99$, $n = 6$)]. In both populations, range expansion was biased to the north of each release site (Table 1). In Covington, northward expansion as of 2004 was 10.5 km (or 41%) farther than the mean expansion for the other three directions. In Norwood, the difference as of 2006 was 23.5 km (or 40%).

The rate of spread of *P. tricuspis* varied tremendously among years between the Covington and Norwood releases

Table 1
Pseudacteon tricuspis cumulative spread radius (km), annual spread distance (radius at year *t* minus radius at $t-1$; in parentheses), and estimated area occupied (km^2) for different transects and years at the Covington and Norwood releases

Release location	Year	North	South	East	West	Mean radii ± SE	Area occupied (km^2)[a]
Covington	1999	0.1	0.1	0.1	0.1	0.1 ± 0.0	0.03
	2000	0.8 (0.8)	0.4 (0.4)	0.4 (0.4)	0.4 (0.4)	0.5 ± 0.1	0.8
	2001	1.6 (0.8)	0.8 (0.4)	1.6 (1.2)	0.8 (0.4)	1.2 ± 0.2	4.5
	2002	3.3 (1.7)	1.6 (0.8)	4.4 (2.8)	1.6 (0.8)	2.7 ± 0.7	22.9
	2003	12.4 (9.1)	11.6 (10)	14.2 (9.8)	8.6 (7)	11.7 ± 1.2	430.0
	2004	36.5 (24.1)	24.5 (13.1)	27.2 (13)	26.1 (17.5)	28.6 ± 2.7	2569.7
	2005	59.8 (23.3)	[b]	[c]	47.1 (21)	50.7 ± 3.0	8075.4
	2006	—	—	—	—	74.3 ± 5.9[f]	17,343.1
	2007	—	—	—	—	102.1 ± 9.2[f]	32,749.2
Norwood	2000[d]	0.1	0.1	0.1	0.1	0.1 ± 0.0	0.03
	2001	0.1	0.1	0.1	0.1	0.1 ± 0.0	0.03
	2002	0.1	0.1	0.1	0.1	0.1 ± 0.0	0.03
	2003	9.3	1.6	3.2	1.6	4.1 ± 1.95	52.8
	2004	19.4 (10.1)	10 (8.4)	9.1 (5.9)	8.8 (7.2)	11.8 ± 2.5	437.4
	2005	40.7 (21.3)	27.4 (17.4)	34.5 (25.4)	36 (27.2)	34.7 ± 2.8	3782.8
	2006	82.2 (41.5)	55.2 (27.8)	[e]	62.2 (26.2)	68.2 ± 9.7	14,612.3
	2007	—	—	—	—	99.3 ± 12.9[f]	30,977.6
	2008	—	—	—	—	140.3 ± 20.6[f]	61,839.4

[a] Based on the area of a circle (πr^2).
[b] Southward expansion reached Lake Pontchartrain in 2004.
[c] Eastward expansion merged with Mississippi *P. tricuspis* in 2005.
[d] 2000–2002 Norwood radii based on 1999 Covington radii.
[e] Eastward expansion merged with Covington *P. tricuspis* in 2006.
[f] Predicted radii computed from quadratic models (see text).

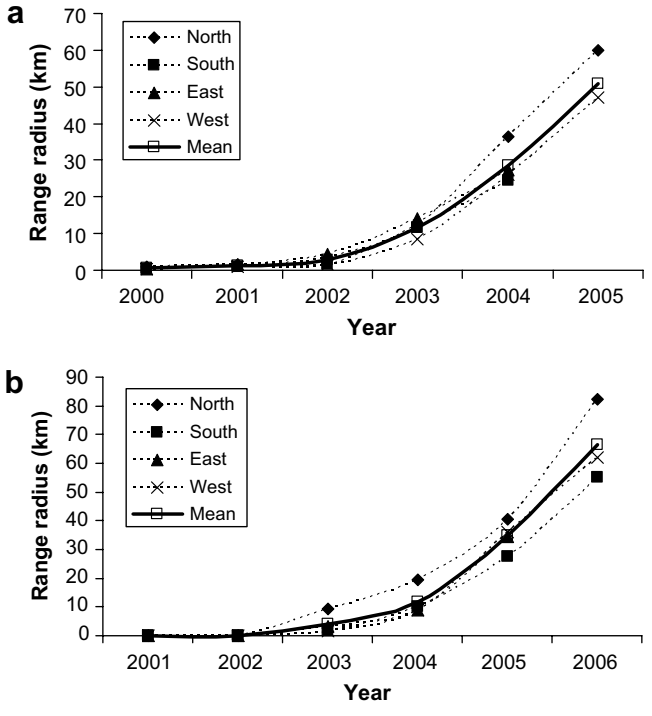

Fig. 1. (a) The change in *Pseudacteon tricuspis* range radius (km) over time in four cardinal directions (and mean of all directions) for two release sites: Covington (a) and Norwood (b), Louisiana. Curves are derived from polynomial least-squares regression (see Section 3).

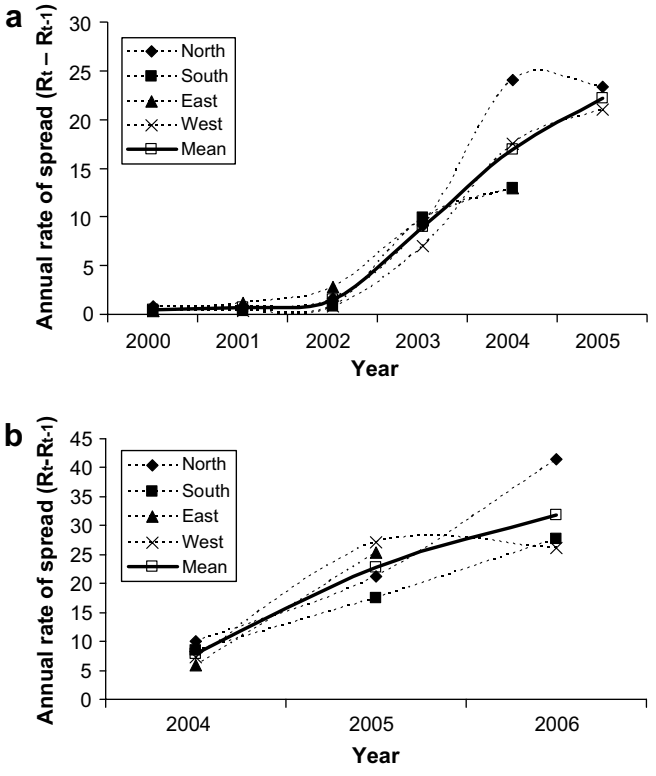

Fig. 2. Annual directional rate of spread (km/year = radius at $time_t$ − radius at $time_{t-1}$) for *P. tricuspis* at the Covington (a) and Norwood (b) release sites. A logistic growth curve (see Section 2) is fit to each individual transect and the mean of all four transects.

(Fig. 2). The annual rate of spread at the Covington site was sigmoidal over time – the spread rate was very low

in the first two years following the release, then it increased rapidly during years 3–4, and finally appeared to slow down or level off at a mean maximal rate of spread of 23 km/yr (Table 1 and Fig. 2a). Although, we do not have sufficient data from the Norwood release (Table 1 and Fig. 2b) to compare range expansion in the first couple of years to that from subsequent years, we do observe a steady increase in the rate of spread from years 3–5. The rates of spread during this time period are very comparable to those for the Covington release, differing only by an average of 2.6 km (or 15%). A paired *t*-test (using Prism® 4.03) comparing years 3–5 spread rates between both populations was nonsignificant [$df = 2$, $t = 1.39$, $p = 0.3$].

The logistic models provided a very good fit to the latent, accelerating and plateau phases of the Covington spread rate data: north $y = 0.4528 + [(25.25 - 0.4528)/1 + 10^{\log 4.199 - x}]$ ($R^2 = 0.99$), south $y = 1.0\ e^{-0.007} + [(14.2 - 1.0\ e^{-0.007})/1 + 10^{\log 3.740 - x}]$ ($R^2 = 0.98$), east $y = 0.5659 + [(13.6 - 0.5659)/1 + 10^{\log 3.636 - x}]$ ($R^2 = 0.99$), west $y = 0.2096 + [(21.43 - 0.2096)/1 + 10^{\log 4.336 - x}]$ ($R^2 = 0.99$). Covington asymptotic spread rates are projected by the logistic models to be approximately 25 km/yr (north), 14 km/yr (south and east), and 21 km/yr year (west). The Norwood western spread distance in 2006 was similar to the 2005 spread distance (26 km vs. 27 km).

3.2. Decline of *P. tricuspis* abundances away from release points

For both point-in-time surveys of the abundances of *P. tricuspis* at the edge of the Norwood range, we found that ln fly abundances declined linearly with increasing distance from the release point, [2005 east transect $df = 1,3$ ($F = 133.5$) ($R^2 = 0.98$, $n = 5$) $p < 0.01$; 2006 south transect $df = 1,3$ ($F = 37.59$) ($R^2 = 0.93$, $n = 5$) $p < 0.01$; Fig. 3].

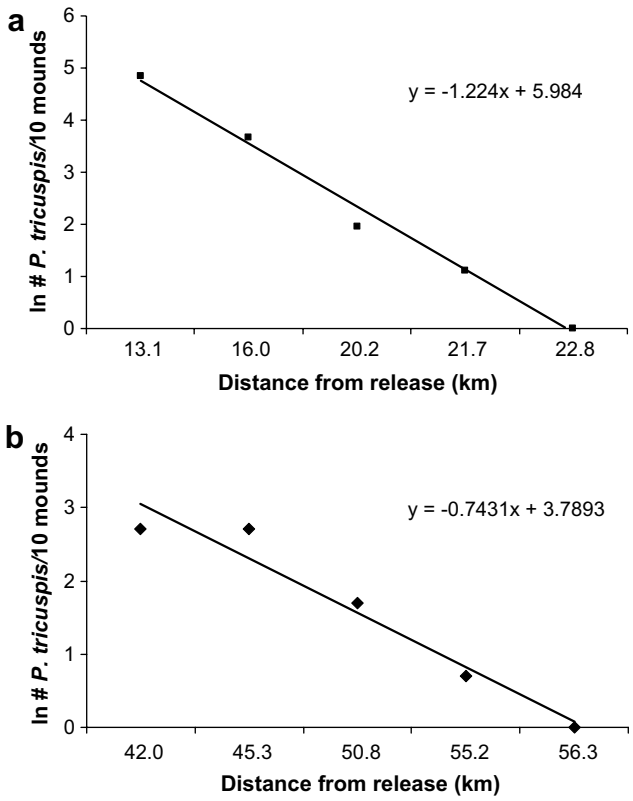

Fig. 3. ln number of *P. tricuspis*/10 mounds at different distances from the release point at Norwood. (a) East transect, 10 October 2005, (b) South transect, 11 October 2006.

4. Discussion

Range expansion by *P. tricuspis* was not linear as predicted by classical models of diffusive spread. Instead, the rate of spread accelerated during the first five years post-release and appeared to slow down or level off in subsequent years (at least for the Covington site). For both Covington and Norwood, populations were spreading at a rate of approximately 15–25 km/yr by the end of the study. The accelerating phase of range expansion is similar to the type 3, bi-phasic curve described by Shigesada et al. (1995). It is also suggestive of stratified dispersal in *P. tricuspis*.

Rapid expansion rates, such as those observed in the third through fourth years following the release of *P. tricuspis* in Covington and Norwood, can occur when a few mated female parasitoids disperse very far in relation to the typical neighborhood movements of most individuals (Hastings, 2000). Jump dispersal can result from intrinsic dispersal heterogeneities within a population, owing to differences in body size, wing morphology and movement behavior (Cronin et al., 2000; Yamamura, 2002). It can also result from human-assisted transport of a small subset of the population (e.g., Buchan and Padilla, 1999; Suarez et al., 2001). Presently, we do not have any information on whether *P. tricuspis* exhibits intrinsic differences in dispersal ability or if humans might assist in their spread.

At low initial population densities, the few long-distance dispersers would have little impact on the velocity of the advancing neighborhood diffusion wave (Hengeveld, 1989). However, as densities increase, the number of long-distance dispersers will increase and may become a dominant component of the advancing wave (Hengeveld, 1989). Eventually, even with stratified dispersal, spread rates should reach an asymptote as densities equilibrate; after which time the mean radius of spread (or square root of area occupied) versus time function would become linear (see Hengeveld, 1989; Moriya et al., 2002; Yamamura, 2002).

Many organisms introduced to a new environment undergo an initial period of little or no expansion, called a 'latent phase' (Turchin, 1998). This is an important first step in the eventual establishment and spread of introduced organisms. It is a time when the population presumably adapts to local conditions and increases its numbers (Turchin, 1998; Andow, 1999). This latent phase may be caused by an Allee effect, whereby introduced insects dispersing into a new environment may become so rare that

males and females often fail to encounter one another (Hopper and Roush, 1993). In their review of the literature, Hopper and Roush (1993) found that establishment success of introduced parasitoids depended on the release density and number of releases. This suggests that Allee effects may represent an important constraint on the success of biological control programs using parasitoids.

Introduced organisms may also have an 'eclipse' period in which abundances shortly after the release fall below a detection threshold, (Hopper and Roush, 1993). This can occur in situations when dispersal rates are high, thereby acting as a 'drain' on local populations at the release site (Kean and Barlow, 2000). Despite high *P. tricuspis* abundances (>5 flies/mound) at the Norwood release site during 2000, flies were not detected at the release site one year later, and only two flies were observed the second year after introduction, despite intensive sampling. By the third year post-release, *P. tricuspis* had already spread up to 10 km away from the release area. A combination of slower-than-expected local increase at the release site (i.e., during the eclipse period), followed by rapidly increasing rates of spread beginning in the third year (Fig. 2), may have been responsible for the sudden appearance of *P. tricuspis* so far from the release site (Kean and Barlow, 2000). Clearly, the negligible population abundances at the Norwood release site 1–2 years post-release were not a reliable indication of the true status of this population. In future releases, more intensive and wider-ranging surveys should be conducted initially when population densities are low.

Porter et al. (2004) documented *P. tricuspis* expansion rates that were comparable to the rates we found in the Louisiana releases—10–30 km/yr in central Florida versus 15–25 km/yr in Louisiana. The Florida releases also appeared to exhibit accelerating spread rates, although Porter et al. (2004) did not attempt to quantify this pattern. Expansion rates in Florida appeared to have accelerated more quickly than in Louisiana, reaching approximately 23 km/yr only three years post-release. Porter et al. (2004) also found that *P. tricuspis* abundances decreased with increasing distances away from release points, and Morrison et al. (1999a) documented declining abundances of *Pseudacteon* parasitoids of *S. geminata* at increasing distances from host colonies in Texas. A species' population density tends to be highest near the center and gradually declines towards the margin of its geographical range (Guo et al., 2005). This can be attributed to an area-dilution effect (Turchin, 1998). As distance from the release point increases, the numbers of organisms reaching that distance are spread over a progressively larger area. The log-linear declines of *P. tricuspis* abundances with increasing distance away from the source population suggest a probability distribution function (kernel) with a long tail of *P. tricuspis* dispersers (i.e., exponential decline in abundance). Similar declines in abundances along other transects near the range edges were observed in both Louisiana populations (Henne and Johnson, unpublished data).

Another similarity between our Louisiana releases and the Florida releases (Pereira and Porter, 2006) is that there is a northward bias in *P. tricuspis* spread. Areas near coastal Louisiana are subjected to afternoon sea breezes that blow north from the Gulf of Mexico and occur almost daily during the warm season (Smith and Fuelberg, 2005). Morrison et al. (1999a) suggested that most *Pseudacteon* remain close to the ground during high winds, but also that passive transport by wind may be an important factor in long-distance dispersal. In support of this claim, *P. tricuspis* have successfully dispersed across the Mississippi river (>1 km) and beyond dense forest stands (e.g., Bogue Chitto National Wildlife Refuge) that were at least 5 km wide and at least 20 km deep (as measured in Google™ Earth).

Microinsects routinely form concentrated well-defined plumes in thermal currents of rising air (Geerts and Miao, 2005) suggesting that long-distance dispersal via winds may be important in the spatial spread of these species. The detection of *P. tricuspis* nearly 42 km further north of the Norwood release site in the 2006 as compared to the 2005 survey was considerably farther than any previous recorded spread distance for this species, including the Florida releases reported in Porter et al. (2004). An explanation for this may have been the influence of two hurricanes (Katrina and Rita) that made landfall in Louisiana in 2005. High winds associated with these large-scale synoptic events as they approached and moved northward through Louisiana (http://www.nhc.noaa.gov/2005atlan.shtml) would have transported dispersing *P. tricuspis* adults farther away than normal. In Florida, four hurricanes with a generally northward trajectory in 2004 (Charley, Frances, Ivan, and Jeanne) (http://www.nhc.noaa.gov/2004atlan.shtml) may explain the enhanced *P. tricuspis* spread rates reported by Pereira and Porter (2006) in Florida. Several studies have shown that tropical cyclones account for long-distance transport of many insects (e.g., Larsen and Pedgley, 1985; Torres, 1988; Richardson and Nemeth, 1991; Clarke and Zalucki, 2004). Thus, model-based predictions of future expansion distances may be prone to considerable directional bias. Regardless of how directional bias occurs, *P. tricuspis* populations do spread considerable distances on an annual basis, a feature that will contribute to its ability to quickly occupy the range of *S. invicta* (see also Porter et al., 2004; Pereira and Porter, 2006).

Nearly 20 species of *Pseudacteon* are known to attack *S. invicta* in South America (Porter and Pesquero, 2001), and at least three species of *Pseudacteon* have already been imported and released in the United States: *P. tricuspis* (Graham et al., 2001; Porter et al., 2004), *P. curvatus* Borgmeier (Graham et al., 2003), and *P. litoralis* Borgmeier (Porter and Alonso, 1999). *Pseudacteon borgmeieri* Schmitz (Folgarait et al., 2002a) and *P. cultellatus* Borgmeier (Folgarait et al., 2002b) are currently under evaluation for possible release in the United States in the next few years. This study provides valuable information about *P. tricuspis* population spread that can be used in predicting spread

rates and distances (with directional bias) for this and other *Pseudacteon* species. The fact that *P. tricuspis* spread patterns and rates are so similar in Louisiana and Florida suggests that our predictions would be robust for releases of this species throughout the southeastern United States.

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