Estimating dispersal rate of the silky cane weevil (Coleoptera: Curculionidae)*

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Abstract: The objective of this study was to estimate the silky cane weevil rate of dispersal under near-natural conditions inside a screened enclosure where an array of buckets was baited with cut sugarcane stalks. One hundred weevils were released and weevils inside the buckets were counted hourly for 8 h, and then 24 and 48 h after release. A passive diffusion model was used to estimate the weevil’s dispersal and disappearance rates, within and between rows of buckets with sugarcane. The weevils concentrated around the release point and slowly moved towards the boundaries of the experimental plot over time with an overall average dispersal rate of 2.8 ± 3.58 cm²/h. Dispersal and disappearance rates within and between rows were not significantly different among the time intervals considered (1–8, 8–24 and 24–48 h after release) except for the 1–8 time interval on the array representing the release point when the dispersal rate, \( D \), was significantly higher than those at other time intervals. Continuum of the substratum to disperse from one side of the array to another via a wooden bridge may explain the higher dispersal rate through this array. The number of buckets exposed to the sun during the morning hours was significantly higher on those rows exposed to the sun (south side of the screen enclosure) than on the shaded side. Longer times of bucket exposure to the sun may explain the predominant distribution of weevils in that area suggesting that the weevil population is constantly expanding and retracting according to micro environmental conditions.

Key words: Metamasius hemipterus, diffusion model, dispersal, dispersal rate, speed of movement

1 Introduction

The silky cane weevil, Metamasius hemipterus sericeus (Olivier) (Coleoptera: Curculionidae) is a pest of sugarcane, palms, banana and pineapple in Central and South America, the Caribbean and Africa (Vaurie, 1966). Giblin-Davis et al. (1994) reported that this weevil was introduced into Florida in the mid-1980s where it later became a significant pest of sugarcane (Saccharum officinarum L.) and ornamental palm species, including Hyophorbe verschaffeltii Wendland, Phoenix canariensis Hortorum ex Chabaud, Ptychosperma macarthurii (Wendland), Ravena rivialis, Roystena rergia (Humbolt, Bonpland and Kunth) and Washingtonia robusta Wendland. In sugarcane, this weevil has caused losses at one sugarcane farm estimated at $402.40 per hectare (Sosa et al., 1997), this amount representing more than 50% loss of revenues. In Colombia, the weevil has been implicated as a possible vector of the nematode, Bursaphelenchus cocophilus (Cobb), responsible for red ring disease of coconut (Cocos nucifera L.) and African oil palms (Elais guineensis Jacq.) (Weissling et al., 1992; Calvache et al., 1995). Because South Florida is a recipient of these major field plantings, it is important, for forecasting and management purposes, to determine the rate at which the weevil populations can spread.

The rate of insect dispersal can be used to predict pest outbreaks (Joyce, 1976) and patterns of host selection (Stanton and Cook, 1984). To develop accurate and efficient sampling procedures that can be used to predict economic populations levels in a crop, it is important to understand how the spatial distribution of an insect pest is achieved after dispersal occurs (Ruesink, 1980; Taylor, 1986). It has been suggested that measuring movement or dispersal rates (Vandermeer, 1989) and using diffusion models (Okubo, 1980; Kareiva, 1983) may be the key to generating optimal indicators of the predictability and reliability of a suggested control technique to reduce insect damage and determining herbivore densities in intercropping schemes (Banks and Ekrom, 1999). Herein, we used mathematical models and results of release-recapture experiments as a first approach to understand the foraging movement of the silky cane weevil, and to quantify its movement behaviour by estimating the weevil’s rate of dispersal.

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2 Materials and Methods

2.1 Trapping

Five black plastic buckets (37 × 30 × 30 cm³, WESSLING et al., 1992) placed on five different sites and baited with 0.5 kg of chopped sugarcane stalks (Saccharum officinarum L.) and pads of Metalure (Chemtica, Costa Rica), a weevil male attractant, were set up at the USDA-ARS-SHRS, Miami FL to collect the weevils for the experiment. Moist sponges were placed inside the buckets and water was added periodically to preserve moisture. Trapping began in March and continued for 8 weeks. Weevils were held in plastic containers (20 × 12 × 12 cm) with moist absorbent paper and pieces of sugarcane stalks until needed.

2.2 Screen enclosure experiments

The study was conducted in a screened enclosure (5 × 16 × 3 m), located at the USDA-ARS-SHRS Miami, FL. For each of the six experiments, 60 plastic buckets (17 × 17 × 18 cm), baited with 50 cm long sugarcane stalks and a moist sponge were placed on two tables (9 m long × 1.5 m wide each) covered with a layer of gravel and the tables were separated by a space of 1.5 m (fig. 1). The purpose of having two tables spaced between them was to simulate the space in between sugarcane rows in the field. The buckets in the array were spaced 0.3 m from each other and arranged in four rows of 15 buckets each row, 1 m between rows. The entire test was set inside the screen enclosure. Rows were arranged East-West with row 1 located on the south side of the array. One hundred weevils were released on the centre of the array on a wooden bridge that connected the two tables. The purpose of the wooden bridge was to provide a platform for releasing the weevils, and provide the weevils with an easy access to the experimental set up of two tables with buckets and sugarcane. The buckets were checked every hour for the first 8 h after release, and subsequently at 24 and 48 h after release. When weevils were found in the external boundary of the sugarcane bucket array, the experiment was terminated. The screen enclosure was divided into 20 subplots of three buckets each. The position and numbers of recaptured weevils were recorded to determine the dispersal rate (or diffusion rate measured in cm²/h) of the weevils within and between rows. Exposure of the buckets to the sun was noted.

2.3 Dispersal rate of sugarcane weevil

In order to use a diffusion model to describe insect dispersal, an assumption of no directionality needs to be satisfied. This assumption was verified for each release experiment. The average displacement of recaptured weevils was calculated using the equation (Turchin and Thony, 1993):

\[ X_j = \frac{\sum_{i=1}^{n} x_i C_{ij}}{\sum_{i=1}^{n} C_{ij}} \]  

where \( C_{ij} \) represent the cumulative recaptures in trap \( i \) over the course of recapture run \( j \), \( x_i \) was the \( x \) coordinate of the location trap \( i \) relative to the central release point, and \( n \) was the number of traps. The average displacement \( X_j \) along the \( x \) coordinate was provided by Equation 1 (BLACKMER et al., 2004). Similar calculations were used to determine average displacements along the \( y \) coordinate. If the average displacement was found not to be significantly different from zero (t-test, SAS Institute, 1999), then the recapture data were fit to a statistical passive diffusion model under the assumption that a diffusion process could explain the weevil’s movement. A passive diffusion model (Skellam, 1951; Dempster, 1957) was used to analyse the movement of weevils over time. This model was chosen because it can separate the effect of mortality from movement per se (Skellam, 1951). Diffusion is the tendency of a group of individuals concentrated initially near a point in space to spread out in time, gradually occupying an even larger area around the initial point (OKANO, 1980). The model assumes that random movement will tend to homogenize differences in insect densities between two areas. Overall changes in insect numbers are determined by emigration, birth or death. The model of Dempster (1957) was modified to allow estimates of the diffusion rate (dispersal rate), \( D \), in two dimensions, such that

\[ \frac{\partial N(x,y,t)}{\partial t} = D_1 \left( \frac{\partial^2 N}{\partial x^2} \right) + D_2 \left( \frac{\partial^2 N}{\partial y^2} \right) - \mu N \]  

where \( \frac{\partial N(x,y,t)}{\partial t} \) expressed the change in number of weevils in a period of time, \( D_1 \) was the dispersal rate within rows, \( D_2 \) was the dispersal rate between rows, \( \mu \) was the disappearance rate of insects (combined migration and death minus birth), and \( N \) was the initial number of weevils found in the centre square of a 3 × 3 lattice square (fig. 2). Each lattice square was comprised by nine of the 20 subplots (of three buckets each) inside the screen enclosure, with a total of six lattice squares (fig. 2). The terms \( \frac{\partial^2 N}{\partial x^2} \) and \( \frac{\partial^2 N}{\partial y^2} \) measure the change in spatial gradient of insect density at point \( (x, y) \). Thus, the net change in insect numbers due to random

![Fig. 1. Distribution of plastic buckets (O) baited with sugarcane stalks and placed on two tables connected by a wooden bridge (X) that provided 100 released weevils to an easy access to the experimental set up](image-url)
movement is proportional to these last terms, according to Fick’s law of diffusion (Okubo, 1980). This method assumes that movement between sections of the area is random and that $D$ and $\mu$ are constant. The dispersal rate ($D_1$ or $D_2$) is interpreted as the number of insects moving between two equal areas with a density gradient of one insect between them in unit time $t$. This method yields the following estimates of the terms above, for a central square surrounded by squares of equal area, arranged as a $3 \times 3$ lattice (Puchin, 1991):

$$\frac{\partial^2 N}{\partial x^2} = \frac{1}{3}(N_{11} - 2N_{12} + N_{13} + N_{21} - 2N_{22} + N_{31})$$

$$+ N_{31} - 2N_{32} + N_{33})$$

and

$$\frac{\partial^2 N}{\partial y^2} = \frac{1}{3}(N_{11} + N_{12} + N_{13} - 2(N_{21} + N_{22} + N_{23})$$

$$+ N_{31} + N_{32} + N_{33})$$.

In these terms $N_{ij}$ denotes the number of insects ($N$) in the central square ($x, y$) of the $3 \times 3$ lattice square (fig. 1). Therefore, this procedure allows for an estimation of dispersal rate of a cohort of weevils moving simultaneously and independently through the bucket array in two directions (within and between rows). Six lattice squares (A–F) were used to determine the dispersal rate within rows (via combinations of lattice squares ABC and DEF) and between rows (via combinations of lattice squares AD, BE and CF) (fig. 1). A series of simultaneous equations was developed for the central square of each $3 \times 3$ lattice square in the 20-subplot plot using Equation 1 (for lattice squares A through F, fig. 2). Using the densities of weevils in each subplot, the equations were then solved by minimal squares and the values of $D_1$, $D_2$ and $\mu$ were obtained (Sternwood, 1978). These values were calculated for every hour after release for the first 8 h and for the time intervals 1–8, 8–24, and 24–48 h after release.

### 2.4 Statistical analysis

Data were tested for homogeneity of variances and normality to meet the assumptions for parametric tests. An ANOVA was used to detect effects of time intervals on the dispersal rates, $D$ and the disappearance rate, $\mu$ if normality was not found, to normalize the data and stabilize the variance, estimated values of $D$ and $\mu$ were square root transformed ($x + 0.5$) and an ANOVA was used to detect effects of time intervals. When no transformation normalized the data, the non-parametric Kruskal–Wallis ANOVA was used followed by a non-parametric multiple comparison procedure (Siegel and Castellan, 1988) to detect differences of $D$ and $\mu$ among time intervals tested. A $t$-test was used to determine if average displacement of recaptures was significantly different from zero along the $x$ and $y$-axes. A Mann-Whitney $U$-test was used to compare movement within ($D_1$) and between rows ($D_2$). Number of buckets exposed to the sun, and number of hours that buckets were exposed to the sun during the morning (8:00–11:55 a.m.) and afternoon (12:00–3:00 p.m.) hours were grouped according to rows in the screen enclosure array. An ANOVA was used to detect differences on number of buckets exposed to the sun and hours that buckets were exposed to the sun among the four rows of buckets (SAS Institute, 1999).

### 3 Results

The average ($\pm$SE) overall dispersal rate of the silky cane weevil was 2.8 ± 3.58 cm$^2$/h (table 1). The weevils moved slowly (walking and flying) from the centre of the array (the release point, fig. 3a) towards the boundary of the array (fig. 3b,c) during the first 24 h after release. However, movement appeared to be negligible between 24 and 48 h after release (fig. 3d).

The average displacement of recaptures was not significantly different from zero along the $x$-axis. The mean recapture displacement for $X_j$ was 0.028 ± 0.011 ($t = -2.595$, d.f. = 4, $P < 0.05$). The mean recapture displacement in the $y$-axis was small but significantly shifted to the southeast. $Y_j$ was 0.049 ± 0.009 ($t = -5.323$, d.f. = 4, $P < 0.05$). Even though the shift along the $y$-axis was significant, directional biases were considered slight enough because the order of magnitude of the dispersal movement was greater than the shift along the $y$-axis (Blackmer et al., 2004). Therefore, data can be fit to the diffusion model. The mean hourly dispersal rates, $D$ (cm$^2$/h), the first 8 h after release in the within-row arrays (ABC and DEF) and the between row arrays (AD, BE and CF) are shown in table 2. In the ABC array most of the dispersal occurred the first 4 h after release (positive values, within rows) followed by a reduced dispersal between 5 and 7 h. This result was reiterated by the mean hourly disappearance rate, $\mu$, which was positive the first hour after release and then became negative or
close to zero after this time (table 2). The mean hourly dispersal rates, $D$, via the DEF array (northerly side of the within row array) were all negative indicating that movement within rows was negligible through that array (Dempster, 1957). In contrast, the mean hourly disappearance rate, $\mu$, was positive during the first 2 h after release (table 2) indicating that the weevils were leaving the DEF array during these times, but then became negative. In the between row AD array, $D$ and $\mu$ were positive 1 h after release but became negative afterwards. This result suggests that weevils flew towards the AD array in the morning but then movement was negligible. On the CF array, $D$ and $\mu$ were positive and very close to zero only 1 and 4 h after release and then became negative, suggesting that weevil’s movement was negligible through the CF array. However, on the BE array, the mean hourly $\mu$ were positive the first 5 h after release suggesting that weevils were moving through the release point during this period of time.

Comparisons of dispersal and disappearance rates between time-intervals are shown in table 1. The only difference detected was in the BE array among time intervals. $D$ was significantly higher at the 1–8 time interval compared with the 8–24 and 24–48 time intervals (table 1; Wilcoxon signed-rank test, $P < 0.05$). Values of $D$ and $\mu$ were grouped according to type of movement (within and between rows), but they were not significantly different (Wilcoxon signed-rank test, $P > 0.05$, for both $D$ and $\mu$, respectively).

The number of buckets (B) exposed to the sun during the morning hours was significantly higher for rows 1 and 2 (south side of screen enclosure or combined ABC array) than for rows 3 and 4 (north side or combined array DEF; Wilcoxon signed-rank test, $P < 0.05$, table 3). The number of hours (h) of the morning sampling scheme that the buckets were exposed to the sun was not significantly different for rows 1 and 2 (combined array ABC) than for those in rows 3 and 4 (combined array DEF) (Wilcoxon signed-rank test, $P > 0.05$).

### Discussion

The dispersal rate of the silky cane weevil during the first 48 h after release followed a simple diffusion...
Table 2. Mean (± SE) hourly dispersal rates, D and disappearance rates, μ for the silky-cane weevil movement through the within-row arrays (ABC and DEF) and the between-row arrays (AD, BE and CF) the first 7 h after release.

<table>
<thead>
<tr>
<th>Hours after release</th>
<th>Within-rows</th>
<th>Between-rows</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ABC</td>
<td>DEF</td>
</tr>
<tr>
<td>D (cm²/h)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>4.2 ± 2.00</td>
<td>0.7 ± 0.42</td>
</tr>
<tr>
<td>2</td>
<td>1.9 ± 1.26</td>
<td>0.3 ± 0.71</td>
</tr>
<tr>
<td>3</td>
<td>1.8 ± 1.27</td>
<td>-2.0 ± 1.14</td>
</tr>
<tr>
<td>4</td>
<td>5.8 ± 5.14</td>
<td>0.9 ± 1.07</td>
</tr>
<tr>
<td>5</td>
<td>-0.1 ± 0.25</td>
<td>0.7 ± 0.30</td>
</tr>
<tr>
<td>6</td>
<td>0.1 ± 0.17</td>
<td>0.6 ± 0.29</td>
</tr>
<tr>
<td>7</td>
<td>0.1 ± 0.19</td>
<td>-0.5 ± 0.24</td>
</tr>
<tr>
<td>μ (weevils/h)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>1.5 ± 2.29</td>
<td>0.4 ± 0.24</td>
</tr>
<tr>
<td>2</td>
<td>-0.1 ± 0.10</td>
<td>1.9 ± 2.03</td>
</tr>
<tr>
<td>3</td>
<td>-0.3 ± 0.21</td>
<td>-2.0 ± 1.14</td>
</tr>
<tr>
<td>4</td>
<td>0.2 ± 0.27</td>
<td>-0.9 ± 1.07</td>
</tr>
<tr>
<td>5</td>
<td>-0.2 ± 0.13</td>
<td>-0.7 ± 0.30</td>
</tr>
<tr>
<td>6</td>
<td>0.2 ± 0.13</td>
<td>-0.6 ± 0.29</td>
</tr>
<tr>
<td>7</td>
<td>0.3 ± 0.045</td>
<td>-0.5 ± 0.24</td>
</tr>
</tbody>
</table>

Table 3. Number of buckets exposed to the sun (± SE) during the morning hours, and number of hours (± SE) of the morning sampling scheme that the buckets were exposed to the sun, for rows 1 through 4 contained in the within row arrays: ABC (south side of screen enclosure) and DEF (north side of screen enclosure).

<table>
<thead>
<tr>
<th>Array</th>
<th>Row</th>
<th>Buckets</th>
<th>Hours</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABC</td>
<td>1</td>
<td>44.6 ± 11.81 a</td>
<td>3.8 ± 0.83 a</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>40.6 ± 10.70 a</td>
<td>3.2 ± 0.62 a</td>
</tr>
<tr>
<td>DEF</td>
<td>3</td>
<td>10.6 ± 5.92 b</td>
<td>1.4 ± 0.61 a</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>9.6 ± 5.81 b</td>
<td>1.6 ± 0.70 a</td>
</tr>
</tbody>
</table>

Means in a column followed by different letters are significantly different (Wilcoxon signed-rank test, P < 0.05).

process. High numbers of individuals were concentrated around the release point and slowly moved towards the boundaries of the experimental plot. Analogous patterns of dispersal have been observed with other beetles where cumulative trap catch remained highest near the release point with an outward spread over time (Banks et al., 1988; Rieske and Raffa, 1990; Arbogast et al., 2000; Smith et al., 2001; Arbogast et al., 2003).

The Dempster’s model used in this study was based on the assumptions that (1) all weevils, on average, forage in the same way; and that (2) the weevils do not interact and move independently from each other (Okubo, 1980). These assumptions were justified based on the average displacement of recaptures. These displacements were either not significantly different from zero along the x-axis or had a negligible deviate along the y-axis, indicating that weevils diffused equally in all directions and foraged independently from each other. The Dempster’s model was used to determine the flux in numbers of weevils through different portions of the sampled area via the central squares (N₃) of all the 3 x 3 lattice squares (A–F). The value of this flux was then used to evaluate the dispersal ability of a population of weevils (in contrast to an individual weevil) providing that movement of each individual weevil was independent from each other and that no forces were acting in the same direction upon an individual weevil (as was explained above). Movement of an individual weevil can rarely be at random because each individual possesses sense organs that are influenced by the immediate environment (Dempster, 1957). Therefore, when the qualities of the environment (shelter, food, oviposition site, etc.) are perceived by the individual weevils, movement will be directed and unlikely will be at random. However, movement by individuals may not affect the total movement of the population. The Dempster’s model (1957) was used to estimate the dispersal rate of the population of weevils moving on an experimental set up. Other equations have been proposed to estimate the dispersal rate of moving organisms but those approaches take into account only movements of individual organisms (Kareiva and Shigesada, 1983; Boyet and Benshamou, 1988; Chronin et al., 1999; Byers, 2001) instead of simultaneous movement of groups of individuals, that is, populations, which is the case that we are studying here. In addition, with this model (Dempster, 1957), it was possible to separate movement and disappearance rates, providing ways to discern the causes producing changes in the population density of the weevils.

Weevil movement within rows was greater than between rows most likely because weevils had to fly between rows of the experimental plot but could easily walk within a row. Similarly, dispersal rate through the release point (BE array) was higher than those at other places (arrays AD and CF) because the bridge that connected the bucket array represented a continuum of substrate to disperse to the other side of the array. This hypothesis may explain the lower disappearance rate at the point of release (where a physical bridge was placed to connect the two tables with buckets, BE array) compared with those at the end of the tables (arrays AD and CF) that did not have a bridge. Dispersal rates through the ABC array (within rows, facing south) were higher than those through the DEF array (within rows, facing north). Data were collected in the morning when the sun was on the south side of the experimental plot (ABC array), while the north side of the plot (DEF array) was in the shade. The higher
number of buckets in that array exposed to the sun may explain the predominant distribution of weevils on that array compared to the DEF array. The changing distribution of weevils within these arrays over time may indicate that the weevil population is constantly expanding and retracting according to micro environmental conditions as indicated by the hourly dispersal rate and disappearance rate from the arrays. As a result the spread of the population, i.e. dispersal, takes place and the movement puts the individuals in advantageous circumstances. This hypothesis was postulated by Okubo (1980) who suggested that in a changing environment through space and time, the most probable strategy for a new individual to adapt or survive and reproduce may be to migrate to a new habitat that would supply the factors necessary for its existence, in our case, warmer buckets in the cool mornings. This result is in contrast to those reported by Arbogast et al. (2003) that showed that numbers of the beetle, Lasioderma serricone (Coleoptera: Anobiidae) had no significant association with mean, minimum or maximum temperature. Therefore, further investigations are needed to determine the effect of temperature on the weevil’s dispersal.

Higher dispersal and disappearance rates in the BE array during the 1–8 h time interval compared to 8–24 and 24–48 h may be explained by the weevil’s relative daily activity which has been found to have two peaks: (1) between 6:00 and 10:00 a.m. and (2) between 6:00 and 8:00 p.m. (Weissling, unpublished data). In the present investigation, data were collected from 6:00 a.m. until 3:00 p.m. Therefore, the higher dispersal rates the first 8 h after release may correspond to the daily patterns of flight activity. Because the weevils were then counted once 24 and 48 h after release, the weevil population may have already reached a level of threshold density inside the buckets by that time, and may have not moved further from their previous day’s hiding places.

Our study has been conducted in the near-natural screen enclosure setting. Therefore, our results indicate the intrinsic propensity and ability of the silky cane weevil to colonize cut sugarcane, but do not quantify the amount of such movement under field conditions. Movement between and within rows of sugarcane in the field is likely to be affected by abiotic factors as well as placement of the sugarcane from the release point. Dispersal of other insects was affected by wind speed (Blackmer et al., 2004), mechanical disturbance, crowding, drought or predation (Bailey et al., 1995). Therefore, weevils may be susceptible to environmental perturbations or by predation by other arthropods that may affect their dispersal, but no information is available on this matter. Furthermore, the effect of placement of sugarcane from the release point on the dispersal rate of the weevils warrant further study, because dispersal might vary according to the distance of plant hosts and to the spatial distribution of those hosts, as reported for the beetle Anoplophora glabripennis Motschulsky (Smith et al., 2001). However, the present study provides initial insight into the mechanisms of dispersal of the silky cane weevil, but further investigations are required to find out the extent of the weevil’s movement between sugarcane plants in the field.

Quantitative information on the dispersal rate of a pest is critical in predicting the rate of range expansion. Expansion rate can be predicted empirically by determining the population rate of spread, $c^*$, based on the rate of population growth, $\alpha$, and the diffusion coefficient, $D$, as $c^* = 2(\pi D)^{1/2}$ (Okubo, 1980). The strength of this type of approach is that, with the right kind of data, one can build more detail and realistic models of movement for predicting population spread of the weevil and the consequences of its movement in a wide variety of settings. If the rate of range expansion is known, the arrival of the weevil can be forecasted in nearby areas and control operations can begin before damage to sugarcane or palms trees occurs. Therefore, the rate of the weevil’s range expansion requires further investigations.

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