

ORIGINAL CONTRIBUTION

Life-history traits of *Encarsia guadeloupae*, a natural enemy of the invasive spiralling whitefly *Aleurodicus dispersus*G. Mollot^{1,2}, N. Borowiec^{2,3}, P.-F. Duyck², S. Glénac² & S. Quilici²¹ CNRS, Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), UMR 5175, Montpellier Cedex 5, France² CIRAD, UMR PVBMT, CIRAD / Université de La Réunion, Pôle de Protection des Plantes, Saint-Pierre, La Réunion, France³ INRA, Equipe Recherche et Développement en Lutte Biologique, UMR 1355 ISA, Sophia Antipolis, France**Keywords**

alternative host, classical biological control,
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Abstract

On south-west Indian Ocean islands, many crops and ornamental plants are threatened by the spiralling whitefly *Aleurodicus dispersus* (Hemiptera: Aleyrodidae), which is a polyphagous pest that is native to the Caribbean region. *Aleurodicus dispersus* causes economic damage to various crops on all the islands in the south-west Indian Ocean. The hymenopteran parasitoid *Encarsia guadeloupae* (Hymenoptera: Aphelinidae) is a natural enemy of *A. dispersus* on the Caribbean islands. In this study, we assessed the geographical distribution of the parasitoid in La Réunion, an island in the south-west Indian Ocean where the parasitoid was first observed in 2004. We also investigated its main life-history traits. Field surveys indicated that the parasitoid is widespread in most of the low-lying areas of the island and exhibits high parasitism rates on *A. dispersus* populations. At 25°C, *E. guadeloupae* adults had a mean longevity of 33.6 days, and its pre-imaginal development required 23 days. The lower temperature threshold and thermal constant were estimated to be 7.9°C and 132 degree-days, respectively. Females of *E. guadeloupae* preferred to deposit eggs in early rather than in late instars of *A. dispersus*, and oviposition rates were highest in the second larval instar. Females of *E. guadeloupae* were able to oviposit in larvae of other species of whiteflies found in La Réunion (*Bemisia tabaci* and *Dialeurolonga simplex*), although subsequent development of the parasitoid was not monitored. Finally, we discuss the potential use of *E. guadeloupae* for the control of whitefly populations on islands in the south-west Indian Ocean.

Introduction**The spiralling whitefly: a worldwide pest**

Whiteflies (family Aleyrodidae) are sap-sucking hemipterans whose body and wings of adults are coated with white wax (Martin and Mound 2007). Whiteflies, which are often polyphagous, feed on phloem sap and thus reduce the growth of their host plants. Because whitefly numbers can increase very rapidly, the damage to crops and ornamental plants can be severe (Geetha 2000; Banjo 2010). The spiralling whitefly *Aleurodicus dispersus* Russell is

native to the Caribbean and Central America and was first described in 1965 based on individuals collected in Barbados, Brazil, Canary Islands, Costa Rica, Cuba, Dominica, Ecuador, Haiti, Martinique, Panama, Peru and the USA (Florida). This species was recorded as a pest in Hawaii in 1978 (Kumas-hiro et al. 1983) and has been passively dispersed, mostly with infested plant material (Mani and Krishnamoorthy 2002), to some Pacific Islands, Sri Lanka and the Maldives (Waterhouse and Norris 1989), Asia (Wen et al. 1995), Africa (D'Almeida et al. 1998), the Americas (Evans 2007) and Australia (Lambkin 2004). *A. dispersus* recently invaded

several islands in the south-west Indian Ocean including Mauritius in 2000 (S. Quilici, unpublished data), the Seychelles in 2003 (Hazell 2005), La Réunion in 2004 (S. Quilici, unpublished data) and Madagascar in 2006 (N. Borowiec, unpublished data). *A. dispersus* populations can develop on more than 300 plant species (Lambkin 2004) including economically important crops (guava, banana, cassava, soya bean and papaya) (Mani and Krishnamoorthy 2002) and ornamental plants (*Acalypha* spp. and *Euphorbia* spp.) (Dubey and Sundararaj 2002; Lambkin 2004). The spiralling whitefly now occurs in almost all tropical and subtropical regions of the world and is considered one of the most important pests worldwide (D'Almeida et al. 1998; Mani and Krishnamoorthy 2002).

Spiralling whitefly biology and damage

The adult of *A. dispersus* is 2 mm long (D'Almeida et al. 1998; Dubey and Sundararaj 2002; Ramani et al. 2002; Banjo and Banjo 2003) and has white wings that are sometimes coated with black or white patches (Chin et al. 2007). Females deposit their 0.2-mm-long, yellow, elliptical eggs in a spiral pattern usually on the underside of leaves but sometimes on the upper side and also on stems, fruits and even seeds (Chin et al. 2007). Whiteflies affect the physiology and development of the host plants by removing nutrients, which reduces growth, and sometimes have direct, phytotoxic effects (Byrne and Bellows 1991). In addition to this direct damage, whiteflies produce honeydew that may support the development of sooty mould (Banjo and Banjo 2003; Rashid 2003). The fungal mycelium blocks sunlight and thus decreases photosynthesis. Most of the pesticides used against *A. dispersus* are effective against only a specific developmental stage of the pest, and side effects on natural enemies are often shown to decrease the natural regulation of pests (Croft 1990; Foster et al. 2003; Desneux et al. 2007). In addition, chemical control is constrained by the diversity and abundance of host plants and by the wide distribution of the whitefly (Mani and Krishnamoorthy 2002).

One alternative to the application of pesticides for the control of whiteflies and other pests is classical biological control (CBC). In CBC, a specific and generally co-evolved exotic natural enemy is introduced into an area invaded by the pest. Once established, the natural enemy may contribute to the permanent control of the pest populations in the invaded area (Eilenberg et al. 2001).

Classical biological control of *A. dispersus*

CBC of spiralling whitefly populations has been reported in several countries, and most of the natural enemies used have been Chalcidoid parasitoids belonging to the genus *Encarsia* (Aphelinidae). These CBC programmes included the use of *Encarsia dispersa* Polaszek in Australia (Lambkin and Zalucki 2010), *Encarsia guadeloupae* Viggiani in India (Mani and Krishnamoorthy 2006), *Encarsia haitiensis* Dozier in Hawaii and other Pacific Islands (Kumashiro et al. 1983; D'Almeida et al. 1998), *E. dispersa* and *E. guadeloupae* in Benin (Obinna et al. 2011) and *E. guadeloupae* and *E. haitiensis* in Taiwan (Chien et al. 2000).

Native to the Caribbean region (Viggiani 1987), *E. guadeloupae* is an endoparasitoid that reproduces by thelytokous parthenogenesis: fertilized eggs produce male offspring, and unfertilized ones produce haploid female offspring (Cook 1993). To date, males are unknown, perhaps because of the presence of symbiotic bacteria that can skew the sex ratio in favour of females, as occurs with other hymenopteran parasitoids with thelytokous reproduction (Zchori-Fein et al. 2001). *E. guadeloupae* is recognized as a specific endoparasitoid of *A. dispersus* nymphs (Zhou et al. 2013), but has also been reported on the whitefly species *Bemisia tabaci* (Gennadius) and *Trialeurodes vaporariorum* (Westwood) (Noyes 2013). Despite its use as a biological control agent of *A. dispersus* in several countries, biological and ecological information for *E. guadeloupae* is scarce; most information concerns its ability to control *A. dispersus* populations in the field. *E. guadeloupae* was reported to attain a parasitism rate up to 68% on *A. dispersus* on poinsettia (*Euphorbia pulcherrima* Willd) in Taiwan (Chien et al. 2000) and was reported to be the main natural enemy responsible for the decrease of *A. dispersus* populations in India (Mani et al. 2004).

In the south-west Indian Ocean, *E. guadeloupae* was first reported in La Réunion in 2008 (Assani 2008), where its presence probably resulted from a fortuitous introduction with plant materials co-infested by *A. dispersus* and the parasitoid. This parasitoid might be a promising candidate for the biological control of *A. dispersus* on all islands in the south-west Indian Ocean, where *A. dispersus* causes significant damage to crop and ornamental plants. To date, La Réunion is the only island in the Indian Ocean where *E. guadeloupae* has been recorded.

Objectives

The main goal of this study was to determine whether *E. guadeloupae* can be used as a part of a CBC to control *A. dispersus* populations in the Indian Ocean. The underlying condition to achieve this goal is the ability to rear the parasitoid in the laboratory before its release in the field. Our experiments were designed to obtain such information that would help to plan mass rearing of the parasitoid and to predict its geographical distribution as a function of environmental variables. We first assessed the geographical distribution of *E. guadeloupae* and the rate at which it parasitizes *A. dispersus* in La Réunion. We also recorded sites where only *A. dispersus* was observed and sites where neither of the two species were observed. Second, we investigated the parasitoid's pre-imaginal development cycle and adult longevity at four constant temperatures. Information on the pre-imaginal development cycle and on the geographical distribution of the species enabled us to compute the thermal requirement and the lower developmental threshold and to predict the probability of the presence of the parasitoid as a function of temperature and rainfall. Finally, we observed the parasitic behaviour of the parasitoid (developmental stages of *A. dispersus* preferentially attacked and host specificity) to assess possible non-target effect of mass parasitoid releases in non-invaded areas.

Materials and Methods

Geographical distribution and parasitism rates

Between March and May 2009, we recorded the presence/absence of *E. guadeloupae* based on the observation of *A. dispersus* nymphs collected at 100 sites in La Réunion. The GPS coordinates of each site were recorded with a Garmin 60 (Garmin International, Kansas). The nymphs were collected on the following plants growing along the coastline at altitudes between 0 and 600 m a.s.l.: *Acalypha* sp., *E. pulcherrima*, *Carica papaya* L., *Psidium guajava* L., *Hibiscus* sp. and *Terminalia catappa* L. We recorded the presence/absence of *A. dispersus* at each site by the observation of potential host plants. When *A. dispersus* was present, we collected 3–5 leaves of the host plant to record the presence/absence of *E. guadeloupae*. The nymphs were examined in the laboratory for parasitism by *E. guadeloupae*. Based on these data, the geographical distribution of *E. guadeloupae* in La Réunion was mapped using the GIS software ArcGIS version 9 (ESRI 2009).

To assess parasitism rates of *E. guadeloupae*, observations were carried out at five sites at altitudes ≤ 200 m a.s.l. At each of these sites, we collected 10 leaves infested with *A. dispersus* colonies on *Acalypha* sp., which is one of the preferred hosts of the whitefly. The parasitism rate, which was assessed with the aid of a binocular microscope, was based on *a posteriori* signs. Because *A. dispersus* adults emerge from *A. dispersus* puparia through T-shaped exit holes whereas parasitoids emerge through O-shaped exit holes, parasitism rate was calculated as [the number of nymphs with O-shaped exit holes/(number of nymphs with O-shaped exit holes + number of nymphs with T-shaped exit holes)*100]. We verified that the parasitism was exclusively due to *E. guadeloupae* by isolating parasitized puparia and identifying the adult parasitoids that emerged.

Rearing of *A. dispersus*

Aleurodicus dispersus rearing was initiated with samples collected in the field from sites located near the laboratory. Between 2008 and 2009, *A. dispersus* was reared on *E. pulcherrima* (poinsettia) in climate chambers at 25°C and 60% RH in the CIRAD laboratory, La Réunion. To obtain newly infested plants for our experiments, healthy *E. pulcherrima* plants (<15 cm tall) were placed near plants infested with *A. dispersus* for 48 h in 'insect proof' cages. With this method, we were able to obtain plants that were infested only by *A. dispersus*.

Collection of *E. guadeloupae* adults

We collected leaves of *Acalypha* sp. on which *A. dispersus* nymphs were present and showing signs of parasitism by *E. guadeloupae*. Samples (parasitized nymphs) were collected in the field from sites located near the laboratory. Because parasitized larvae are black and healthy larvae are white, observation of the underside of leaves with a binocular microscope enabled us to discriminate between healthy and parasitized larvae. The parasitized larvae were removed and isolated in small plastic boxes on a piece of leaf; the larvae were placed on the new leaf such that their orientation was the same as on the original leaf to avoid disturbing adult emergence. Boxes containing parasitized larvae were then placed in a climate chamber at 25°C. The newly emerged parasitoid adults were isolated every day in individual boxes, provided with water and honey (20%) and placed in a climate chamber at 25°C.

Pre-imaginal development of *E. guadeloupae*

To assess the pre-imaginal development of *E. guadeloupae*, 48-h-old females of the parasitoid were brought into contact with *A. dispersus* larvae developing on newly infested poinsettia. The oviposition behaviour of the parasitoid was observed with the aid of a binocular microscope to locate the position on the leaf of each parasitized larva of *A. dispersus*; the time required for the development of the parasitoid (from oviposition until adult emergence) in each of 19 parasitized larvae was determined. The plants supporting *A. dispersus* larvae parasitized by *E. guadeloupae* were placed in a climate chamber at 15, 20, 25 or 30°C. The date of adult emergence was recorded by daily observations.

Longevity of *E. guadeloupae* adults

The longevity of *E. guadeloupae* adults was measured by individually placing newly emerged adults in Petri dishes (diameter 7 cm; height 2 cm) containing a piece of paper towel (5 × 5 mm) soaked with a 20% solution of honey in water. The dishes were placed in climate chambers at 15, 20, 25 or 30°C. Each dish was examined daily for adult mortality. The honey and water solution were renewed every day until the end of the experiment (75 days).

Parasitic behaviour of *E. guadeloupae*

To assess the development stages of *A. dispersus* preferentially attacked by *E. guadeloupae*, *E. guadeloupae* females ($n = 20$) were brought into contact with the four larval instars of *A. dispersus* at ambient temperature (24°C), and each oviposition event (contact, coupling and oviposition) was recorded. Our pretests showed that the majority of individuals required <10 min to achieve an oviposition; to standardize the experiment, we decided to allocate 10 min per replicate. Each female was presented with six *A. dispersus* infested leaves (from the laboratory colony of *A. dispersus*). The six leaves were infested with 93.6 ± 13.1 (SE) whitefly nymphs at the four larval stages; the proportions of the larval stages were not recorded.

Preliminary observations on host specificity of *E. guadeloupae*

We collected leaf samples infested by other species of whiteflies in the field and observed the oviposition behaviour of *E. guadeloupae* on larvae in Petri dishes

with the aid of a binocular microscope. Ten females of *E. guadeloupae* were tested for each of the following four whitefly species: *Aleurotrachelus atratus* Hempel, *Aleurotrachelus trachoides* Back, *Bemisia tabaci* biotype B and *Dialeurolonga simplex* Takahashi. *A. atratus* was collected on *Acanthophoenix rubra* (Barbel palm) with 32.8 ± 8.9 nymphs per leaf (mean \pm SD); *A. trachoides* was collected on *Capsicum* sp. (Chili pepper) with 40.1 ± 9.6 nymphs per leaf; *B. tabaci* biotype B was collected on *Brassica* sp. with 50.4 ± 17.8 nymphs per leaf; and *D. simplex* was collected on *Citrus* spp. with 36.9 ± 8.1 nymphs per leaf. After being exposed to an alternative host, each female parasitoid was exposed to its preferred host, *A. dispersus*, for 10 min; if the parasitoid failed to oviposit on *A. dispersus*, we assumed that its oviposition behaviour was altered, and we excluded this female from the analysis. These assays were conducted at ambient temperature (24°C) in the laboratory.

Statistical analysis

The effect of temperature on the mean pre-imaginal development time of *E. guadeloupae* was assessed with an ANOVA; *post hoc* Tukey HSD tests were used to detect differences between each pair of temperatures. We adopted a temperature summation model approach based on the assumption that, above a certain lower threshold for development, the temperature–development rate relationship is linear (Fletcher 1989). Therefore, a constant number of heat units (usually expressed as degree-days) above this threshold is required to complete development (Wagner et al. 1984; Fletcher 1989). Development rate (i.e. 100/developmental time) was plotted against temperature. The lower development threshold t (i.e. the temperature at which the development rate is zero) was then determined by extrapolation of the regression line back to the X -axis. The thermal constant K (i.e. the number of degree-days above the lower threshold required to complete development) was calculated from the regression equation using the relationship $y = K/(x - t)$ (Fletcher 1989).

The data concerning the field distribution of *E. guadeloupae* (its presence or absence at 100 sites) as related to temperature and rainfall were analysed by the generalized linear model (GLM) with binomial error; the independent variables were mean annual temperature, mean annual rainfall and the interaction between temperature and rainfall. The significance of each term was assessed based on the change in deviance between models with and without that term. The quadratic effects of rainfall and temperature were

also tested and were removed from the model because they were not significant.

We compared adult longevity at four temperatures (15, 20, 25 and 30°C) with the nonparametric log-rank test. Analysis of *E. guadeloupae* survival was based on Kaplan–Meier statistics with censored data (some individuals kept at 15 °C were still alive at the end of the experiment) and was performed with the OASIS package (Yang et al. 2011).

The proportions of eggs laid as a function of larval instar of *A. dispersus* were compared with the exact version of the pairwise proportion test, which is based on repeated Fisher's exact tests instead of chi-square tests, and on a Bonferroni method for P-value adjustment.

For the host specificity experiment, the number of each behavioural event (contact, coupling and oviposition) as a function of host species was analysed by the generalized linear model (GLM) with Poisson error. Analyses were performed using the R statistical package, version 3.0.2 (R Development Core Team 2012).

Results

Geographical distribution of the parasitoid and parasitism rates

Nymphs of *A. dispersus* were found at 72 of the 100 sites assessed in La Réunion, and *E. guadeloupae*-parasitized nymphs were recorded at 45 of the sites; no whitefly was found in the eight sites that were prospected beyond 498 a.s.l. (Le Tampon). The altitude of the sites with parasitized nymphs ranged from 5 m a.s.l. (Rivière des Roches) to 486 m a.s.l. (Saint-Gilles les Hauts) (fig. 1). Parasitism rates of *E. guadeloupae* on *A. dispersus* at the five monitored sites ranged from 74% (Saint Benoit, 36 m a.s.l.) to 99% (Anse des Cascades, 106 m a.s.l.).

Temperature and rainfall were significantly associated with the probability that *E. guadeloupae* was present (fig. 2). The presence of the parasitoid increased with increasing annual mean temperature (GLM with binomial error: $\Delta\text{dev}_{1,97} = 9.988$, P-value = 0.0016) and decreased with increasing annual rainfall ($\Delta\text{dev}_{1,97} = 4.659$, P-value = 0.0308); the interaction between temperature and rainfall was not significant ($\Delta\text{dev}_{1,96} = 0.622$, P-value = 0.4305).

Life history traits of *E. guadeloupae*

The mean pre-imaginal developmental time for *E. guadeloupae* was 13, 23, 18.5 and 31 days at 30, 25,

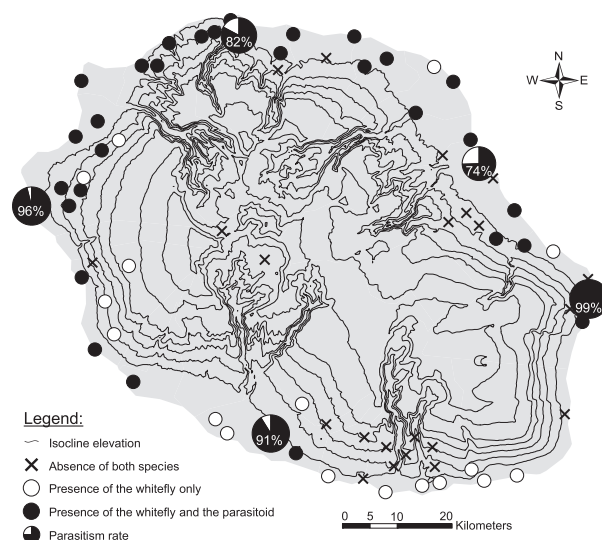


Fig. 1 Geographical distribution and parasitism rates of *Encarsia guadeloupae* in La Réunion. The presence of *A. dispersus* and *E. guadeloupae* was assessed at 100 sites ranging from 0 to 600 m a.s.l. in La Réunion. At five sites, infested leaves were collected, and the percentage of *A. dispersus* nymphs parasitized by *E. guadeloupae* was determined.

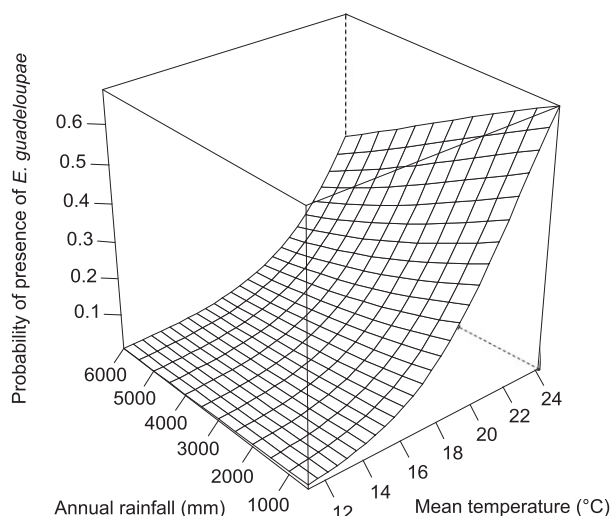


Fig. 2 Probability of the presence of *Encarsia guadeloupae* as a function of annual rainfall and annual mean temperature (fitted from GLM with binomial error). The geographical distribution of the parasitoid (GPS coordinates) was used to compute the probability of *E. guadeloupae* presence as a function of rainfall and temperature.

20 and 15°C, respectively. ANOVA indicated that the effect of temperature was significant ($F_{3,15} = 112.59$, P-value <0.001), and the Tukey HSD test indicated that all pairs of temperature treatments were significantly different (P-value <0.001).

Table 1 Survival time and age (in days) at a given level of mortality (25–100%) for *E. guadeloupae* adults after emerging from *A. dispersus* nymphs

Temperature (°C)	n	Survival time (restricted mean)			Age in days at the indicated mortality level						Shapiro–Wilk test P-value
		Days	SE	95% CI	25%	50%	75%	90%	100%	95% Median CI	
15	30	67.30	2.79	61.83–72.77	65	–	–	–	–	66–76	0.0430
20	30	41.73	3.30	35.27–48.20	35	42	49	71	75	39–46	0.3518
25	30	33.47	2.25	29.06–37.87	28	33	44	45	58	31–42	0.0477
30	30	11.50	1.18	9.18–13.82	6	13	15	17	29	6–14	0.1905

A strong and positive linear relationship was observed between temperature and *E. guadeloupae* development ($y = 0.756 \times -5.980$; P-value <0.0001, d.f. = 1; 17; $R^2 = 0.64$). The lower temperature threshold and thermal constant were estimated to be 7.9°C and 132 degree-days, respectively.

The mean longevity of *E. guadeloupae* adults after emergence from *A. dispersus* ranged from 11.5 ± 1.2 days at 30°C to 67.3 ± 2.8 days at 15°C (table 1), and the comparison of the survival curves indicated significant differences between all temperatures (log-rank test, P-value <0.001). At 15°C, the survival analysis was censored because 18 individuals were still alive at the end of the experiment (75 days).

Parasitic behaviour of *E. guadeloupae*

When presented with leaves infested with L1, L2, L3 and L4 instars of *A. dispersus*, *E. guadeloupae* females preferentially oviposited in the early instars, especially in the L2 instars (table 2). The proportion of oviposition events was significantly higher in L2 than in L3 (pairwise Fisher test, P-value = 0.0074) or L4 instars (P-value <0.0001). The percentage of oviposition events did not significantly differ between L1 and L2 instars (P-value = 0.1349).

Host specificity experiments showed that *E. guadeloupae* accepted other whitefly species for oviposition. The number of contacts (GLM with Poisson error: $\Delta dev_{4,75} = 223.8$, P-value <0.0001), couplings ($\Delta dev_{4,75} = 36.3$, P-value <0.0001) and ovipositions ($\Delta dev_{4,75} = 50.7$, P-value <0.0001) was significantly different among the tested whitefly species. We observed a total of 17 oviposition events (60% of females) on larvae of *B. tabaci*, and one oviposition event (10% of females) on a larva of *D. simplex* (fig. 3).

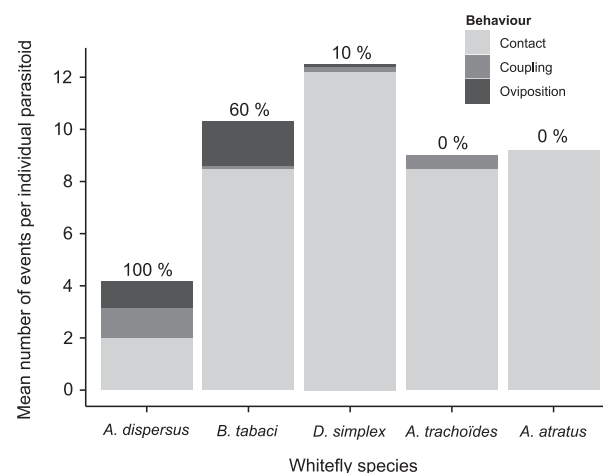
Discussion

The increasing geographical distribution of the parasitoid *E. guadeloupae* and the current data describing development as a function temperature indicate that

Table 2 Oviposition preference of *Encarsia guadeloupae* females (n = 20) among larval instars of *A. dispersus*. After each female was presented with a Poinsettia leaf infested with four instars of *A. dispersus*, the parasitic behaviour of the parasitoid (number of oviposition events) was recorded for 10 min

Host instar	Number of ovipositions exhibited by 20 females	Percentage of ovipositions in each instar	Pairwise Fisher test (P-value)		
			L2	L3	L4
L1	8	26.7	0.1349	1.0000	0.1179
L2	16	53.3	–	0.0074*	<0.0001**
L3	5	16.7	–	–	1.0000
L4	1	3.3	–	–	–

Significant P-values are indicated in bold. *P < 0.01; **P < 0.001.

**Fig. 3** Oviposition of *Encarsia guadeloupae* on the larvae of five whitefly species. The cumulative bar chart indicates the mean number of parasitoid events (contact with the host, coupling with the host and oviposition in the host) observed (10 min) per *E. guadeloupae*. Ten female parasitoids were presented with nymphs of each of the five whitefly species for 10 min. The value above each bar indicates the percentage of females that deposited eggs in the indicated host.

E. guadeloupae dispersal has benefited from tropical abiotic conditions and human activities. In 2008, *E. guadeloupae* was found for the first time on the

northern and western coasts of La Réunion (Assani 2008). One year later, the parasitoid had already spread to the eastern and south-western coasts at altitudes between 0 and 600 m a.s.l. The rapid dispersal observed in La Réunion can be expected in other areas with similar climatic conditions and human activities. The exchange of plant materials through human activities or the ability of the species to disperse probably accounts for its rapid dispersal. Other Chalcidoid wasps in the Mymaridae family have been shown to disperse as aeroplankton (Petit et al. 2009). The initially high population density of *A. dispersus* on the island probably facilitated the rapid establishment of the parasitoid. Despite the presence of *A. dispersus* on the southern coast, however, *E. guadeloupae* was not observed in this region (fig. 1). The absence of *E. guadeloupae* along the southern coast of La Réunion might result from the limited transport of infested plant material into this region.

In the five sites where parasitism rates were measured in the current study, the rates were high; in one site, for example, 99% of the *A. dispersus* nymphs on a leaf were parasitized by *E. guadeloupae*. Although measured within a few sites, the very high parasitism rates recorded in this study suggest that *E. guadeloupae* has a potential to regulate *A. dispersus* in La Réunion. We suspect that high parasitism rates may also be attained in other regions where climatic conditions are suitable.

Our results indicate that *E. guadeloupae* tolerates a wide range of temperatures that are representative of those observed in tropical and subtropical regions. A large percentage of the adults kept at 15°C were still alive after 75 days, and as expected, longevity decreased as the temperature increased. These results are consistent with observations made for other *Encarsia* species. Adults of *Encarsia formosa* Gahan (a parasitoid of the greenhouse whitefly *Trialeurodes vaporariorum*), for example, emerge in 15 days at 22.5–25°C and achieve maximal longevity (52 days) at 20°C (Hoddle 1999). Our results also suggest that the probability that *E. guadeloupae* is present decreases as annual rainfall increases. Under dry conditions in Benin, *E. guadeloupae* has been shown to become dominant compared to the other whitefly parasitoid, *Encarsia dispersa* (Obinna et al. 2011).

Our research indicates that *E. guadeloupae* preferentially deposits eggs in the early stages of *A. dispersus*. The 2nd instar seemed to be favoured over the first instar, perhaps because the first instar is mobile. The appearance of cirri on the 3rd instar may make it difficult for the female parasitoid to reach the instar with her ovipositor.

Encarsia guadeloupae has been reported on five species of whiteflies (Noyes 2013), including *B. tabaci*. In

the current study, *E. guadeloupae* oviposition was 100% with *A. dispersus* (i.e. all females deposited eggs in *A. dispersus*) but only 60% with *B. tabaci*. We observed a very low oviposition rate with *D. simplex*, which has not been previously recorded as a host. We also observed a few specimens of *E. guadeloupae* attempting to couple to larvae of *A. trachoides*, but no oviposition was recorded. The successful development of *E. guadeloupae* in larvae of *B. tabaci*, *D. simplex* and *A. trachoides* remains to be demonstrated.

Encarsia guadeloupae shows substantial potential for use in a regional biological control programme against *A. dispersus*. As demonstrated in the current study, the parasitoid tolerates the abiotic conditions observed in tropical and subtropical regions where *A. dispersus* is present and inflicts high parasitism rates on *A. dispersus* populations. However, a more accurate assessment of its specificity and ability to develop on other species of Aleyrodidae is needed. For instance, the parasitoid may be able to parasitize an indigenous whitefly species, part of the species complex of *B. tabaci* (known as Indian ocean species), which is present on the south-west of the Indian Ocean Islands and East Africa (Delatte et al. 2011). To guide the conservation of *E. guadeloupae* in La Réunion and its introduction on other islands in the Indian Ocean, however, we require more information about its host range among whitefly species and its ability to regulate populations of whitefly species.

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