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Short-distance dispersal behavior and establishment of the parasitoid *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae) in Tahiti: Implications for its use as a biological control agent against *Homalodisca vitripennis* (Hemiptera: Cicadellidae)

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Abstract

The egg parasitoid *Gonatocerus ashmeadi* Girault (Hymenoptera: Mymaridae), was introduced into French Polynesia as a biological control agent to control the invasive plant feeding pest *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae). The short-distance dispersal of *G. ashmeadi* was monitored as part of the biological control program. *G. ashmeadi* showed exponential dispersal capacity with 47 m/day being a minimum estimate of its natural rate of spread at high host densities (>150 nymphs per minute of sweep net sampling) in urbanized areas at sea level, which were characterized by a high diversity of exotic ornamental plants. This rate of spread contrasted starkly with almost nonexistent establishment and dispersal where host densities were very low (<2 nymphs per minute of sweep net sampling) at high elevation (800 m) with relatively undisturbed native vegetation. Survey results across different altitudes revealed an effect of vegetative diversity and host density on the measurable mobility and establishment of *G. ashmeadi*. In contrast, no significant influence of wind direction was found on *G. ashmeadi* dispersal rate or direction. Survey results for *G. ashmeadi* from French Polynesia suggest that the best release establishment strategies for classical biological control of *H. vitripennis* are: (1) many small releases where host density is high, or (2) larger and fewer releases where host densities are low.

Keywords: *Gonatocerus ashmeadi*; *Homalodisca vitripennis*; Classical biological control; Dispersal rate

1. Introduction

The glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) [formerly *Homalodisca coagulata* (Say) (Takiya et al., 2006)] (Hemiptera: Cicadellidae) is a serious plant pest in the South Pacific. This xylem feeding cicadellid is a major threat to agricultural, native and urban landscapes because of its ability to acquire and transmit a lethal xylem-dwelling plant pathogenic bacterium, *Xylella fastidiosa*. Native to the southeast USA and northeast Mexico (Triapitsyn and Phillips, 2000), *H. vitripennis* was inadvertently introduced into California in the late 1980's (Sorensen and Gill, 1996) and invaded French Polynesia in 1999 (Secretariat of the Pacific Community 2002), Hawaii in 2004 (Hoover, 2004), Easter Island in 2005 (Sandra Ide personal communication 2005), and the Cook Islands in 2007 (Maja Poeshco personal communication 2007). Grandgirard et al. (2006) documented the arrival of *H. vitripennis* on the island of Tahiti and the problems resulting from this biological invasion. Subsequently, this pest has spread to at least nine other islands in three archipelagoes within French Polynesia (see Petit et al., 2007).

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In May 2004, a classical biological control program against *H. vitripennis* was initiated in French Polynesia using the highly specific egg parasitoid *Gonatocerus ashmeadi* Girault (Hymenoptera: Mymaridae). This parasitoid is a solitary endoparasitoid attacking eggs of Proconiini sharpshooters (Cicadellidae: Cicadellinae: Proconiini) (Triapitsyn et al., 1998), the group to which *H. vitripennis* belongs. *G. ashmeadi* is a minute insect, <2 mm in length with an average longevity of <12 days (at 25 °C) and exhibits optimal reproduction between 20 and 30 °C (Pilkington and Hoddle, 2006). After risk assessment studies indicated an acceptably low level of risk by *G. ashmeadi* to native 'non-target' species in French Polynesia (Grandgirard et al., in press-a), 13,786 parasitoids were released at 27 sites on the island of Tahiti between May 2 and October 25, 2005. *G. ashmeadi* had an extremely rapid and catastrophic impact on high density *H. vitripennis* populations at release sites in Tahiti, reducing their numbers by >90% within seven months of release with parasitism levels averaging 80–100% (Grandgirard et al., in press-b).

The control of *H. vitripennis* was very efficient, in part, because of the extremely rapid widespread dispersal of *G. ashmeadi*. Dispersal abilities of natural enemies are considered important factors affecting establishment success and efficacy of biological control agents for pest suppression (Hopper and Roush, 1993; Saavedra et al., 1997; McDougall and Mills, 1997). Excellent dispersal capabilities are desirable for natural enemies because maximum reduction of pest densities is attained once control agents have infiltrated and colonized all suitable habitats harboring pest populations (Sallam et al., 2001).

Despite the assumed critical role of dispersal in biological control programs, there are few studies that have systematically examined rates of parasitoid dispersal and subsequent impact on target populations (Corbett and Rosenheim, 1996; Barlow et al., 1998; Munro, 1998; Goldson et al., 1999; Sallam et al., 2001; Wright et al., 2001; Langhof et al., 2005; Canto-Silva et al., 2006; Henne et al., 2007). Biotic and abiotic factors can strongly influence natural enemy dispersal and survivorship rates, as well as dispersal pathways. Wind and other climatic factors, for example, can influence the natural dispersal patterns of some biological control agents, particularly for small organisms such as parasitoids. Consequently, these factors may play an important role in the efficacy of biological control programs (Canto-Silva et al., 2006). Similarly, host plants and landscape characteristics can influence greatly the dispersal of parasitoids. Thies et al. (2003), showed that host plants and landscape diversity directly affect the strength of interactions between herbivores and their parasitoids. Parasitoid spread is also likely to be influenced by the abundance of hosts, which is in turn influenced by the abundance of resources utilized by potential hosts (Doak, 2000).

We hypothesized that the spread of *G. ashmeadi* on and across islands in French Polynesia would follow a stratified dispersal process. Stratified dispersal is a combination of: (1) a short-distance localized dispersal by the organism (<5 km), through natural progression (e.g., flying or walking for *G. ashmeadi*), and (2) rapid long-distance dispersal mediated by either abiotic factors (e.g., wind) or biotic factors (e.g., the unintentional transportation by humans of parasitized *H. vitripennis* egg masses on plants within and between islands) (Hengeveld, 1989).

The aim of the present study was to use survey data collected as part of the classical biological control program against *H. vitripennis* with *G. ashmeadi* to describe the short-distance dispersal of this parasitoid in French Polynesia (i.e., the first component of the stratified dispersal process), and in particular, to assess the potential influence of wind and host density on the dispersal capacities of this natural enemy. Understanding the factors influencing the natural short-distance dispersal of *G. ashmeadi* in French Polynesia will help to determine the optimal spatial arrangement for future releases of this parasitoid on other islands as part of the biological control campaign against *H. vitripennis* in the South Pacific.

2. Material and methods

Because *G. ashmeadi* did not previously occur in French Polynesia before its release as part of the classical biological control program against *H. vitripennis*, it was possible to follow directly the colonization behavior of this parasitoid by examining selected field sites over time for the presence of the parasitoid and the distribution and density of parasitized *H. vitripennis* eggs. Dispersal of *G. ashmeadi* was studied across three different habitats: at sea level, at low inland elevations, and at high elevations.

2.1. Release of G. ashmeadi in Tahiti

Detailed release methods for *G. ashmeadi* are described in Grandgirard et al. (in press-a, in press-b). Briefly, *G. ashmeadi* was imported from the University of California at Riverside (USA) in September 2004, and reared in quarantine at the French Polynesia Agricultural Research Facility in Papara on the island of Tahiti. *G. ashmeadi* was released at two monitoring sites on the north of the island of Tahiti: (1) at sea level in Papenoo (S17°30′25″ W149°27′30″), and (2) at 800 m in Pirae (S17°34′21″ W149°31′26″) (Fig. 1). From May 2, 2005 to June 30, 2005, ~820 parasitoids released each week for a total of 6,574 *G. ashmeadi* released in Papenoo. From June 7, 2005 to October 25, 2005, 1652 parasitoids were released in Pirae. Initially, ~275 parasitoids were released every two weeks June 7 to July 25 and then on a month basis after July 25, 2005. Because of the difficult access to this site, parasitoids were not released weekly in Pirae. Further, parasitoids were not released at both sites during the same period, because of limitations in mass rearing, and parasitoid releases were a priority at sea level because the need for classical biological control of *H. vitripennis* was highest in these urban areas. Numbers of parasitoids released were dependant on the success of

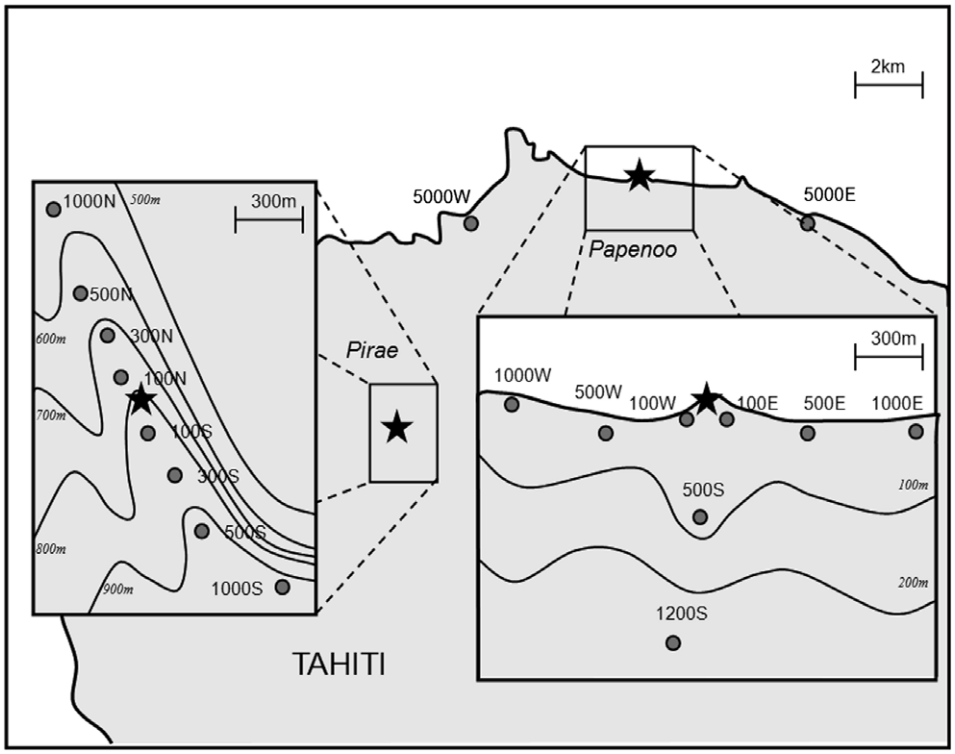

Fig. 1. Release sites in Tahiti at sea level in Papenoo and at 800 m elevation in Pirae (black stars) and short-distance dispersal monitoring sites (dark grey circles).

mass rearing at any given time. Consequently, parasitoid releases were maintained for five months in Pirae (vs. 2 months in Papenoo) because measurable parasitism rates were almost zero during the first two months of surveys at this site. Subsequent releases were made on the rest of Tahiti in August and September 2005 as part of the classical biological control program. The Pirae release site was >15 km from the monitoring sites being studied at sea level and did not affect the results of this study.

2.2. Measuring natural dispersal of G. ashmeadi at sea level

Short-distance dispersal of *G. ashmeadi* was studied at both of the initial release sites (Papenoo and Pirae) on Tahiti. The site at sea level (Papenoo) was characterized by: (1) an extremely high host density, with an average of 156 *H. vitripennis* nymphs collected on *Hibiscus rosa-sinensis* (Malvaceae) hedges in one minute of sampling effort (Petit et al., 2007). *H. vitripennis* density was monitored on *H. rosa-sinensis* because this plant is widespread and is a highly preferred host for the pest. However, high density*H. vitripennis* populations were found on almost every species of exotic tree and shrub at sea level in Tahiti. Sea level sites were disturbed habitats composed almost exclusively of exotic ornamental vegetation (mostly grasses, *H. rosa-sinensis*, *Cordyline* sp. and *Polyscias* sp. edges, *Tiare tahiti* and *Scaevola* sp. shrubs, *Plumeria* sp. and *Cocos nucifera* trees), with a mean annual temperature averaging 27 °C (Grandgirard et al., in press-b) and a predominant easterly wind (Laurent et al., 2004). Site topography was characterized by flat terrain approximately 100–200 m in width that lay between the ocean and steeply rising interior mountains (Fig. 1).

Parasitoid dispersal from the Papenoo release site was studied along the coast 5000 m westward and 5000 m eastward of the release site using two methods. First, the presence and absence of *G. ashmeadi* was monitored every second week from 16 days to 113 days after the initial parasitoid release on May 2, 2005. At approximately 200–500 m intervals along the 5 km transect, *H. rosa-sinensis* hedges were sampled for a one minute interval by sweep netting with an insect sweep net (38 cm diameter). The presence or absence of *G. ashmeadi* at was recorded after site sampling was completed. At each sampling date, the maximum distance colonized by *G. ashmeadi* westward and eastward (furthest individuals dispersed) was noted. The rate of dispersal was estimated by comparing the date of release with the date of recovery at different locations. To test the effect of wind on dispersal pattern, the colonization pattern westward (upwind) and eastward (downwind) were compared with Logistic Regression of dispersal distance over time and the Wald Test was used to determine statistical significance at the 0.05 level (SAS, 1990).

Second, naturally occurring *H. vitripennis* eggs masses were collected every second week at sampling sites at various distances from the release site (100, 500, 1000, and 5000 m) in both the easterly and westerly directions (Fig. 1). At least 10 *H. vitripennis* egg masses were collected

at each site from mixed plant species (several host plant species were inspected in order to collect the desired minimum number of egg masses). Old enclosed egg masses collected were checked for parasitism (i.e., circular emergence holes), and fresh unenclosed egg masses were held in labeled individual Petri dishes in the laboratory at 25 °C for parasitoid or *H. vitripennis* emergence. The presence or absence of parasitoid activity and percentage parasitism of collected egg masses was calculated from survey data. The *H. vitripennis* egg mass survey had the additional advantage of being used to confirm parasitoid dispersal rate estimates calculated from presence or absence data from sweep netting and by calculating parasitism rates, an indicator of subsequent reproductive and dispersal ability.

2.3. Measuring natural dispersal of G. ashmeadi at low inland elevations

Parasitoid dispersal from the Papenoo release site was also studied at inland survey sites. At the same time intervals as the sea level dispersal monitoring, *H. vitripennis* egg masses were collected at two inland sites that were not part of the linear coastal transect. The first inland site was 500 m south and inland from the Papenoo release site (65 m elevation) and the second was 1200 m south and inland from the Papenoo release site (245 m elevation) (Fig. 1). Both inland sites were non-urbanized and consisted mainly of unmanaged natural vegetation. These vegetation differences had a significant negative effect on *H. vitripennis* densities, with 1.7 nymphs on average collected per minute of sweep net sampling on *H. rosa-sinensis* at the first inland site and 1.9 at the second (Petit et al., 2007). These inland sites with significantly different vegetative characteristics and pest densities were used for comparison of *G. ashmeadi* data collected from the urbanized coastal areas where the linear transect measurements were conducted.

2.4. Measuring natural dispersal of G. ashmeadi at high inland elevations

The high elevation monitoring site at Pirae (800 m elevation, 10 km southwest from Papenoo release site, and six km south from coast) was characterized by: (1) a very low host density of *H. vitripennis*, with an average of 1.3 nymphs collected on native *Metrosideros colina* in one minute of sweep net sampling effort (Petit et al., 2007); (2) a habitat consisting almost exclusively of mixed native vegetation (i.e., ferns, *M. colina*, *Weinmannia parviflora*, *Dodonea* sp., and *Vaccinium cereum*); and (3) a mean annual temperature averaging 20.5 °C (Grandgirard et al., in press-b). Dispersal from the release site at high elevation was studied along a linear transect extending 1000 m north (and 210 m lower in elevation) to 1000 m south (and 117 m higher in elevation) from the release site (Fig. 1). The presence of *G. ashmeadi* was determined by sampling sites at set distances of 100, 300, 500, and 1000 m from the release point. A minimum of 10 *H. vitripennis* egg masses were collected every second week from 13 days to 125 days after release, at each of the four release sampling distances north and south of the release site. Egg masses harvested from mixed native plant species (mostly from ferns, *M. colina* and *W. parviflora*) were checked for parasitism as described previously.

3. Results

3.1. Short-distance dispersal of G. ashmeadi at sea level

At sea level, the presence/absence sampling methods showed progressive dispersal of *G. ashmeadi* from the release site at Papenoo. Parasitoids were found 100 m west 16 days after the initial release and at 200 m east 27 days after release. As adult *G. ashmeadi* only live for a maximum of ~12 days under the prevailing temperature conditions at sea level (Pilkington and Hoddle, 2006), these measurements suggested that the first generation of *G. ashmeadi* oviposited in the field was dispersing at 6.3 m/day westward and 7.4 m/day eastward. Continued monitoring indicated that parasitoid dispersal increased markedly with *G. ashmeadi* being found 4600 meters west of the release site 113 days post-release (equivalent to a dispersal rate of 40.7 m/day) and 5000 m east of the release site 106 days post-release (dispersal rate of 47.2 m/day). This increase in measured dispersal distance followed an exponential pattern on the west ($R^2 = 0.95$) and east sides ($R^2 = 0.94$) of the release point (Fig. 2). Statistical comparison of west and east dispersal curves demonstrated that exponential dispersal patterns eastward and westward were not significantly different (Wald test, $W = 0.129$, $p < 0.05$). The short-distance dispersal survey was discontinued 113 days post-release, because at this time, the colonization front was no longer clearly discernible as parasitoid colonies were being simultaneously discovered in numerous different sites on Tahiti (data not presented). Thus, a dispersal rate of 47.2 m/day could be considered the minimum natural dispersal rate for *G. ashmeadi* on Tahiti across low elevation coastal sites with high *H. vitripennis* populations.

The field collection of *H. vitripennis* eggs that were laboratory reared for evidence of parasitism showed a progressive dispersal pattern and rates of dispersal similar to that observed for adult *G. ashmeadi* (Table 1). However, a few irregularities in the dispersal pattern of *G. ashmeadi* were detected with this monitoring method suggesting some local-scale discontinuous dispersal: (1) 100 m east of the release site and 27 days post-release, no parasitized *H. vitripennis* eggs were collected whereas adult parasitoids were found 200 m east of the release site on the same sampling date. (2) Parasitized *H. vitripennis* eggs were collected 1000 m east of the release site and 100% parasitism was recorded, yet no parasitized egg masses were detected 500 m east of release site. These data suggest that the easterly dispersal rate of *G. ashmeadi* between 34 and 43 days after release increased from 5.6 to 20.1 m/day.

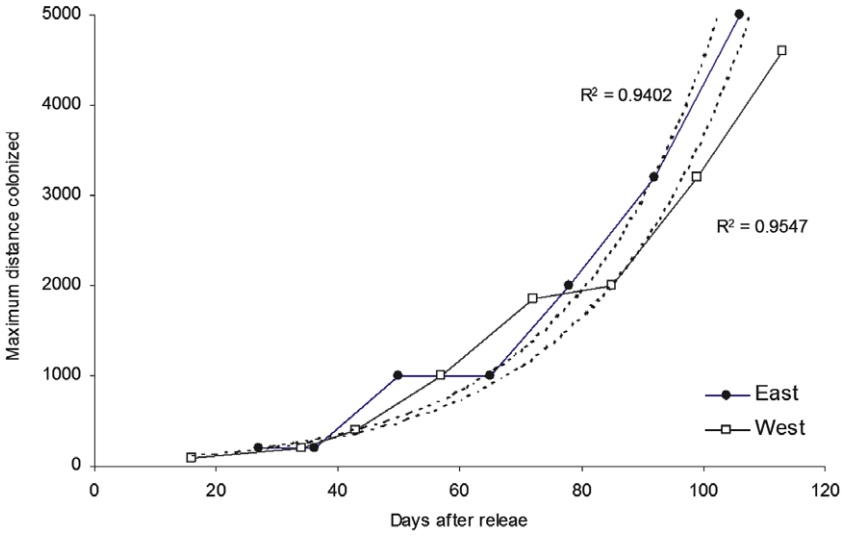

Fig. 2. Maximum distance colonized by *Gonatocerus ashmeadi* west and east from the release site in Papenoo Tahiti (high host density at sea level). Dotted lines are fitted exponential regression lines.

Table 1
Percentage parasitism of *Homalodisca vitripennis* eggs by *Gonatocerus ashmeadi* at set distances west and east from the parasitoid release site in Papenoo Tahiti (high host density, sea level), and the number of host egg masses collected for parasitism estimates are shown in parentheses

West					At site	East				
Days	5000 (m)	1000 (m)	500 (m)	100 (m)	0 (m)	100 (m)	500 (m)	1000 (m)	5000 (m)	Days
16	—	—	—	**31% (19)**	**87%**	0% (7)	—	—	—	27
34	—	—	0% (5)	50% (12)	61%	**78% (9)**	0% (6)	—	—	36
43	—	0% (8)	0% (7)	50% (10)	94%	55% (9)	0% (9)	**100% (7)**	—	50
57	—	**29% (7)**	**40% (10)**	80% (10)	95%	—	**40% (15)**	92% (14)	—	65
72	0% (5)	10% (10)	100% (11)	—	89%	100% (14)	100% (15)	92% (12)	0% (12)	78
85	0% (7)	75% (12)	93% (15)	100% (12)	94%	100% (5)	100% (10)	100% (9)	0% (10)	92
113	0% (5)	100% (4)	100% (4)	100% (4)	80%	—	100% (11)	100% (9)	**40% (5)**	106
141	**100% (7)**	67% (3)	100% (3)	83% (6)	94%	100% (10)	100% (6)	100% (7)	100% (4)	134

Bolded values are first appearance of parasitoid on each site, shaded portion is for parasitism rate >0.

3.2. Natural dispersal of G. ashmeadi at intermediate elevation sites

At both sites monitored inland from the release site at Papenoo, dispersal was substantially less than that observed along the coastal linear transect. At the 500 m site, the parasitism rate of *H. vitripennis* eggs was zero 92 days after release and reached 45% ($n = 11$ egg masses) 113 days after parasitoid release. At the 1200 m site, parasitism was 0% ($n = 12$ egg masses) 141 days after release, whereas *G. ashmeadi* was widespread along the Tahitian coastline at this time. *G. ashmeadi* appeared to have difficulty establishing in sites characterized by mixed native vegetation and low *H. vitripennis* densities.

3.3. Natural dispersal of G. ashmeadi at high elevation sites

Parasitism rates at the high elevation release site were very low after parasitoid releases (0–15%) and almost no dispersal was observed until 97 days post-release (Table 2). However, 300 m north from the release site, one parasitized egg mass was collected 13 days after the first release, suggesting an initial dispersal rate of 23 m per day. Parasitism subsequently declined at this site to zero and then increased to 100% 71 days post-release. Widespread parasitoid dispersal at the high elevation site began 97 days post-release. At this time, *G. ashmeadi* became widespread northward from the release site with parasitism rates reaching 37–100%. South of the release site, *G. ashmeadi* colonized two sites at 100 and 500 m with average parasitism reaching 66%. Finally, 125 days post-release, *G. ashmeadi* was widespread at every high elevation monitoring site, occurring 1000 m north and 1000 m south of the release site.

4. Discussion

Strong dispersal capabilities are considered essential attributes of a successful biological control agent (Sallam et al., 2001). Short-distance dispersal monitoring at sea level and high elevation sites have provided data on the natural dispersal capacities of*G. ashmeadi* and an estimation of the rate at which this natural enemy was able to dis-

Table 2
Percentage parasitism of *Homalodisca vitripennis* eggs by *Gonatocerus ashmeadi* at set distances north and south from the parasitoid release site in Pirae (low host density, 800 m elevation), and the number of host egg masses collected are shown in parentheses

Days	North (downhill)				At site	South (uphill)			
	1000 (m)	500 (m)	300 (m)	100 (m)	0 (m)	100 (m)	300 (m)	500 (m)	1000 (m)
13	—	0% (8)	**11% (9)**	0% (6)	**3%**	0% (11)	0% (11)	0% (3)	—
27	0% (8)	0% (5)	0% (10)	0% (9)	0%	0% (6)	0% (13)	0% (5)	0% (3)
43	0% (6)	0% (7)	0% (7)	0% (9)	15%	0% (8)	0% (2)	0% (3)	0% (16)
71	—	0% (3)	100% (2)	0% (2)	4%	0% (3)	0% (8)	—	—
97	**75% (4)**	**67% (6)**	100% (9)	**37% (8)**	87%	**66% (6)**	0% (2)	**66% (3)**	0% (5)
125	75% (8)	87% (8)	100% (8)	87% (8)	96%	70% (10)	—	91% (11)	**56% (16)**

Bolded values are first appearance of parasitoid on each site, shaded portion is for parasitism rate >0.

perse through markedly different habitat types. The rapid suppression of *H. vitripennis* by *G. ashmeadi* in French Polynesia (Grandgirard et al., in press-b), may have resulted, in part, because of the parasitoid's excellent dispersal capacity at sea level sites that resulted in rapid population build up. These large parasitoid populations at sea level subsequently emigrated in abundant numbers into habitats where previously modest establishment and impact due lower parasitoid densities had been observed.

4.1. Natural dispersal capacities of G. ashmeadi

At sea level, natural dispersal of *G. ashmeadi* followed an exponential pattern increasing from 6.3 (16 days after release) to 47.2 m/day (106 days after release). The natural dispersal rate may have continued to increase, but it was difficult to separate natural dispersal from the human-mediated dispersal that was likely occurring in Tahiti via the unintentional movement of plants bearing parasitized *H. vitripennis* egg masses. This exponential expansion pattern contrasts with linear dispersal patterns that have been observed for other parasitoid species (Corbett and Rosenheim, 1996; Barlow et al., 1998; Munro, 1998; Goldson et al., 1999; Wright et al., 2001; Canto-Silva et al., 2006). However, exponential dispersal of the ant parasitoid, *Pseudacteon tricuspis* Borgmeier (Diptera: Phoridae), has been observed (Henne et al., 2007).

On both the west and east sides of the release site at sea level, the dispersal of*G. ashmeadi* exhibited homogeneous expansion from the release site. Nevertheless, some discontinuous colonization patterns, notably at 200 m east and 1000 m east were observed. This finding indicated that parasitoid sub-populations were establishing away from the main population fringe, suggesting that parasitoids had dispersed over host patches and then were rapidly merging with the expanding leading edge of the source population. These jumping sub-population events created significant increases in dispersal rates (e.g., from 5.6 to 20 m/day at 1000 m east). Further, as the exponential growth in parasitoid abundance continued it likely multiplied the frequency of these jumping sub-populations. This observed jumping phenomenon could explain, in part, the exponential pattern of natural colonization by *G. ashmeadi* at sea level in Tahiti.

Mobility in terms of diffusion rate has been quantified for a small number of parasitoids. A review of the literature gives dispersal rates for parasitoids ranging from 2.7 to 65 m per day (Table 3). These estimates are not strictly comparable with data taken during this study, but if a dispersal estimate for *G. ashmeadi* of 47.2 m per day is used as a minimum estimate of natural mobility (i.e., no human assistance), then this parasitoid is among the faster dispersing parasitic Hymenoptera for which data on dispersal are available.

4.2. Factors influencing G. ashmeadi dispersal

Wind is recognized as being an important environmental factor affecting the aerial dispersal of organisms (McManus, 1988). As *G. ashmeadi* is a tiny insect, one would expect its flight capacity to be slight and its ability to fly against prevailing winds limited. Thus a pattern of downwind dispersal would be expected for this parasitoid (Messing and Rabasse, 1995). However, our study showed no evidence that prevailing wind direction influenced the dispersal pattern of *G. ashmeadi*. Work in California citrus orchards monitoring the flight activity of *G. ashmeadi* has shown that significantly more parasitoids are caught on sticky cards at ground level as opposed to one and two meters above the ground. This result suggests that *G. ashmeadi* may fly in a relatively calm boundary layer close the ground where flight is more easily controlled (Hoddle and Boyd unpublished data). Similar results suggesting that wind direction has no prevalent effect on flight direction have been observed for *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) (Saavedra et al., 1997) and *Trissolcus basalis* (Hymenoptera: Scelionidae) (Justo et al., 1997). While such results for *G. ashmeadi* in Tahiti do not definitively prove that wind played no role in dispersal, they suggest that it might not be an important factor for this parasitoid over relatively small spatial scales and short time periods.

Landscape characteristics and plant composition have a significant effect on parasitoid dispersal and efficacy (Thies et al., 2003). In this study, *G. ashmeadi*'s dispersal was faster in disturbed urbanized habitats characterized by high numbers of exotic plant species than in relatively undisturbed natural habitat with a relatively lower diversity of

Table 3
Estimated diffusion rates for selected hymenopterous parasitoids

Parasitoid	Dispersal rate	Method	Source
Microctonus hyperodae (Hymenoptera: Braconidae)	2.7 m/d	Parasitized hosts (3 years)	Goldson et al. (1999)
Shecophaga vesparum (Hymenoptera: Ichneumonidae)	2.7–4.1 m/d	Parasitized host (5 years)	Barlow et al. (1998)
Gryon gallardoi (Hymenoptera: Scellionidae)	7.6 m/d	Mark recapture (24 h)	Canto-Silva et al. (2006)
Aphidius colemani (Hymenoptera: Braconidae)	16 m/d	Parasitized hosts (5 days)	Langhof et al. (2005)
Cotesia flavipes (Hymenoptera: Braconidae)	21.3 m/d	Parasitized hosts (3 days)	Sallam et al. (2001)
Anagrus epos (Hymenoptera: Mymaridae)	24.5 m/d	Mark recapture (24 h)	Corbett and Rosenheim (1996)
Trichogramma ostriniae (Hymenoptera: Trichogrammatidae)	30 m/d	Parasitized hosts (180 days)	Wright et al. (2001)
Trigonospila brevifacies (Diptera: Tachinidae)	21.9–41 m/d	Parasitized hosts (8 years)	Munro (1998)
Gonatocerus ashmeadi (Hymenoptera: Mymaridae)	47 m/d	Parasitized hosts (113 days)	Present study
Xanthopimpla rhopaloceros (Hymenoptera: Ichneumonidae)	35–65 m/d	Parasitized hosts (8 years)	Munro (1998)
Pseudacteon tricuspis (Diptera: Phoridae)	41–68 m/d	Parasitized hosts (6 years)	Henne et al. (2007)

Gonatocerus ashmeadi shaded.

native species. This observation suggests that in French Polynesia *H. vitripennis* and *G. ashmeadi* spread readily in disturbed urban habitats with a high diversity of exotic plants.

Host density and distribution patterns could be additional factors affecting the movement of *G. ashmeadi*. Parasitoids are thought to use two major environmental stimuli in order to successfully locate and parasitize hosts. First, they use the resource (e.g., plant) of their host as a long range (e.g., volatile infochemicals) cue to locate potentially suitable habitats. Second, once they are in suitable habitat, they use short range cues (e.g., host excreta) to search for hosts (Dout, 1959). Low host densities or lack of suitable host plants could result in areas being devoid of natural enemies and thus cause barriers to continuous linear dispersal (Esch et al., 2005). Several studies have found a positive relationship between high host densities and high parasitoid dispersal rates (Stireman and Singer, 2003; Cronin and Haynes, 2003). The present study is consistent with the hypothesis that high host densities uniformly distributed in a suitable climatic environment facilitate rapid parasitoid reproduction and subsequent dispersal. The dispersal of *G. ashmeadi* at high host densities at sea level sites in Tahiti was extremely rapid, whereas at low host densities at high elevation sites parasitoid spread was extremely limited.

At the high elevation release site, the majority of monitoring sites were not colonized until 10 weeks after initial parasitoid releases. Released parasitoids may have been unable to persist in the high elevation release area because of the low densities of *H. vitripennis* eggs. Further, low temperatures at high elevation (mean daily temperature of 20.5 vs. 27 °C at sea level) may also have played a significant role in the poor dispersal (and possible reduced reproduction) of *G. ashmeadi* in this zone. However, poor dispersal was also observed at the two intermediate elevation inland monitoring sites on Tahiti that also comprised mainly native vegetation and had climatic conditions similar to sea level sites. Thus, these comparative observations suggest that high host availability is likely to be an important factor affecting *G. ashmeadi* dispersal in Tahiti. Similarly, parasitism rates and subsequent population growth by *Eretmocerus eremicus*, a white fly parasitoid, have been observed to respond positively to increasing host numbers (Bellamy et al., 2003). An extremely abrupt boundary between high and low *H. vitripennis* densities is related to a high diversity of cultivated exotic plants in urbanized areas (Petit et al., 2007). This human influenced biotic boundary appears to be an important limiting factor for pest population development and the subsequent infiltration of natural areas by dispersing founder populations of parasitoids.

Another factor affecting the dispersal of *G. ashmeadi* may be the sheer density of a rapidly increasing parasitoid population. Grandgirard et al. (in press-a, in press-b) speculated that the late and abrupt establishment of *G. ashmeadi* at the high elevation site was due to the natural invasion of this site by large numbers of parasitoids colonizing progressively up the mountain from sea level. The results presented here support this suggestion that high densities of parasitized *H. vitripennis* eggs at sea level produced substantial numbers of vagile parasitoids that invaded high elevation sites and overcame earlier establishment barriers caused by low host densities. Parasitoid dispersal at high elevation then followed an ascending pattern across monitoring sites 97 days after release. Further, the date of this massive upward invasion of parasitoids from sea level is consistent with the period that *G. ashmeadi* populations were rapidly increasing throughout Tahiti (Grandgirard et al., in press-b). Therefore, observations on the colonization pattern by *G. ashmeadi* of high elevation sites suggests that at very low host density rapid dispersal and subsequent establishment is possible only when parasitoids are present in sufficiently high numbers to overcome establishment problems associated with host scarcity. Therefore, in instances of low host density, parasitoid dispersal and subsequent establishment rates are closely linked with propagule pressure (i.e., naturally occurring infiltration or deliberate releases).

4.3. Implications for biological control of Homalodisca vitripennis

Understanding the dispersal and establishment capacity of a parasitoid is important in terms of developing effective release protocols (Wright et al., 2001). This study increased our knowledge on the natural dispersal behavior*G. ashmeadi* by showing that wind direction was not a major factor affecting dispersal of *G. ashmeadi* while landscape characteristics and host density were very important. The rate of natural dispersal by *G. ashmeadi* was shown to average ~47 m/day and this rate of spread appears to be vastly greater than that of *H. vitripennis*, at 17 vs. 5 km/year, respectively (Petit et al., 2007). This finding supports the hypothesis that dispersal rates exhibited by an organism depend on its trophic level. Typically, upper trophic level organisms exhibit higher mobility than prey in order to rapidly locate and exploit ephemeral host patches (Holt, 1996; Jones et al., 1996). Results presented here strongly suggest that *G. ashmeadi* should be able to suppress rapidly *H. vitripennis* in every new area that this pest establishes high density populations if the climate is permissive enough to allow year round reproduction by the pest (Hoddle, 2006).

Host density appears to have had a significant influence on *G. ashmeadi* establishment. Therefore, the size, frequency, and subsequent efficacy of releases of this parasitoid as part of a classical biological control program in new areas will depend on pest density. Mathematical models and empirical data suggest that, in most classical biological control programs, a minimum of about 1000 insects per release is necessary to increase the likelihood of establishment of introduced parasitoids in new areas (Hopper and Roush, 1993). This study indicates that this suggested release threshold of ~1000 parasitoids is not fixed, and can be modulated with respect to host density. For example, it may be possible to release fewer parasitoids when host densities are uniformly high and liberating more natural enemies when host densities are low and populations are widely dispersed.

At high host density at sea level in Papenoo (>150 *H. vitripennis* nymphs/min of sweep netting) the dispersal and establishment capacity of *G. ashmeadi* was very high. Moreover, at this level of host abundance, parasitoid dispersal ability seems not to be related to initial propagule pressure. Additional field surveys have determined that *G. ashmeadi* has established successfully through unintentional human-assisted movement of plant material on remote islands (e.g., the Austral Islands which are ~600 km south of Tahiti [Petit unpublished data]) from invaders that were almost certainly below the release threshold of 1000 insects determined by Hopper and Roush (1993). Therefore, to establish *G. ashmeadi* rapidly and to provide quick control of high density contiguous populations of *H. vitripennis*, it may be more efficient to release fewer parasitoids at several dispersed locations than a massive release at just one central location. This scenario of multiple low density parasitoid introductions leading to widespread natural enemy establishment and rapid pest suppression may have occurred on Moorea (separated from Tahiti by 17 km of open ocean) where *G. ashmeadi* rapidly colonized the whole island from what were probably several accidental human-mediated and widely spaced introductions of a few parasitoids into different parts of the island. These parasitoid introductions probably occurred from the introduction of plants from Tahiti bearing parasitized *H. vitripennis* egg masses (Petit unpublished data). This multiple inoculation pattern scenario of low numbers of parasitoids may have allowed *G. ashmeadi* to colonize Moorea more rapidly across similar distances as seen in Tahiti where sequential large introductions were made at just one site.

However, at very low host densities such as those observed at high elevation in Pirae (<2 nymphs/min of sampling), *G. ashmeadi* establishment and dispersal was very limited. High parasitoid densities were necessary to overcome the lack of abundant hosts before establishment was achieved. In this instance, a release threshold of more than 1000 natural enemies would be necessary to obtain successful establishment of *G. ashmeadi* when *H. vitripennis* densities are very low and widely dispersed.

In conclusion, this study has increased greatly our understanding of the natural dispersal and establishment ecology of *G. ashmeadi* and data presented here should improve our ability to use this parasitoid as an effective classical biological control agent in areas where releases are planned to establish new perennial populations. Careful design of release strategies based on empirical field data will be especially important if resources are limited for maintaining colonies of *G. ashmeadi* and *H. vitripennis* for large mass rearing programs. When taken together, these data can be used to guide development of release strategies of *G. ashmeadi* for classical biological control of *H. vitripennis* on other islands in the South Pacific invaded by this pest.

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References

Barlow, N.D., Beggs, J.R., Moller, H., 1998. Spread of the wasp parasitoid *Sphecophaga vesparum vesparum* following its release in New Zealand. New Zealand Journal of Ecology 22, 205–208.

Bellamy, D.E., Asplen, M.K., Byrne, D.N., 2003. Impact of *Eretmocerus eremicus* (Hymenoptera: Aphelinidae) on open-field *Bemisia tabaci* (Hemiptera: Aleyrodidae) populations. Biological Control 29, 227–234.

Canto-Silva, C.R., Kolberg, R., Romanowski, H.P., Redaelli, L.R., 2006. Dispersal oft he egg parasitoid Gryongallardoi (Brethes) (Hymenoptera:Scelionidae) in tobacco crops. Brazilian Journal of Biology 66, 9–17.

Corbett, A., Rosenheim, J.A., 1996. Quantifying movement of a minute parasitoid, *Anagrus epos* (Hymenoptera: Mymaridae), using fluorescent dust marking and recapture. Biological Control 6, 35–44.

Cronin, J.T., Haynes, K.J., 2003. Parasitoid and host movement and population dynamics in a heterogeneous prairie landscape. Journal of Insect Science (Tucson) 3, 6.

Doak, P., 2000. The effects of plant dispersion and prey density on parasitism rates in a naturally patchy habitat. Oecologia (Berlin) 122, 556–567.

Dout, R.L., 1959. The biology of parasitic hymenoptera. Annual Review of Entomology 4, 161–182.

Esch, S., Klinkhamer, P.G.L., Van der Meijden, E., 2005. Do distances among host patches and host density affect the distribution of a specialist parasitoid? Oecologia (Berlin) 146, 218–226.

Goldson, S.L., Proffitt, J.R., McNeill, M.R., Baird, D.B., 1999. Linear patterns of dispersal and build up of the introduced parasitoid *Microctonus hyperodae* (Hymenoptera: Braconidae) in Canterbury, New Zealand. Bulletin of Entomological Research 89, 347–353.

Grandgirard, J., Hoddle, M.S., Roderick, G.K., Petit, J.N., Percy, D., Putoa, R., Garnier, C., Davies, N., 2006. Invasion of French Polynesia by the glassy-winged sharpshooter, *Homalodisca coagulata* (Hemiptera: Cicadellidae): a new threat to the South Pacific. Pacific Science 60, 429–438.

Grandgirard, J., Hoddle, M.S., Petit, J.N., Percy, D., Roderick, G.K., Davies, N., in press-a. Pre-introductory risk assessment studies for *Gonatocerus ashmeadi* (Girault) (Hymenoptera: Mymaridae) for use as a classical biological control agent against *Homalodisca coagulata* (Say) (Hemiptera : Cicadellidae) in the Society islands (French Polynesia). Biocontrol Science and Technology.

Grandgirard, J., Hoddle, M.S., Petit, J.N., Roderick, G.K., Davies, N., in press-b. Engineering an invasion: classical biological control of the glassy-winged sharpshooter, *Homalodisca vitripennis*, by the egg parasitoid *Gonatocerus ashmeadi* in Tahiti and Moorea, French Polynesia. Biological Invasions.

Henne, D.C., Johnson, S.J., Cronin, J.T., 2007. Population spread of the introduced red imported fire ant parasitoid, *Pseudacteon tricuspis* Borgmeier (Diptera: Phoridae), in Louisiana. Biological Control 42, 97–104.

Hengeveld, R., 1989. Dynamics of Biological Invasions. Chapman and Hall, London.

Hoddle, M.S., 2006. Are glassy-winged sharpshooter populations regulated in California? Long-term phenological studies and construction of multi-cohort life tables for glassy-winged sharpshooter in citrus orchards. California Department of Food and Agriculture Symposium Proceedings, 2006 Pierce's Disease Research Symposium. November 27–29, 2006, San Diego, California, pp. 73–75.

Holt, R.D., 1996. Food webs in space: an island biogeographic perspective. In: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs, Integration of Patterns and Dynamics. Chapman & Hall, pp. 313–323.

Hoover, W., 2004. New invader may threaten crops. Honolulu Advertiser, 14 May 2004.

Hopper, K.R., Roush, R.T., 1993. Mate finding, dispersal, number released, and the success of biological control introductions. Ecological Entomology 18, 321–331.

Jones, T.H., Godfray, H.C.J., Hassell, M.P., 1996. Relative movement patterns of a tephridid fly and its parasitoid wasps. Oecologia 106, 317–324.

Justo Jr., H.D., Shepard, B.M., Elsey, K.D., 1997. Dispersal of the egg parasitoid *Trissolcus basalis* (Hymenoptera: Scelionidae) in tomato. Journal of Agricultural Entomology 14, 139–149.

Langhof, M., Meyhoefer, R., Poehling, H.M., Gathmann, A., 2005. Measuring the field dispersal of *Aphidius colemani* (Hymenoptera: Braconidae). Agriculture Ecosystems & Environment 107, 137–143.

Laurent, V., Maamaatuaiahutapu, K., Maiau, J., Varney, P., 2004. Atlas climatologique de la Polynésie française. Météo France—Direction Interrégionale de la Polynésie française (ed.), p. 201.

McDougall, S.J., Mills, N.J., 1997. Dispersal of *Trichogramma platneri* Nagarkatti (Hym., Trichogrammatidae) from point-source releases in an apple orchard in California. Journal of Applied Entomology 121, 205–209.

McMannus, M.L., 1988. Weather, behavior and insect dispersal. Memoirs of the Entomological Society of Canada 146, 71–94.

Messing, R.H., Rabasse, J.M., 1995. Oviposition behaviour of the polyphagous aphid parasitoid *Aphidius colemani* Viereck (Hymenoptera: Aphidiidae). Agriculture Ecosystems and Environment 52, 13–17.

Munro, V.M.W., 1998. A retrospective analysis of the establishment and dispersal of the introduced Australian parasitoids *Xanthopimpla rhopaloceros* (Krieger) (Hymenoptera: Ichneumonidae) and *Trigonospila brevifacies* (Hardy) (Diptera: Tachinidae) within New Zealand. Biocontrol Science and Technology 8, 559–571.

Petit, J.N., Hoddle, M.S., Grandgirard, J., Roderick G.K., Davies N., 2007. Invasion dynamics of the glassy-winged sharpshooter *Homalodisca vitripennis* in French Polynesia. Submitted to Biological Invasions.

Pilkington, L.J., Hoddle, M.S., 2006. Reproductive and developmental biology of *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae), an egg parasitoid of *Homalodisca coagulata* (Hemiptera: Cicadellidae). Biological Control 37, 266–275.

Saavedra, J.L.D., Torres, J.B., Ruiz, M.G., 1997. Dispersal and parasitism of *Heliothis virescens* eggs by *Trichogramma pretiosum* (Riley) in cotton. International Journal of Pest Management 43, 169–171.

Sallam, M.N., Overholt, W.A., Kairu, E., 2001. Dispersal of the exotic parasitoid *Cotesia flavipes* in a new ecosystem. Entomologia Experimentalis et Applicata 98, 211–217.

SAS Institute, 1990. SAS/STAT User's Guide: Statistics Version 6. SAS Institute, Cary, North Carolina.

Sorensen, J.T., Gill, R.J., 1996. A range extension of *Homalodisca coagulata* (Say) (Hemiptera: Clypeorrhyncha: Cicadellidae) to southern California. Pan-Pacific Entomologist 72, 160–161.

Stireman, J.O., Singer, M.S., 2003. What determines host range in parasitoids? An analysis of a tachinid parasitoid community. Oecologia 135, 629–638.

Takiya, D.M., McKamey, S.H., Cavichioi, R.R., 2006. Validity of *Homalodisca* and of *H. vitripennis* as the name for glassy-winged sharpshooter (Hemiptera: Cicadellidae: Cicadellinae). Annals of the Entomological Society of America 99, 648–655.

Thies, C., Steffan-Dewenter, I., Tscharnetke, T., 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos 101, 18–25.

Triapitsyn, S.V., Mizell, R.F., Bossart, J.L., Carlton, C.E., 1998. Egg parasitoids of *Homalodisca coagulata* (Homoptera: Cicadellidae). Florida Entomologist 81, 241–243.

Triapitsyn, S.V., Phillips, P.A., 2000. First record of *Gonatocerus triguttatus* (Hymenoptera: Mymaridae) from eggs of *Homalodisca coagulata* (Homoptera: Cicadellidae) with notes on the distribution of the host. Florida Entomologist 83, 200–203.

Wright, M.G., Hoffmann, M.P., Chenus, S.A., Gardner, J., 2001. Dispersal behavior of *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae) in sweet corn fields: Implications for augmentative releases against *Ostrinia nubilalis* (Lepidoptera: Crambidae). Biological Control 22, 29–37.