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
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-fitting, 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
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 $24.851314^\circ$S, $113.731267^\circ$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

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

<table>
<thead>
<tr>
<th>Name</th>
<th>x-coordinate (m)</th>
<th>y-coordinate (m)</th>
<th>Crop</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field 0</td>
<td>0</td>
<td>0</td>
<td>Green beans</td>
</tr>
<tr>
<td>Field 300-NW</td>
<td>−175</td>
<td>300</td>
<td>Green beans</td>
</tr>
<tr>
<td>Field 700-N</td>
<td>−75</td>
<td>675</td>
<td>Soybeans</td>
</tr>
<tr>
<td>Field 700-E</td>
<td>700</td>
<td>0</td>
<td>Green beans</td>
</tr>
<tr>
<td>Field 2000-NE</td>
<td>1500</td>
<td>1375</td>
<td>Green beans</td>
</tr>
<tr>
<td>Field 2900-NE</td>
<td>2375</td>
<td>1675</td>
<td>Green beans</td>
</tr>
<tr>
<td>Field 3600-NE</td>
<td>2750</td>
<td>2375</td>
<td>Green beans</td>
</tr>
</tbody>
</table>

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.

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![Carnarvon Release and Sampling Locations](image-url)  
Fig. 2. The ‘Carnarvon’ site is situated on the mid-west coast of Western Australia, Australia, to the east of the town of Carnarvon.
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,

$$\text{flight distance} = f \times \text{wind speed} \times \text{flight time},$$  \[1\]

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 whitely density in the female’s current location (Hodde 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 whitely 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 synovogenic and therefore oviposition begins soon after emergence.

**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
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 the 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

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.
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 emergence. 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 $f = 2.52$, the flight
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.
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 dispersal. The model fitted and tested here presents a radically different perspective on parasitoid and \textit{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 \textit{E. hayati} as compared with other \textit{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 \textit{E. hayati} as an effective biocontrol agent for \textit{Bemisia}, the results of this study are encouraging. \textit{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. 5. The relative density of female \textit{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 \textit{E. hayati} from sites at Fassifern.](image-url)
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 \( \approx 2 \) 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**

We thank Gregory Simmons for his comments and providing us with an early version of his manuscript. This project has been funded in part by Horticulture Australia Limited using the AUSVEG Levy and matched funds from the Australian Government, and by the Plant Biosecurity CRC.


Received 25 August 2012, accepted 30 July 2013.