Wind-Borne Dispersal of a Parasitoid: the Process, the Model, and its Validation

Nadiah P. Kristensen,[1,2] Nancy A. Schellhorn,[1] Andrew D. Hulthen,[1] Lynita J. Howie,[1] and Paul J. De Barro[1]

ABSTRACT The aphelinid parasitoid *Eretmocerus hayati* Zolnerowich & Rose (Hymenoptera: Aphelinidae) was recently released in Australia as a biocontrol agent against the crop pest *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae). It was found that the parasitoid can spread over several kilometers in a single generation and continue laying eggs for over a fortnight. A simple wind-advection model was fitted to emergence data from a first release between Fassifern and Kalbar, Queensland, and its predictive ability was tested against the second release near Carnarvon, Western Australia. The fitting of the model was used to develop several hypotheses about the dispersal of *E. hayati*, which were validated by the second release: *E. hayati* flies in the same direction as the wind to a distance proportional to the wind speed; this wind-borne flight takes place at any time during daylight hours; a flight is attempted every day after emergence unless there are high wind conditions during that day; and the high wind condition that will delay flight is wind speeds in excess of ≈ 2 m/s. This model of *E. hayati* dispersal may be contrasted with previous models fitted for *Eretmocerus* species, for which dispersal was dominated by diffusion processes, and parasitoid spread was constrained to the scales of tens and hundreds of meters.

KEY WORDS *Eretmocerus hayati*, *Bemisia tabaci*, advection, spread, landscape scale

Despite the potential importance of the wind-borne component to small parasitoid dispersal (Pasek 1988, Chapman et al. 2004), the literature in this area is limited, and no validated wind-advection model on the kilometers scale exists. This has bearing on the assessment of the potential efficacy of biocontrol agents like *Eretmocerus* species. Its host *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) is known to disperse long distances (Blackmer and Byrne 1993), dispersing >2.7 km within a morning (Byrne et al. 1996), and it has been suggested that the relatively poor dispersal capability of one of its natural enemies, *Eretmocerus eremicus* (Hymenoptera: Aphelinidae) Rose and Zolnerowich, was responsible for its weak performance (Bellamy et al. 2004).

The linear parasitoid dispersal distances that have been observed in the literature are meters (Kölliker–Ott et al. 2004, Takasu et al. 2004, Darrouzet–Nardi et al. 2006, Ayvaz et al. 2008, Suverkropp et al. 2009), tens of meters (Sallam et al. 2001, Langhof et al. 2005, Paranhos et al. 2007, Scarratt et al. 2008, Chapman et al. 2009), hundreds of meters (Wright et al. 2001, Schellhorn et al. 2008), and kilometers (Doutt and Nakata 1973, McKenzie and Beirne 1973, Williams 1984, Antolin and Strong 1987, Smith 1988). With the exceptions of Antolin and Strong (1987) and Grillen-

berger et al. (2009), previous studies only consider a single scale per investigation. Significantly, the exceptions revealed much longer distance dispersal than would have been estimated using a single smaller scale, raising the possibility that longer-distance dispersal has been overlooked.

Studies of long-distance dispersal may be compromised by the constraints of the methods used. Mark–release–recapture methods or mark–capture methods (Antolin and Strong 1987, Corbett and Rosenheim 1996, Wright et al. 2001, Desouhant et al. 2003, Takasu et al. 2004, Paranhos et al. 2007, Scarratt et al. 2008, Schellhorn et al. 2008, Chapman et al. 2009, Grillenberger et al. 2009, Suverkropp et al. 2009) or baiting with sentinel hosts (Sallam et al. 2001, Kölliker–Ott et al. 2004, Langhof et al. 2005, Darrouzet–Nardi et al. 2006, Ayvaz et al. 2008, Chapman et al. 2009) may change the insect's behavior. Direct methods are also unable to provide critical information about the location of egg-laying (Hastings 2000). The first-time release of a biocontrol agent offers an excellent opportunity to monitor dispersal without these shortcomings (Petit et al. 2008).

Dispersal data can be inferred from emergence data under certain conditions (e.g., the univoltine *Torymus sinensis* Kamijo in Moriya et al. 1989). Therefore, we used the release (De Barro and Coombs 2009) of a biocontrol agent, *Eretmocerus hayati* Zolnerowich & Rose (Hymenoptera: Aphelinidae), and its emergence from its host the silverleaf whitefly, *B. tabaci* Middle
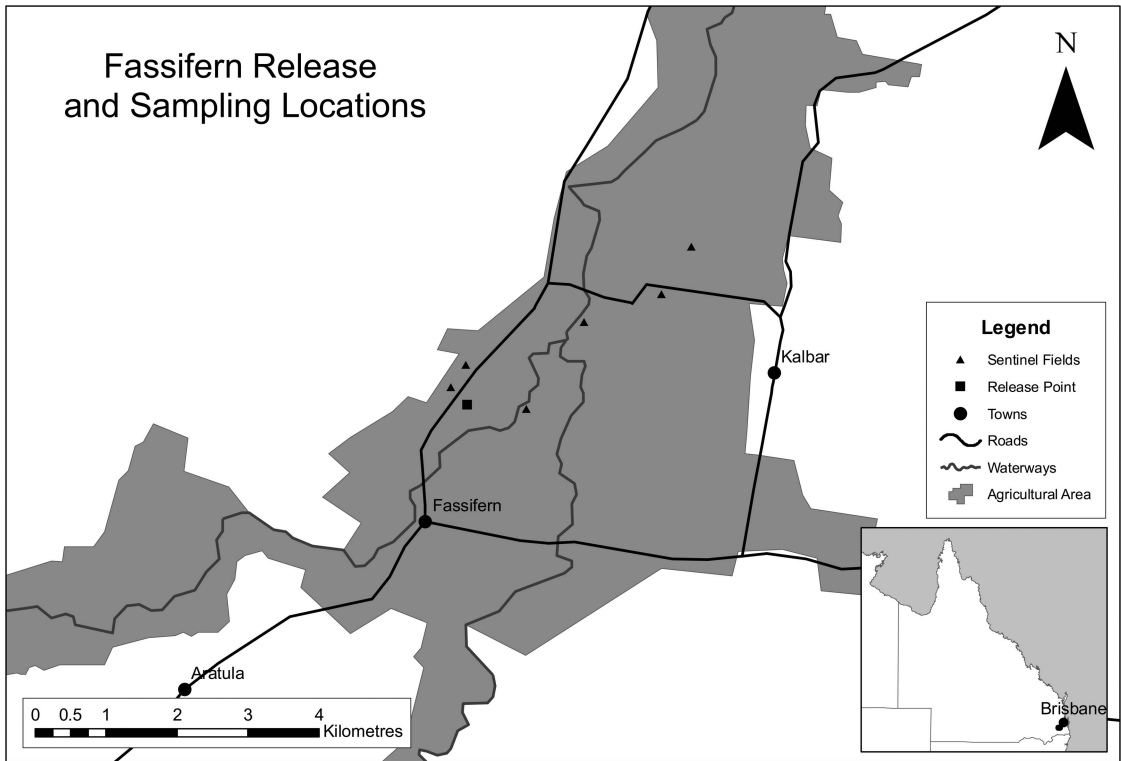
Fig. 1. The 'Fassifern' site is situated in south–eastern Queensland, Australia, near the townships of Fassifern and Kalbar. The sentinel collection fields were located at increasing distances from the release field in a northeasterly direction.

East-Asia Minor 1 (also commonly known as the B biotype Gennadius [Hemiptera: Aleyrodidae]), to infer parasitoid dispersal.

Parasitoid dispersal studies may be used to derive and fit a dispersal model. With a few exceptions (Corbett and Rosenheim 1996, Brewster et al. 1997), the models fitted for parasitoid dispersal have been diffusion models (Simmons 2000, Desouhant et al. 2003, Darrouzet–Nardi et al. 2006, Chapman et al. 2009), and the authors know of no study in which wind-advection alone was modeled. Wind is known to influence parasitoid dispersal (Hendricks 1967, Chapman 1982, Keller and Lewis 1985, Smith 1988, Corbett and Rosenheim 1996, Sallam et al. 2001, Wright et al. 2001, Desouhant et al. 2003, Langhof et al. 2005, Grillenberger et al. 2009); however, the objective of most studies was to determine whether and when parasitoids are able to disperse up- and down-wind (Chapman 1982), rather than investigating wind-advection as a dispersal mechanism specifically.

For *Eretmocerus* species, diffusion kernel fitting has only been undertaken for scales <1 km (Brewster et al. 1997, Simmons 2000). In light of the observation that *E. hayati* can disperse several kilometers (Kristensen et al. 2013), both the mechanism and dispersal scale of most models in the literature appear unsuited to this species. Further, none of the models developed were validated against a second independent data set. Such model validation is necessary to avoid over-fit-

ting, to test the robustness of the model, and to improve confidence in the dispersal mechanisms identified by the model fitting.

In this study, we used a first-time biocontrol release (Kristensen et al. 2013) to develop a hypothesis of *E. hayati* wind-borne dispersal via a model-fitting procedure. The model was validated using independent data from a second first-time release.

Materials and Methods

Study Site. *Fassifern.* The first release occurred between Fassifern and Kalbar, south–eastern Queensland, Australia, 27.945752° S, 152.58474° E (Fig. 1). A detailed account may be found in Kristensen et al. (2013), but an abbreviated description is provided here. At the time of release (12 March 2005), sunrise was at 5:49 a.m. and sunset at 6:10 p.m. The site consists of one release field, Field 0, and six sentinel fields from which leaves containing hosts were collected to estimate emergence.

Field 0 is a 17-ha field flanked by a two-lane highway on the northwest edge, a tree-lined creek on the southeast, and a bare field on the northeast. The bottom edge of the Field 0 runs 32 east of the north–south alignment, and the release point was placed near the center of the field, where there is a bare patch of ground that is used as a tractor turning circle. At the

Table 1. Coordinates of sentinel plots, in meters, used for monitoring dispersal on the landscape scale

Name	x-coordinate (m)	y-coordinate (m)	Crop
Field 0	0	0	Green beans
Field 300-NW	−175	300	Green beans
Field 700-N	−75	675	Soybeans
Field 700-E	700	0	Green beans
Field 2000-NE	1500	1375	Green beans
Field 2900-NE	2375	1675	Green beans
Field 3600-NE	2750	2375	Green beans

The release field, Field 0, is taken as (0,0), North as positive y, and East as positive x. Fields are named by their radial distance and compass direction from the release field.

time of release, Field 0 was planted with beans (variety Yates 'Stringless Pioneer').

The sentinel fields were located at increasing distances from the release field in the northeast direction. Table 1 lists the crops and locations of each field relative to the release field (where coordinates are defined by taking Field 0 as [0,0], north as positive y, and east as positive x).

Carnarvon. The second release occurred near Carnarvon, on the mid-west coast of Western Australia, Australia, at 24.851314° S, 113.731267° E (Fig. 2). At the time of release (30 March 2008), sunrise was at 6:33 a.m. and sunset at 6:26 p.m. The study area consists of one release field, Field 0, and 20 sentinel fields from which leaves containing parasitized hosts were collected to estimate emergence.

The Carnarvon irrigation area is surrounded to the north, south, and east by desert vegetation, and to the west by the Indian Ocean. It consists of a series of irrigated blocks that flank the Gascoyne River. Blocks extend no further than 1.5 km from the river. Field 0 is on the south bank of the Gascoyne River, on the corner of South River Road and Research road. At the time of release, Field 0 was planted with rockmelons; however, the crop had started to die before the second collection on the 26 April.

The sentinel fields were located to the northeast and west of the release field, on both sides of the Gascoyne River. Table 2 lists the crops and locations of each field from which emergence was recorded relative to the release field (where coordinates are defined by taking Field 0 as [0,0], north as positive y, and east as positive x).

The Release, Collection of Emergence Data, and Recording of Weather Conditions. *Fassifern.* A center-point release of *E. hayati* was conducted in Field 0 at 8:30 a.m. on 12 March 2005. Four mesh bags (1 by 1 cm) measuring 35 by 15 by 10 cm were filled with soybean leaves infested with *B. tabaci* parasitized by *E. hayati*. Approximately 130,000 wasps emerged (estimated from sample density per leaf and number of leaves). At the time of release, all *B. tabaci* had reached
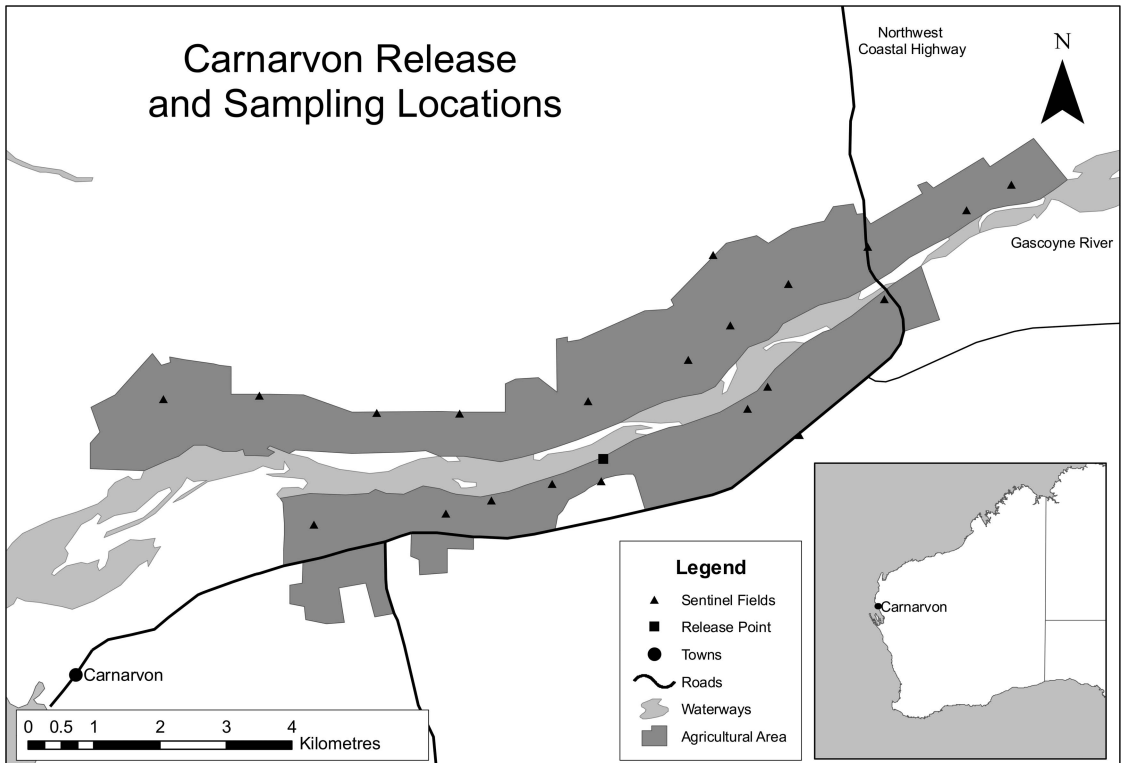
Fig. 2. The 'Carnarvon' site is situated on the mid-west coast of Western Australia, Australia, to the east of the town of Carnarvon.

Table 2. Coordinates of 'Carnarvon' sentinel plots from which emergence was recorded, in meters, and the host in each field

Name	x-coordinate (m)	y-coordinate (m)	Crop
Field 0	0	0	Thistles
Field 6300-NE	5100	3780	Thistles
Field 3500-NE	1600	3090	Thistles
Field 2800-NE	1810	2080	Thistles
Field 1200-NE	1220	1510	Thistles
Field 3200-W	3140	770	Thistles
Field 1300-NE	1050	800	Thistles
Field 300-E	50	−300	Thistles
Field 700-SW	−630	−340	Thistles
Field 1600-W	−1470	−560	Thistles
Field 2300-W	−2110	−790	Thistles
Field 4000-W	−3870	−950	Thistles

The release field is taken as (0,0), North as positive y, and East as positive x.

pupal stage and 5% of *E. hayati* had just begun to emerge.

To evaluate long distance dispersal, on 31 March 2005, 270 leaves were collected from each sentinel field, and placed in containers so that parasitoid and host emergence could be measured. *Encarsia* were differentiated from *E. hayati* by visual inspection. Females of *Eretmocerus mundus* (Mercet), a species that is known to attack *B. tabaci* at very low levels (De Barro et al. 2000), look similar to females of *E. hayati.* There is no confusion between males of the two species because *E. mundus* only produces females (De Barro and Hart 2001). Therefore, DNA analysis was used to verify that all emerged female *Eretmocerus* were *E. hayati.*

Weather data were collected from 12:00 a.m. on 13 March to 11:30 p.m. on 30 March 2005 in 30-min intervals using a Vantage Pro2 from Davis Instruments. The weather station was placed in the center of the field next to the release cage, on the standard tripod 1.8 m tall. Recordings included temperature, humidity, precipitation, wind speed, and wind direction. Wind velocity was averaged over each 30-min interval. Wind direction was recorded in 1 of 16 compass directions.

Carnarvon. On 30 March 2008, ≈40,000 parasitized hosts were released into Field '0' (Fig. 2). In contrast with the Fassifern release, the emergence of *E. hayati* released at Carnarvon was spread over ≈12 d.

To determine the spread of *E. hayati*, collections of leaves with hosts were made at each of 18 points within the release field and at each sentinel field on three occasions, 23, 27, and 31 d post release. The first collection was made 23 d postrelease (22 April 2008), and a minimum of 30 nymphs were collected at all points. The second collection was made 27 d postrelease (26 April 2008). Owing to death of the crop in the release field, the minimum of 30 nymphs could not be obtained for 8 of the 18 points within the release field. The final collection was made 31 d postrelease (30 April 2008). No leaves were collected from the release field for the final collection.

Weather data were collected in 30-min intervals from 5:30 p.m. on 30 March to 4:00 p.m. on 30 April 2008, again using the Vantage Pro2 from Davis Instruments. The weather station was located in the center of the release field. Wind speed was averaged over the 30-min interval, and wind direction was recorded in one of 16 compass directions.

Modeling. *Using Emergence to Infer the Presence of Females.* It is assumed that the presence of released parasitoids may be fitted to the emergence data with an appropriate time-shift. For example, if one parasitoid emerges 3 d after another at a certain location, then it is assumed that it was oviposited 3 d earlier than the other, and therefore, the respective females were present at those times at that location. This assumption may be justified by observing that the development time for *Eretmocerus* spp. is neither sensitive to the instar parasitized (17.6, 16.8, and 16.4 d for first through third instars, respectively, at 27°C; McAuslane and Nguyen 1996) nor to temperature variability for the range over which temperature varied during the experiment (Qiu et al. 2004). In this way, emergence data can be used to infer presence data for the released parasitoid females.

Flight Vector is Proportional to Wind Velocity. The dispersal of the parasitoids was modeled using a simple advection model. The model assumes that female E. hayati will undertake wind-borne flights in the same direction as the wind, to a distance proportional to the wind's speed by a factor *f.* Therefore,

$$flight \ distance \ = \ f \times \text{wind speed} \times \text{flight time,}$$

[1]

Wind velocities are determined from the 30-min averages recorded during the experiment. There are two major ways in which this assumption will introduce errors into the model: the use of 30-min averages, and the use measurements that were made near the ground level.

Wind speed and direction is highly variable, and so any temporal averaging of wind velocity loses information. However, what is critical is that the input data are sufficient for the purposes of the model and the resolution of the empirical data to which it is fitted. The purpose of the model is to demonstrate that, in contrast to previous models using diffusion kernels, *E. hayati* can disperse on the kilometers scale and that this dispersal is by advection. Female *E. eremicus* have been observed to fly for up to 108 min in flight chambers, with mean flights of 10 min for mated females and 34 min for unmated females (Bellamy and Byrne 2001); therefore, wind data averaged over time intervals of the same order of magnitude—30 min—are most suitable. Fitting such a model also offers the opportunity to identify environmental factors, such as time-of-day and weather conditions, that may influence flight on this scale.

Owing to the boundary layer effect, wind speeds are lower when closer to the ground. It is not known exactly how high *E. hayati* fly when undertaking wind-borne dispersal; however, it is possible that it is higher

than 1.8 m (Glick 1939, Freeman 1945, Elzinga et al. 2007), and so the wind speeds measured by our weather station will likely have underestimated the wind speeds *E. hayati* use. This difference is accounted for by the factor *f* such that an underestimate of the wind speed will be corrected by fitting an *f* that is >1. In addition, the factor *f* can account for errors that may reduce the distance traveled by *E. hayati*, such as the possibility that the mean flight time of 10 min taken from flight-chamber experiments is an overestimate of flight time (e.g., because of the harsher field conditions).

The diffusion component of dispersal is not explicitly included in the model for two reasons. First, because the number of grid-points that would be required to adequately represent both the diffusion scale (hundreds of meters) and the wind-borne advection scale (on the order of kilometers) would not be computationally feasible. Second, and more significantly, because the field data obtained are of such a low resolution that the detailed density-distribution data required to fit a diffusion model are not available. However, although there is no explicit diffusion component, the coarse grid used in the model in-effect simulates the spread of insects over the area defined by the grid-square. A grid size of 500 by 500 m was used.

Female Flight Time. It is assumed that the flight time is the same for all females. Using a single uniform flight time simplifies the model; however, it ignores many real-world complicating factors, including dependence of flight time on mating status (Bellamy and Byrne 2001), increased patch-leaving tendency at low host density (Bellamy et al. 2004), a variety of responses to visual plant cues (Blackmer and Cross 2001), potential self-direction toward host cues (Guerrieri 1997, Hagler et al. 2002), relationships between flight-tendency and time-of-day and temperature (Hagler et al. 2002), relationships between egg-load, weight, and host-feeding opportunities (Asplen et al. 2001), and the effects of dessication (Berlinger et al. 1996).

A flight time of 10 min is used in the model, taken from the mean flight time reported for mated *E. eremicus* females in flight-chamber experiments (Bellamy and Byrne 2001, Blackmer and Cross 2001). It should be noted that Bellamy and Byrne (2001) reported a significant difference in flight time with respect to mating status, with unmated females flying for a mean time of 34 min. Because *E. hayati* are arrhenotokous, if the dependence on mating status is similar in the *E. hayati* species, it will manifest as a spatial bias in the sex ratio with more males emerging further from the release field. However, no such bias is evident in the Fassifern emergence data (Fig. 3).

It is unlikely that the *E. hayati* in our experiment flew for an average of exactly 10 min for a number of reasons, including the difference in species and the difference in conditions between the field and the flight chamber. However, the estimate of 10 min provides as reasonable a starting point as possible given the information available, and the error in it will be accounted for during the fitting process (see discussion of the coefficient *f* above).

Conditions for Wind Borne Flight. It is assumed that all females modeled will undertake one wind-borne flight per day, unless certain conditions preventing that flight are met. Conditions identified in the literature under which females may choose not to undertake a wind-borne flight include a high whitefly density in the female's current location (Hoddle et al. 1998, Jones et al. 1999), time of day (Hagler et al. 2002), and weather conditions that make flight difficult or dangerous. For example, Walters and Dixon (1984) showed that the take-off time of cereal aphids could be delayed by several hours if the wind speed was high enough. Response to whitefly density was investigated in the initial exploratory model runs (see Supp. Material [online only]), and both the maximum wind speed constraint and the time-of-day at which flights occurred were used as genetic algorithm fitting parameters in the final models. Because our model assumes that *E. hayati* will fly in the same direction as the prevailing wind at that time, the time of day was used with the wind data collected to determine when flights were undertaken, and to determine whether this was related to the time of day and the wind speed at that time.

Number and Distribution of Eggs Oviposited. It is assumed that the number of eggs oviposited per day is equal over the study period. Villanueva–Jimenez et al. (2012) observed that *E. hayati* show parasitisation up to 25 d postemergence, with a peak in female progeny 5 d postemergence and in male progeny 13 d postemergence, summing to a flattened (though still dual-peaked) profile over 17 d, tapering-off until 25 d postemergence. For comparison, *E. eremicus* has been observed with two peaks in egg-laying, one on the day of emergence and one ≈5 d after emergence (Headrick et al. 1999), and *E. mundus* has been observed laying eggs for ≈10 d after emergence (Qiu et al. 2005). In contrast to *E. hayati*, both *E. eremicus* and *E. mundus* have been observed to lay most of their eggs within a few (≈3) days after emergence (Qiu et al. 2004). Further, dispersal and the egg-laying profile are also thought to be traded-off against one another (Byrne et al. 2001), and may further depend on the protein-availability circumstances in which individuals find themselves (Asplen et al. 2001). As no more detailed information about the egg-laying profile of *E. hayati* is available, assuming a flat profile is the simplest assumption that can be made, and is reasonable given the published data (Villanueva–Jimenez et al. 2012).

It is also assumed that oviposition occurs on the first day of emergence, in the field of emergence. This is justified because *Eretmocerus* is synovigenic and therefore oviposition begins soon after emergence. For example, preoviposition periods of 0.29 d 20°C, 0 d at 29°C (Powell and Bellows 1992), and 0.61 d at 28°C (Headrick et al. 1999) have been observed.

Fitting. After an initial manual fitting process that served to familiarize us with the behavior of the model (Supp. Material [online only]), the key parameters were selected for model fitting: start and end time of
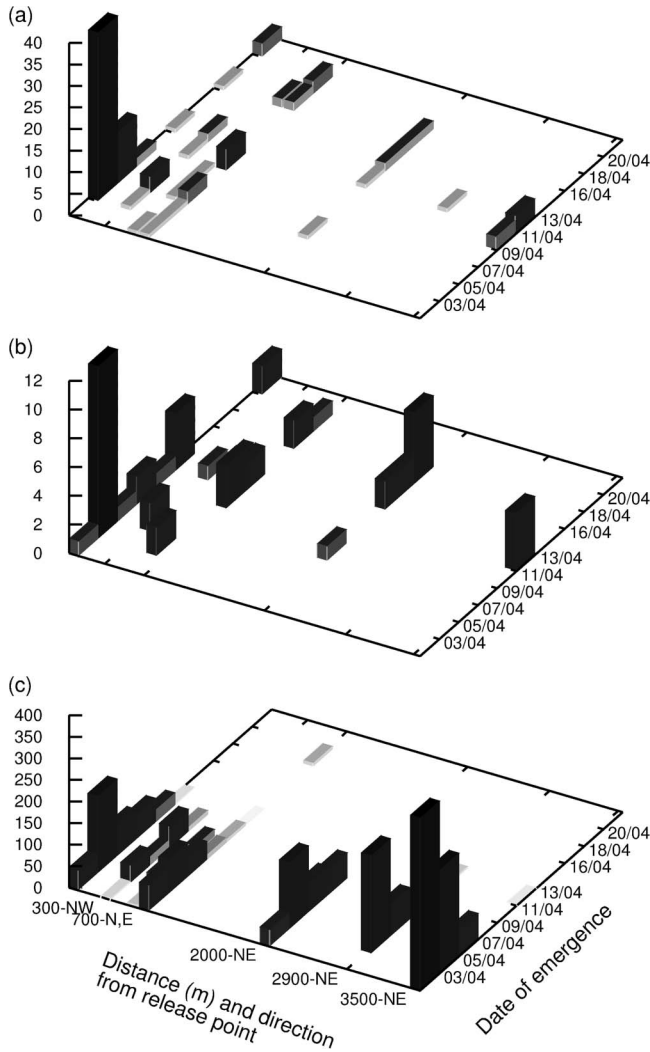
Fig. 3. Number of (a) female *E. hayati*, (b) male *E. hayati*, and (c) host *B. tabaci* emerged over time (day/mo of 2005) from leaves sampled from 'Fassifern' site.

flights, maximum wind speed at which flights occur, and coefficient *f*.

The model was fitted using PyGene, the genetic algorithm library for Python. A genetic algorithm (GA) is an algorithm that searches the parameter space for values that optimize a fitness function using a process that mimics natural selection (Holland 1975). Each individual or phenotype was one set of possible parameter values. Individuals were permitted to reproduce and produce mutations, and their survival to the next generation depended on how well the model with that set of parameter values predicted the data. The code, together with input data, sample runs, and instructions and assistance on the code's use, is available from the lead author.

Owing to the coarseness of the data and the uncertainties introduced by inferring presence from emergence, the GA was run with the objective of matching the presence–absence data. The fitness function *F*

applied a penalty for each incorrect prediction. *F* was increased from 0 by 2 for every 2 d in which no emergence was observed, but the model predicted presence of parasitoids on at least one of those days. *F* was increased by 4 for every 2 d for which emergence was observed, and the model predicted no parasitoids present on either of those days. Erroneously predicting that the parasitoids would be present when none were observed was less heavily penalized than the reverse error, to account for the various ways in which parasitoids may have been present without being detected (e.g., death of the offspring, not collecting enough leaves to detect low densities, etc.). Alternative fitness functions are explored in the Supp. Material (online only).

Validation. The best-fitting model for the Fassifern data set, as found by the GA, was rerun using the initial emergence and wind conditions for Carnarvon. To check for over-fitting, a best-fitting model for the

Carnarvon data set was also rerun on Fassifern. In both cases, model performance was assessed in terms of the GA fitness function and the ability of the models to predict key qualitative features of each data set.

Results

Weather. *Fassifern.* The mean daily temperature recorded over the period was 22°C, and ranged from 19 to 24°C. Rain was recorded during two 30-min intervals: 0.25 mm was recorded at 2.30 a.m., 14 March, and 0.51 mm was recorded at 4:00 p.m., 28 March.

The predominant wind direction during the experimental period was from the south. Generally, faster winds came from the southeast and slower winds from the southwest. Morning wind speeds tended to be slower than those later in the day. A period of high wind speed occurred from 19 to 23 March, with speeds frequently over 2 m/s in the mornings. Days 16, 17, 22–25, and 29 March had wind from a northerly direction, usually occurring later in the day.

Carnarvon. The average temperature over the study period was 23.8°C, ranging between a minimum of 12.6°C and a maximum of 35.4°C. There were several rain days during the experimental period: 9.4 mm was recorded on 31 March, 6.2 mm on 03 April, 53.4 mm on 4 April, and 16.8 mm on 29 April. The predominant wind direction was from the south and southeast, with the highest winds tending to occur in the mid-afternoon.

E. hayati Emergence From Leaves From Release and Sentinel Fields. *Fassifern.* The emergence of male *E. hayati*, female *E. hayati*, and *B. tabaci* from leaves collected from the sentinel fields is presented in Fig. 3. *E. hayati* emerges from the fourth instar, so we chose leaves infested with these.

The start and peak of *E. hayati* emergence is later in fields further from the release field. This pattern is not evident in the emergence of *B. tabaci*, which peaks near the start of the period regardless of the field's distance. Therefore, the pattern of *E. hayati* emergence is suggestive of the dispersal of females.

Carnarvon. The emergence of the host and of *E. hayati* from leaves collected at sentinel fields is presented in Fig. 4.

In contrast with the Fassifern release, leaf collection was made at three different times for the Carnarvon release, allowing for the possibility of collecting second-generation parasitoids. The parasitoids that emerged late in the experiment from Fields 3500-NE and 2300-W were most likely second generation, as they only emerged from leaves that were collected 31 d postrelease, and emerged ≈24 d after the bulk of the emergence from the release field.

Although no time-to-emergence relationships are published for the *E. hayati* species specifically, using relationships derived for related *E. eremicus* and *E. mundus* species (Greenberg et al. 2000, Qiu et al. 2004) emergence time should be between 18 and 22 d

(Greenberg et al. 2000, Qiu et al. 2004). Therefore, it is likely that all late emergence from Fields 3500-NE, 1600-W, and 2300-W after 12 May were second generation. In light of this, for the model fitting, these parasitoid emergence data points were shifted in time to approximate when their female parents would have emerged in the same fields. This is in keeping with the assumption that the synovogenic *Eretmocerus* will oviposit on the first day of emergence in the field of emergence, as is observed for release generation.

Modeling. *Using Emergence to Infer Presence of Release Females.* The rearing of the *E. hayati* was timed such that most emergence would occur on 13 March, so this was set as the start date for the model. Initial manual exploration of the model revealed that key features of the empirical data could be reproduced by changing the maximum wind speed at which flight would occur and the time-of-day during which flights were undertaken. Reducing the maximum wind speed to ≈2 m/s prevented the *E. hayati* from being blown out of the study area altogether by the fast winds that occurred from 19 March onwards. When combined with extending the time-of-day at which flights occurred to include the afternoon (c.f. Hagler et al. 2002, who found that most *E. emiratus* were captured between 6:00 a.m. and 10:00 a.m.), the bimodal shape of emergence in Fields 0, 300-NW, and 700-NW could be reproduced (Supp. Material [online only]).

The GA was then used to find the maximum wind speed, flight period, and *f*, which provided the best fit to the empirical data. A fitness $F = 52$ was obtained when the maximum wind speed was 2.2 m/s, $f = 1$, the flight period start time was 6:30 a.m., and the end time was 5:00 p.m. (Fig. 5a).

Fassifern Model's Performance on Carnarvon. The model fitted for Fassifern was rerun using the wind conditions recorded for Carnarvon, with the additional assumption that emergence was spread uniformly over 12 d to reflect the change in the host nymph stages released. The Fassifern model had mixed success predicting the Carnarvon data (Fig. 6a). The model did correctly predict an increase in parasitoid concentrations in the release field ≈7 d after first emergence, which corresponded to days for which the wind velocities were above 2.2 m/s, preventing the parasitoids from flying. This result gives weight to the hypothesis that *E. hayati* will delay flight during high-wind conditions. The model also correctly predicted the presence of parasitoids in Fields 1600-W and 2300-W soon after the release, matching our deduction that the late emergence in those fields were second-generation parasitoids. However, the predictions for NE Fields, 3200-W, and 300-E are poor, and the model parasitoids did not reach Field 6300-NE at all.

Fitting the Carnarvon Model. The GA was used to find the parameter values that led to the best-fitting model, where the maximum wind speed at which parasitoids would fly was held at 2.2 m/s (Fig. 6). A fitness $F = 82$ was obtained when $f = 2.02$, the flight
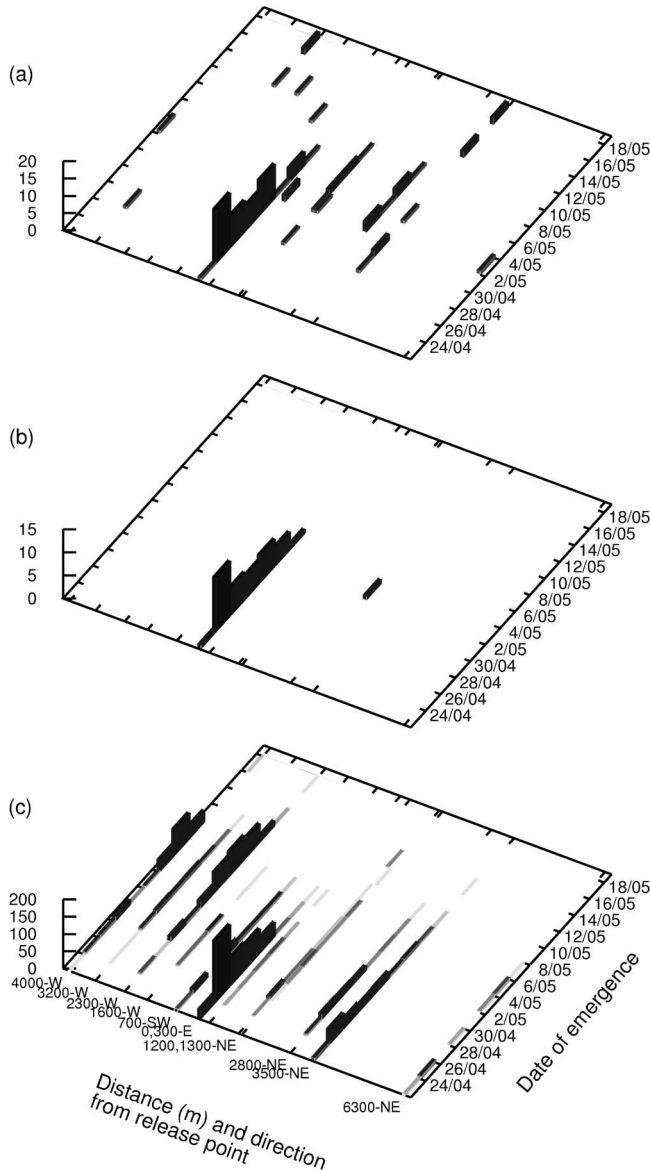
Fig. 4. Number of (a) female *E. hayati*, (b) male *E. hayati*, and (c) host *B. tabaci* emerged over time (day/mo of 2008) from leaves sampled from 'Carnarvon' site.

period start time was 5:00 a.m., and the end time was 7:00 p.m. So the GA extended the flight time slightly compared with the best-fit for Fassifern; however, the most significant difference was the doubling of the factor *f*, which effectively doubles the distance that the parasitoids traveled.

The model found by the GA was better able to predict parasitoid presence for NE Fields, 3200-W, and 300-E; however, it still could not predict the arrival of parasitoids at field 6300-NE in comparably high numbers. One possible reason for this failure is that the model makes the simplifying assumption that all parasitoids remain airborne for the average length of time. However, Bellamy and Byrne (2001) also observed a

wide range of flight times for *E. eremicus*, from 2 s for one mated male to >108 min for one unmated female, so it is possible the emergence at this field was from rare parasitoids that flew further than the average.

Carnarvon Model's Performance on Fassifern. To test how reasonable the model found by the GA for the Carnarvon data were, and to check for over-fitting, the model was rerun on the Fassifern site (Fig. 5c). The Carnarvon model has a fitness of $F = 82$ on the Fassifern data, as compared with 52 from the best-fitting model. However, comparing Fassifern's best fit to Carnarvon's best fit (Fig. 5a and b), it can be seen that the difference between the two model predictions is small. The new Carnarvon-fitted parameter
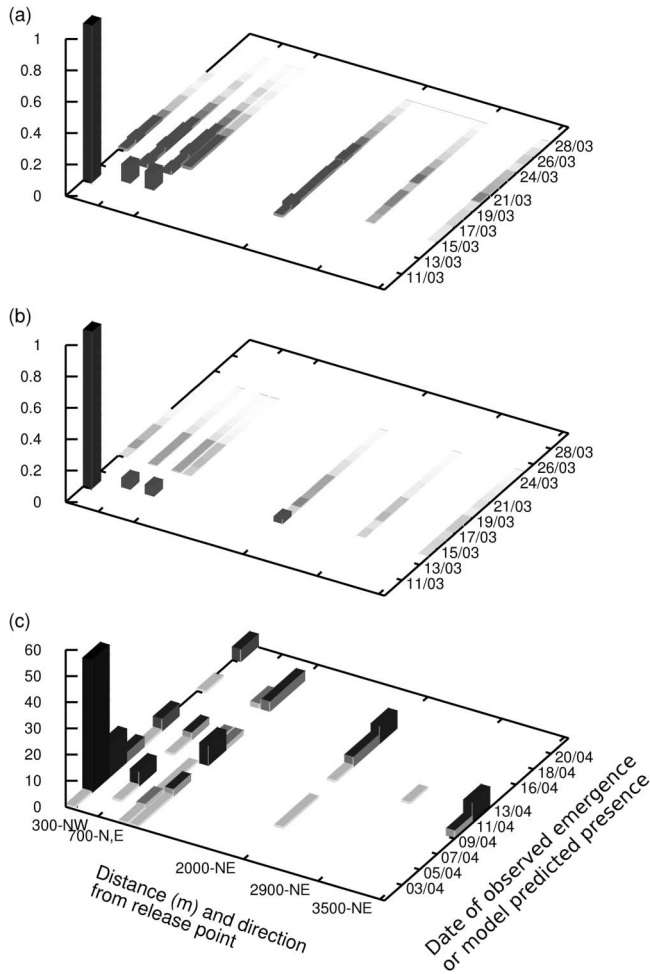
Fig. 5. The relative density of female *E. hayati* parasitoids through time (d/mo of 2005, solid) as predicted by (a) the best-fitting model ($F = 52$) for Fassifern, and (b) the best-fitting model ($F = 82$) for Carnarvon, and (c) the observed emergence of *E. hayati* from sites at Fassifern.

values make predictions that still retain key features from the Fassifern-fitted values, namely, the return of parasitoids to Fields 0, 300-NW, and 700-NW after dispersal, and the general tendency for parasitoids to arrive at further fields later in the experiment.

Discussion

This study provides evidence that supports the view expressed in Petit et al. (2008) that a first-time release of a biological control agent is an excellent opportunity with which to study dispersal. Without the methodological limitations of direct marking and recapture studies, first-generation emergence data provided enough information to infer the presence of females released, to test the hypothesis of wind-advection, and to identify the broad factors governing it.

This study also supports the authors' previous recommendation (Kristensen et al. 2013) that a hierarchical sampling design be used for measuring disper-

sal. The model fitted and tested here presents a radically different perspective on parasitoid and *Eretmocerus* dispersal compared with that presented in the literature so far. While this may be a result of real differences in the dispersal mechanism between the species considered—that is, wind-advection may be peculiar to *E. hayati* as compared with other *Eretmocerus* for which diffusion dispersal models have been used (Brewster et al. 1997, Simmons 2000)—this study's result raises the possibility that the preponderance of such models may be an artifact of the sampling methodology used, rather than a true representation of parasitoid dispersal mechanisms.

To the specific question of *E. hayati* as an effective biocontrol agent for *Bemisia*, the results of this study are encouraging. *Bemisia* is known to travel on the wind for long times over long distances (Blackmer and Byrne 1993, Byrne et al. 1996), and so an effective biocontrol agent will need to have dispersal capabilities to match that. Evidence of wind-borne dispersal
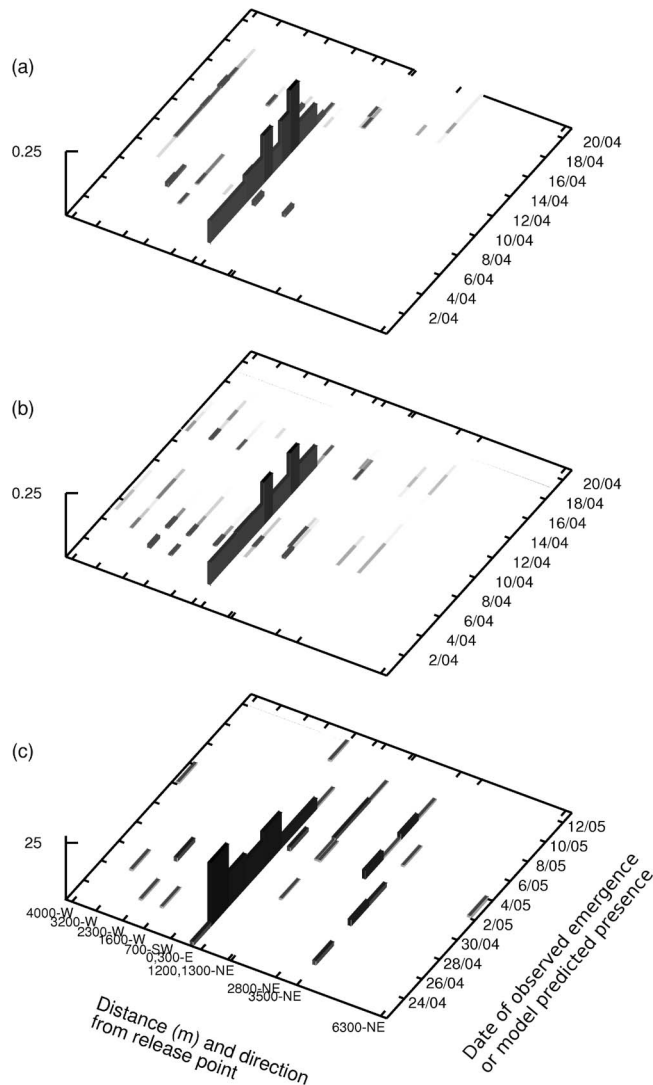
Fig. 6. The relative density of female *E. hayati* parasitoids through time (d/mo of 2008) as predicted by (a) the best-fitting model for Fassifern (Fig. 3) applied to the Carnarvon ($F = 114$), and (b) the best-fitting model for Carnarvon ($F = 82$), and the (c) observed emergence of *E. hayati*, including a time-shifted second-generation emergence. The assumption that parasitoids will not fly above 2.2 m/s led to a predicted increase in parasitoid concentrations in Field 0 corresponding to 1 May 2008 and 2 May 2008 in the observed data.

over several kilometers suggests that *E. hayati* will be a more successful *B. tabaci* biocontrol agent than *E. eremicus*. The relatively poor dispersal capability of *E. eremicus* has been cited as a key reason behind its failure (Bellamy et al. 2004).

The model validation step used increases our confidence that wind dispersal is an important component of *E. hayati* dispersal. Our model also suggests that the flights take place at any time during daylight hours; that a flight is attempted every day after emergence unless there are high wind conditions during that day; and that the flight will be delayed for wind speeds above ≈2 m/s. However, as only one additional site was available for model validation, we recommend

that the specifics of this description be treated with caution. We hope that this preliminary description of *E. hayati* dispersal can provide a basis from which further work on parasitoid dispersal using *E. hayati* as a model species may be performed.

Acknowledgments

References Cited

Antolin, M., and D. Strong. 1987. Long-distance dispersal by a parasitoid (*Anagrus delicatus*, Mymaridae) and its host. Oecologia 73: 288–292.

Asplen, M., D. Bellamy, and D. Byrne. 2001. Eggs of *Eretmocerus eremicus*, a whitefly parasitoid, pp. 11–13. *In* D. Byrne and P. Baciewicz (eds.), Vegetable Report Series P-127, University of Arizona, College of Agricultural and Life Sciences.

Ayvaz, A., E. Karasu, S. Karabörklü, and S. Yilmaz. 2008. Dispersal ability and parasitization performance of egg parasitoid *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae) in field and storage conditions. Turk. J. Biol. 32: 127–133.

Bellamy, D., and D. Byrne. 2001. Effects of gender and mating status on self-directed dispersal by the whitefly parasitoid *Eretmocerus eremicus*. Ecol. Entomol. 26: 571–577.

Bellamy, D., M. Asplen, and D. Byrne. 2004. Impact of *Eretmocerus eremicus* (Hymenoptera: Aphelinidae) on open-field *Bemisia tabaci* (Hemiptera: Aleyrodidae) populations. Biol. Control 29: 227–234.

Berlinger, M., N. Lehmann–Sigura, and R. Taylor. 1996. Survival of *Bemisia tabaci* adults under different climatic conditions. Entomol. Exp. Appl. 80: 511–519.

Blackmer, J., and D. Byrne. 1993. Flight behaviour of *Bemisia tabaci* in a vertical flight chamber: effect of time of day, sex, age and host quality. Phys. Entomol. 18: 223–232.

Blackmer, J., and D. Cross. 2001. Response of *Eretmocerus eremicus* to skylight and plant cues in a vertical flight chamber. Entomol. Exp. Appl. 100: 295–300.

Brewster, C., J. Allen, D. Schuster, and P. Stansly. 1997. Simulating the dynamics of *Bemisia argentifolli* (Homoptera: Aleyrodidae) in an organic cropping system with a spatiotemporal model. Environ. Entomol. 26: 603–616.

Byrne, D., R. Rathman, T. Orum, and J. Palumbo. 1996. Localized migration and dispersal by the sweet potato whitefly, *Bemisia tabaci*. Oecologia 105: 320–328.

Byrne, D., D. Bellamy, and M. Asplen. 2001. Behavior and physiology associated with short-range migration by small insects. NCR 148 report.

Chapman, R. F. 1982. The insects: structure and function. Harvard University Press, Cambridge, MA.

Chapman, J., D. Reynolds, A. Smith, and I. Woioda. 2004. An aerial netting study of insects migrating at high altitude over England. Bull. Entomol. Res. 94: 123–136.

Chapman, A., T. Kuhar, P. Schultz, and C. Brewster. 2009. Dispersal of *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae) in potato fields. Environ. Entomol. 38: 677–685.

Corbett, A., and J. Rosenheim. 1996. Impact of a natural enemy overwintering refuge and its interaction with the surrounding landscape. Ecol. Entomol. 21: 155–164.

Darrouzet–Nardi, A., M. Hoopes, J. Walker, and C. Briggs. 2006. Dispersal and foraging behaviour of *Platygaster californica*: hosts can't run, but they can hide. Ecol. Entomol. 31: 298–306.

De Barro, P., and M. Coombs. 2009. Post-release evaluation of *Eretmocerus hayati* Zolnerowich and Rose in Australia. Bull. Entomol. Res. 99: 193–206.

De Barro, P., and P. Hart. 2001. Antibiotic curing of parthenogenesis in *Eretmocerus mundus* (Australian parthenogenic form). Entomol. Exp. Appl. 99: 225–230.

De Barro, P., F. Driver, I. Naumann, S. Schmidt, G. Clarke, and J. Curran. 2000. Descriptions of three species of *Eretmocerus* Haldeman (Hymenoptera: Aphelinidae) parasitising *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) and *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) in Australia based on morphological and molecular data. Aust. J. Entomol. 39: 259–269.

Desouhant, E., G. Driessen, L. Lapchin, S. Wielaard, and C. Bernstein. 2003. Dispersal between host populations in field conditions: navigation rules in the parasitoid *Venturia canescens*. Ecol. Entomol. 28: 257–267.

Doutt, R., and J. Nakata. 1973. The Rubus leafhopper and its egg parasitoid: an endemic biotic system useful in grape-pest management. Environ. Entomol. 2: 381–386.

Elzinga, J., S. Van Nouhuys, D. Van Leeuwen, and A. Biere. 2007. Distribution and colonisation ability of three parasitoids and their herbivorous host in a fragmented landscape. Basic Appl. Ecol. 8: 75–88.

Freeman, J. 1945. Studies in the distribution of insects by aerial currents. J. Anim. Ecol. 14: 128–154.

Glick, P. 1939. The distribution of insects, spiders, and mites in the air. US Department of Agriculture, Washington, DC.

Greenberg, S., B. Legaspi, W. Jones, and A. Enkegaard. 2000. Temperature-dependent life history of *Eretmocerus eremicus* (Hymenoptera: Aphelinidae) on two whitefly hosts (Homoptera: Aleyrodidae). Environ. Entomol. 29: 851–860.

Grillenberger, B., J. Gadau, R. Bijlsma, L. Van De Zande, and L. Beukeboom. 2009. Female dispersal and isolation-by-distance of *Nasonia vitripennis* populations in a local mate competition context. Entomol. Exp. Appl. 132: 147–154.

Guerrieri, E. 1997. Flight behaviour of *Encarsia formosa* in response plant and host stimuli. Entomol. Exp. Appl. 82: 129–133.

Hagler, J., C. Jackson, T. Henneberry, and J. Gould. 2002. Parasitoid mark-release-recapture techniques–II. Development and application of a protein marking technique for *Eretmocerus* spp., parasitoids of *Bemisia argentifolii*. Biocontrol Sci. Tech. 12: 661–675.

Hastings, A. 2000. Parasitoid spread: lessons for and from invasion biology, pp. 70–82. *In* M. Hochberg and A. Ives (eds.), Parasitoid Population Biology. Princeton University Press, Princeton, NJ.

Hendricks, D. 1967. Effect of wind on dispersal of *Trichogramma semifumatum*. J. Econ. Entomol. 60: 1367–1373.

Headrick, D., T. Bellows, and T. Perring. 1999. Development and reproduction of a population of *Eretmocerus eremicus* (Hymenoptera: Aphelinidae) on *Bemisia argentifolii* (Homoptera: Aleyrodidae). Environ. Entomol. 28: 300–306.

Holland, J. 1975. Adaptation in natural and artificial systems. MIT Press, Cambridge, MA.

Hoddle, M., R. van Driesche, J. Elkinton, and J. Sanderson. 1998. Discovery and utilization of *Bemisia argentifolii* patches by *Eretmocerus eremicus* and *Encarsia formosa* (Beltsville strain) in greenhouses. Entomol. Exp. Appl. 87: 15–28.

Jones, W., S. Greenberg, and B. Legaspi. 1999. The effect of varying *Bemisia argentifolii* and *Eretmocerus mundus* ratios on parasitism. BioControl 44: 13–28.

Keller, M. A., and W. J. Lewis. 1985. Movements by *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) released into cotton. Southwest. Entomol. Suppl. 8: 99–109.

Kölliker–Ott, U., F. Bigler, and A. Hoffmann. 2004. Field dispersal and host location of *Trichogramma brassicae* is influenced by wing size but not wing shape. Biol. Control 31: 1–10.

Kristensen, N., P. DeBarro, and N. Schellhorn. 2013. The initial dispersal and spread of an intentional invader at three spatial scales. PLoS ONE 8: e62407.

Langhof, M., R. Meyhöfer, H. Poehling, and A. Gathmann. 2005. Measuring the field dispersal of *Aphidius colemani* (Hymenoptera: Braconidae). Agric. Ecosyst. Environ. 107: 137–143.

McAuslane, H., and R. Nguyen. 1996. Reproductive biology and behavior of a thelytokous species of *Eretmocerus* (Hymenoptera: Aphelinidae) parasitizing *Bemisia argentifolii* (Homoptera: Aleyrodidae). Ann. Entomol. Soc. Am. 89: 686–693.

McKenzie, L., and B. Beirne. 1972. A grape leafhopper *Erythroneura ziczac* (Homoptera: Cicadellidae) and its mymarid (Hymenoptera) egg-parasite in the Okanagan Valley, British Columbia. Can. Entomol. 104: 1229–1233.

Moriya, S., K. Inoue, A. Otake, M. Shiga, and M. Mabuchi. 1989. Decline of the chestnut gall wasp population, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae) after the establishment of *Torymus sinensis* Kamijo (Hymenoptera: Torymidae). Appl. Entomol. Zool. 24: 231–233.

Paranhos, B., P. Mendes, N. Papadopoulos, and J. Walder. 2007. Dispersion patterns of *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) in citrus orchards in southeast Brazil. Biocontrol Sci. Tech. 17: 375–385.

Pasek, J. 1988. Influence of wind and windbreaks on local dispersal of insects. Agric. Ecosyst. Environ. 22: 539–554.

Petit, J., M. Hoddle, J. Grandgirard, G. Roderick, and N. Davies. 2008. 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). Biol. Control 45: 344–352.

Powell, D., and T. Bellows. 1992. Development and reproduction of two populations of *Eretmocerus* species (Hymenoptera: Aphelinidae) on *Bemisia tabaci* (Homoptera: Aleyrodidae). Environ. Entomol. 21: 651–658.

Qiu, Y., J. van Lenteren, Y. Drost, and C. Posthuma–Doodeman. 2004. Life-history parameters of *Encarsia formosa, Eretmocerus eremicus* and *E. mundus,* aphelinid parasitoids of *Bemisia argentifolii* (Hemiptera: Aleyrodidae). Eur. J. Entomol. 101: 83–94.

Qiu, B.L., P. J. De Barro, and S. X. Ren. 2005. Development, survivorship and reproduction of *Eretmocerus* sp. nr *furuhashii* (Hymenoptera: Aphelinidae) parasitizing *Bemisia tabaci* (Hemiptera: Aleyrodidae) on glabrous and non-glabrous host plants. Bull. Entomol. Res. 95: 313–319.

Sallam, M., W. Overholt, and E. Kairu. 2001. Dispersal of the exotic parasitoid *Cotesia flavipes* in a new ecosystem. Entomol. Exp. Appl. 98: 211–217.

Scarratt, S., S. Wratten, and P. Shishehbor. 2008. Measuring parasitoid movement from floral resources in a vineyard. Biol. Control 46: 107–113.

Schellhorn, N., J. Bellati, C. Paull, and L. Maratos. 2008. Parasitoid and moth movement from refuge to crop. Basic Appl. Ecol. 9: 691–700.

Simmons, G. S. 2000. Studies on dispersal of a native parasitoid *Eretmocerus eremicus* and augmentative biological control of *Bemisia tabaci* infesting cotton. Ph.D. thesis, University of Arizon, Tucson, AZ.

Smith, S. 1988. Pattern of attack on spruce budworm egg masses by *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) released in forest stands. Environ. Entomol. 17: 1009–1015.

Suverkropp, B., F. Bigler, and J. Lenteren. 2009. Dispersal behaviour of *Trichogramma brassicae* in maize fields. Bull. Insectol. 62: 113–120.

Takasu, K., S. Takano, N. Mizutani, and T. Wada. 2004. Flight orientation behavior of *Ooencyrtus nezarae* (Hymenoptera: Encyrtidae), an egg parasitoid of phytophagous bugs in soybean. Entomol. Sci. 7: 201–206.

Villanueva–Jimenez, J., N. Schellhorn, and P. DeBarro. 2012. Comparison between two species of *Eretmocerus* (Hymenoptera: Aphelinidae): reproductive performance is one explanation for more effective control in the field. Biol. Control 63: 333–338.

Walters, K.F.A., and A.F.G. Dixon. 1984. The effect of temperature and wind on the flight activity of cereal aphids. Ann. Appl. Biol. 104: 17–26.

Williams, E. 1984. The life history and ecology of *Euphydryas gillettii* Barnes (Nymphalidae). J. Lepid. Soc. 38: 1–12.

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