Journal of Economic Entomology, 109(2), 2016, 629–636
doi: 10.1093/jee/tov402
Advance Access Publication Date: 19 January 2016
Research article

How Far Can the Palm Weevil, *Rhynchophorus vulneratus* (Coleoptera: Curculionidae), Fly?

M. S. Hoddle[1,2,3] and C. D. Hoddle[1]

[1]Department of Entomology, University of California, Riverside CA 92521 (mark.hoddle@ucr.edu; christina.hoddle@ucr.edu), [2]Center for Invasive Species Research, University of California, Riverside CA 92521, and [3]Corresponding author, e-mail: mark.hoddle@ucr.edu

Received 5 October 2015; Accepted 17 December 2015

Abstract

The palm weevil, *Rhynchophorus vulneratus*, is native to Southeast Asia and was recovered from an infested Canary Islands date palm in Laguna Beach, California, USA, in 2010. The detection of this potentially destructive palm pest initiated a detection, containment, and eradication program that was reliant, in part, on the deployment of bucket traps loaded with aggregation pheromone and baited with fermenting fruit. A key question that pertained to the deployment of traps was "how far can *R. vulneratus* fly?" This question could not be answered and in response to this knowledge deficit, computerized flight mill studies were conducted with field-captured *R. vulneratus* in an outdoor screen house in Sumatra, Indonesia. Of the 63 weevils tethered to flight mills, ~27% failed to fly >1 km in 24 h and were excluded from analyses. In total, 46 weevils (35 females and 11 males) flew >1 km on flight mills and of these adults, the average total distance flown in 24 h was significantly greater for females (~32 km) when compared with males (~15 km). A small proportion of females (~16%) flew 50-80 km, and one female flew 100.1 km in 24 h. Flying weevils exhibited an average weight loss of ~13–17% and non-flying control weevils ($n = 27$) lost 10–13% body weight in 24 h. The distribution of flight distances for female and male weevils combined was leptokurtic, which suggests that faster than expected spread by *R. vulneratus* may be possible in invaded areas.

Key words: dispersal, Indonesia, leptokurtic dispersion, Sumatra

In its native range, Southeast Asia, the palm weevil, *Rhynchophorus vulneratus* (Panzer) (Coleoptera: Curculionidae), is a pest of coconut palms, *Cocos nucifera* L. (Arecales: Arecaceae) (Wattanapongsiri 1966, Rugman-Jones et al. 2013). In August 2010, inspection of a damaged Canary Islands date palm, *Phoenix canariensis* Chabaud (Arecales: Arecaceae), by a professional arborist in Laguna Beach, Orange County, California, USA, resulted in the unexpected recovery of adult and larval weevils, a pest not previously associated with palms in California. The adult weevils were black with a red stripe on the dorsal surface of the thorax. These specimens were identified by the California Department of Food and Agriculture (CDFA) and the U.S. Department of Agriculture (USDA) as *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae), the red palm weevil (Hoddle 2010). This insect is a highly invasive and notoriously destructive palm pest and internal feeding by larvae kills palms (Murphy and Briscoe 1999, Faleiro 2006, Giblin-Davis et al. 2013). In non-native areas, the invasive color morph of *R. ferrugineus* is orange with black maculation on the thorax and dark striations on the elytra (see Rugman-Jones et al. 2013 for color plates of these weevils).

Work by Hallett et al (2004) with different weevil populations in west Java Indonesia resulted in the synonymization of *R. vulneratus* with *R. ferrugineus* because they were unable to detect significant morphological and molecular differences between these two presumptive species that they separated by color (i.e., black with a red stripe [the color morph detected in Laguna Beach] and orange with black markings [the invasive color morph]). Further, the two color morphs were capable of interbreeding and producing offspring, and male weevils produced the same aggregation pheromones (Hallett et al. 1993, 2004). Rugman-Jones et al. (2013) used DNA-based analyses to determine the identity and origin of the palm weevil population in Laguna Beach. These molecular-based analyses of weevils collected throughout the putative native and invaded ranges of *R. vulneratus* and *R. ferrugineus* concluded that two distinct weevil species existed, *R. vulneratus* and *R. ferrugineus*, they are separable molecularly and have distinct geographic distributions, and the species collected in Laguna Beach was *R. vulneratus* (Rugman-Jones et al. 2013).

The results of these molecular analyses supported previous work by Wattanapongsiri (1966) and confirmed that *R. vulneratus* has a native geographic range confined largely to southern Thailand–northern Malaysia on the Thai-Malay Peninsula, Singapore, and Indonesia, and in this native range, *R. vulneratus* has a range of color forms, including that which is typical of the invasive

R. ferrugineus color morph (Rugman-Jones et al. 2013). *Rhynchophorus ferrugineus* has a more northern native distribution including the Philippines, northern Thailand, Vietnam, Cambodia, and India, and it is this species that has demonstrated high invasion capabilities (Rugman-Jones et al. 2013). The only find of *R. vulneratus* outside of its native range was in Laguna Beach, and the closest molecular match to California's population was Bali, Indonesia (Rugman-Jones et al. 2013).

Rugman-Jones et al. (2013) concluded that Hallett et al. (2004) had been working in west Java with different color morphs of the same species, *R. vulneratus*, not *R. ferrugineus*, and reinstatement of *R. vulneratus* as a legitimate species is recommended. Despite findings by Rugman-Jones et al. (2013), USDA-APHIS considers *R. vulneratus* a synonym of *R. ferrugineus* until there is a combined data set of morphological and DNA information, as well as discrete species diagnoses, to resolve remaining taxonomic uncertainty (Eileen Smith USDA-APHIS, pers. comm. 31 Mar. 2015). Regardless of the USDA-APHIS interpretation of Rugman-Jones et al. (2013), the weevil species discovered in Laguna Beach will be referred to here as *R. vulneratus*.

It is unknown how *R. vulneratus* arrived in Laguna Beach, a small relatively isolated city that lacks an airport, seaport, and interstate border crossings, features that are normally associated with invasion vulnerability. Hoddle (2015) speculated that *R. vulneratus* may have been deliberately introduced from Indonesia into Laguna Beach to supply local demand for palm weevil larvae used in the preparation of traditional Asian dishes.

The detection of *R. vulneratus* in California was considered a significant threat to ornamental (e.g., *P. canariensis*), agricultural (e.g., dates [*P. dactylifera* L.]), and native (e.g., *Washingtonia filifera* [Lindl.] H. Wendl.) palms. In response to this pest detection, a delineation, containment, and eradication effort was initiated. *Rhynchophorus vulneratus* monitoring in Laguna Beach relied heavily on bucket traps loaded with commercially available aggregation pheromone (Ferrolure^{TM} 700 mg, manufactured by ChemTica International S.A., Costa Rica), fermenting fruit bait (e.g., apples), ethyl acetate synergist, and 1 liter of 50:50 mixture of water and propylene glycol to drown and preserve weevils that entered traps. It was anticipated that adult weevils would fly to bucket traps, enter, and subsequently be captured. Despite the deployment of 150 bucket traps within a 15.6-km^2 trapping zone that encompassed palm trees with confirmed *R. vulneratus* infestations, only 1 adult weevil was captured over a three-year trapping period. The reasons for this low capture rate are unclear, but what was apparent from this trapping effort was that short- and long-distance flight dispersal by *R. vulneratus* is poorly understood and a seemingly simple question that pertained to trap deployment decisions, "how far can *R. vulneratus* fly?", could not be answered.

Studies examining the dispersal capabilities of invasive pests can help with the identification of dispersion pathways, and understanding of rates and direction of spread that may help with the development of detection, monitoring, and control programs (David et al. 2014, Lopez et al. 2014). One approach to measuring insect flight is to use flight mills coupled to a computer that records flight activity by insects tethered to an arm that rotates when they fly (David et al. 2014, Lopez et al. 2014, Martini et al. 2014). Flight mills can be useful research tools for quantifying basic attributes such as flight bout frequency and duration, distance flown, flight velocity, and periodicity (Hoddle et al. 2015). Despite the utility of such data, results from flight mill studies may need to be interpreted cautiously because potential unknown effects that result from attachment to the flight mill could affect behavior (Taylor et al. 2010). For example, tethered insects are forced to fly because of lack of tarsal contact with substrate and they don't have to support their own weight (Hollick 1940, Weis-Fogh 1956, Wilson 1961). Further, experimental insects tethered to flight mills in a laboratory are not exposed to daily fluctuations in wind, humidity, or heat; abiotic factors that could either promote or suppress flight (Weissling and Giblin-Davis 1993, Weissling et al. 1994).

Flight distance data collected from flight mill studies can be used to parameterize dispersion equations (Hoddle et al. 2015). These types of data can be used to model rates of spread that could help in the development of management options such as eradication programs (Lockwood et al. 2013). Determining which model to use to describe dispersal depends on model assumptions, and in the case of invasive species, rates of spread may be influenced by relatively few individuals whose travel distances are greater than those predicted by a normal distribution (Lockwood et al. 2013).

Leptokurtic dispersal, for example, is described by a dispersal kernel, the portion of an equation that describes the distribution of dispersal distances, which when leptokurtic, is characterized by having "fat tails." Heavy or fat tails contain more long distance dispersal events in the tail of the distribution than expected when compared with a normal distribution (Lockwood et al. 2013). Fat tailed distributions with more individuals than expected dispersing over long distances may typify the spread of some invasive species (Kot et al. 1996, Leibhold and Tobin 2008). This behavior can result in the establishment of isolated populations in advance of the invasion front that expand and merge, which subsequently increases rates of spread (Leibhold and Tobin 2008). However, gathering the data needed to parameterize long-distance dispersal kernels is difficult, and this, in part, affects the accuracy of models because it limits the ability to reliably forecast the speed of long-distance range expansion (Clark et al. 2003). Flight mill studies have the potential detect and quantify long-distance flight by insects (Hoddle et al. 2015) and these data provide not only basic information on flight distances, but have the potential to detect "super-diffuse" individuals that cause heavy tail dispersal distributions (Reynolds and Rhodes 2009).

In an attempt to answer the question, "how far can *R. vulneratus* fly?" and to determine whether some weevils exhibit "super-diffuse" flight activity, flight parameters of field-captured weevils in North Sumatra, Indonesia, were quantified using computerized flight mill studies. The results of these studies are presented here.

Materials and Methods

Source and Preparation of *R. vulneratus* for Flight Mill Studies

Flight mill studies were conducted at a commercial oil palm plantation in Bandar, Simalungun Regency, North Sumatra, Indonesia over 16–23 February 2012. *Rhynchophorus vulneratus* is native to this region, and the black and red stripe morph is almost exclusively the only color form in this area. Adult *R. vulneratus* were collected daily from decomposing trunks of oil palms or from 12 pheromone bucket traps loaded with aggregation pheromone (Ferrolure^{TM} 700 mg) and baited with pieces of meristematic tissue from coconut or oil palms. Traps were deployed in three different sectors of the plantation. Field-captured weevils of unknown age were placed in large ventilated plastic containers, and provisioned with sugarcane that was split longitudinally. This food was readily consumed by *R. vulneratus*. Weevils were allowed to feed for a minimum of 24 h on sugarcane before being used for experiments. For each flight mill trial, eight weevils were used for flight experiments, and for each trial, weevils not attached to flight mills acted as controls and provided estimates of weight loss and naturally occurring mortality in the absence of food and flight activity over a 24-h period. The number of each sex flown for each trial and used for control treatments was dependent on availability, but priority was given to flying female weevils, as it was assumed this gender presented a greater dispersion risk than males. All females used in trials were assumed to be mated, as copulation was observed frequently in containers with sugarcane. Prior to tethering on the flight mill, individual experimental and control weevils were weighed on an electronic balance (A & D GF2000, Elk Grove, IL) and again post-flight to determine percentage weight change. The size of experimental and control weevils was determined by taking measurements of thorax width and length, and body length was measured from the center-anterior margin of the thorax to the center-posterior margin of the abdomen. Measurements (mm) were made with a stainless-steel electronic caliper (KTools 70186 Electronic Caliper, KTool Int., Wixom, MI).

Experimental Set Up and Brief Description of Flight Mills

Eight flight mills were set up on a table (3 m by 1.1 m by 0.75 m) inside a 12-m by 6-m outdoor shed with a roof constructed of corrugated iron, a concrete floor, and walls constructed of metal mesh screen to exclude insects. All experiments were conducted under ambient light, and naturally occurring temperatures and humidities. A hobo data logger (H08-007-02, Onsett Corp., Bourne, MA) made hourly recordings of temperature and humidity for the duration of trials. Weevils were randomly assigned to flight mills that were evenly distributed on the table. Experimental weevils were set up on flight mills by 9:00 am each morning that experiments were run and trials lasted 24 h. Control weevils were maintained inside ventilated metal mesh containers (10 cm by 10 cm by 16 cm) without access to food or water. These containers were placed on shelves immediately adjacent the flight mills for the duration of each experiment. At the end of the 24-h study period, weevil survivorship by treatment and sex was recorded, weevils were removed from flight mills, and experimental and control weevils were weighed to assess weight loss in relation to treatment and sex.

Lopez et al. (2014) and Hoddle et al. (2015) provide details on procedures used to attach weevils to flight rotors, flight mill manufacture and calibration, data recording, and data file management. Briefly, weevils were attached dorsally by their thorax to an "L"-shaped metal plate (0.59-mm-diameter by 28-mm-long) using high-strength glue. Once the glue was dry, the metal plate with the weevil was connected to an arm of the flight mill rotor. Following attachment to the flight mill arm, tethered weevils were examined to make sure they could open their wings and freely move their legs. A modeling clay counterbalance of similar weight to the experimental weevil was attached to the opposite arm of the rotor. As soon as weevils were tethered to the eight flight mills, data recording began.

The flight mills utilized in this study were custom-manufactured and purposely designed to handle large heavy insects utilizing friction-free ball bearing technology. Customized flight mills were necessary to accommodate adult *Rhynchophorus* spp. that can weigh ~ 2–3 g. Each flight mill was connected to a laptop computer via a USB4 Encoder Data Acquisition Device (US Digital, Vancouver, WA). Custom software recorded flight data, and macros developed in Microsoft Excel analyzed the raw data and provided summaries of performance metrics of interest such as total distance flown, average velocity, total time spent flying or resting, total number of flight bouts (i.e., flight activity had to exceed a 5 s activity threshold before it was included in analyses), average flight bout time, time elapsed until first flight bout, and total run time for the experiment.

Statistical Analyses

Prior to statistical analyses, data were checked for normality and, if necessary, research variables were subjected to Box–Cox procedures to determine power transformations to satisfy model assumptions. The following transformations (where y = research variable) were made (if not indicated, the variable was not transformed before analysis): weight loss: log(y); body length: y^2; total distance flown: log(y); maximum distance flown: $y^{0.5}$; total flying time: log(y); total number of flight bouts: log(y); time elapsed until first flight bout: log(y); flight bout length: log(y); maximum bout length: $y^{0.5}$. Analysis of covariance was used to determine if significant differences in measurement variables (e.g., body size and flight measurements) existed for male and female weevils. Tukey tests at the 0.05 level of significance were conducted when significant effects were detected. All statistical analyses were performed using SAS 9.2 (SAS Institute Inc. 2008) and only significant results are presented.

Quantification of a Dispersal and Redistribution Kernel for *R. vulneratus* Using Flight Mill Data

Flight distance data for all 46 experimental weevils that flew >1 km (see Results) were divided across nine bins (distance interval = 14.11 km with the maximum flight distance recorded acting as the upper bin limit [100.1 km], and the lower bin limit being set at the minimum recorded flight distance [1.34 km]) according to Sturges' formula, where the number of bins = $1 + \log_2(n)$ (Sturges 1926). Binned flight data were used to generate a frequency histogram and the mid-point in each bin was identified. To these mid-points, five different dispersal curves (see Kot et al. 1996 for equations for model curves 1, 2, 3, 4, and 7) with finite integrals were examined for goodness of fit to binned data using sums of squares error (SSE) and coefficient of determination (R^2 =SSE/total sums of squares). Curve equation parameters were determined using the function nls() in R (R Core Team 2013) and the best (determined by size of SSE) parameterized equation standardized by multiplying by bin width (2), number of weevils used (46), and a normalizing constant (1421.43) was fitted to binned flight data. This dispersal curve equation was parameterized and normalized to provide an area under the curve of 1 when reflected about the origin, which generated the redistribution kernel for the distances flown by experimental weevils (Kot et al. 1996). The fitted model was tested for kurtosis using the equation:

$$\text{Excess Kurtosis} = \frac{\int x^4 f(x)dx}{\left[\int x^2 f(x)dx\right]^2} - 3$$

Leptokurtosis is detected if $k > 0$; $k = 0$ and $k < 0$ indicate mesokurtosis and platykurtosis, respectively.

Results

In total, 63 tethered (44 females and 19 males) and 27 control (15 females and 12 males) *R. vulneratus* were used in flight mill studies. Of the weevils tethered to flight mills, 9 females (20% of tethered females) and 8 males (42% of tethered males) failed to fly >1 km and were therefore considered non-fliers (i.e., 27% [$n = 17$] of experimental weevils) and were excluded from analyses. Consequently, 46 weevils (35 females and 11 males [i.e., 73% of tethered weevils])

Table 1. Mean (±SE) body size and flight parameters by gender for *Rhynchophorus vulneratus* on flight mills (flyer; weevils that flew >1 km) and control weevils maintained individually in the same room in ventilated containers without food and water and not subjected to flight studies

Mean (±SE) parameter measured	Female		Male	
	Flyer ($n = 35$)	Control ($n = 12$)	Flyer ($n = 11$)	Control ($n = 10$)
Weight before trial (g)	2.08 ± 0.09ab	1.91 ± 0.19b	2.33 ± 0.12a	2.23 ± 0.15ab
Weight after trial (g)	1.73 ± 0.07ab	1.66 ± 0.16b	2.05 ± 0.12a	2.00 ± 0.14a
% Weight loss	16.58 ± 0.01a	13.42 ± 0.01b	12.53 ± 0.01b	10.39 ± 0.01b
Thorax width (mm)	11.29 ± 0.18a	11.08 ± 0.45a	11.82 ± 0.22a	11.50 ± 0.36a
Thorax length (mm)	12.78 ± 0.22a	12.58 ± 0.46a	13.44 ± 0.33a	12.91 ± 0.32a
Body length (mm)	31.04 ± 0.46a	29.96 ± 1.22a	31.52 ± 0.68a	31.21 ± 0.59a
% Survivorship	100	100	100	100
Velocity (m/s)	1.83 ± 0.13a		1.34 ± 0.19a	
Maximum velocity (m/s)	3.70 ± 0.12a		3.62 ± 0.35a	
Total distance flown (km)	32.48 ± 3.97a		14.80 ± 3.16b	
Max. distance flown (km)	13.37 ± 1.22a		6.44 ± 1.41b	
Total time flying (h)	4.91 ± 0.59a		3.00 ± 0.78b	
Total flight bouts	59 ± 11a		32 ± 15a	
Time elapsed to first flight bout (h)	0.27 ± 0.03a		0.46 ± 0.22a	
Flight bought length (h)	0.31 ± 0.05a		0.12 ± 0.04b	
Max. flight bout length (h)	1.70 ± 0.14a		0.87 ± 0.15b	
Room temp. (°C)		27.46 ± 0.22		
% RH in room		79.80 ± 0.88		

Means in the same row followed by different letters are significantly different at the 0.05 level.

flew >1 km in 24 h and were classified as flyers and used for statistical analyses of measured flight variables (Table 1).

A significant difference in pre-trial weevil weights was detected; male weevils that flew >1 km were, on average, significantly heavier than control females ($F = 4.51$, df = 1, $P = 0.03$; Table 1). Average weight lost measured post-trial was significant with control females weighing less than other experimental weevils ($F = 4.92$, df = 1, $P < 0.03$; Table 1). Average percentage weight loss was significantly different ($F = 5.10$, df = 1, $P < 0.02$) and greatest for female weevils that flew, which, on average, lost ~17% of their body weight (Table 1). No significant differences in average body size measurements (i.e., thorax width and length and body length) were observed for experimental weevils (Table 1).

The total average distance flown by female and male weevils was significantly different ($F = 7.58$, df = 1, $P = 0.009$), with female *R. vulneratus* flying approximately twice as far as male weevils in 24 h (Table 1). The average maximum distance flown in a single flight bout was significantly longer for females ($F = 9.72$, df = 1, $P = 0.003$), being approximately twice that recorded for males (Table 1). Female weevils exhibited significantly longer average flight bouts ($F = 5.40$, df = 1, $P = 0.03$), and the average maximum flight bout length was significantly longer for females ($F = 11.51$, df = 1, $P = 0.002$), being ~ 49% greater than males (Table 1).

Of females flying >1 km, approximately 43% flew between 1 and 30 km (Fig. 1A). A small proportion of females (~16%) exhibited high flight capacity, flying 50–80 km (Fig. 1A), and one individual (2%) exhibited "super-dispersive" flight by flying >100 km in 24 h (Fig. 1A). Of the male weevils that flew >1 km, 53% ($n = 10$) flew less than 30 km, and one male (5%) flew greater than 30 km (Fig. 1A). Weevil flight activity (data for both sexes combined) was observed consistently over a 24-h period. The highest percentage of weevils flying was observed between 9:00 and 11:00 am and cumulative total distance flown was also greatest over this period, before tapering off over 11:00 am to 11:00 pm (Fig. 1B). Flight activity (cumulative distance flown and percentage of weevils flying) increased steadily after 3:00 am until 11:00 am (Fig. 1B). Average flight bout time and distance flown per bout (data for both sexes combined) were highest between 9 and 11:00 am at 21 min and 2.63 km, respectively. For the remaining time, average flight bout times and distance flown per bout were reasonably constant, ranging between 5 and 15 min and 0.54 and 1.78 km, respectively (Fig. 1C).

Dispersal and Redistribution Kernel for *R. vulneratus*

The best fitting of the five curves analyzed from Kot et al. (1996) was Curve 7:

$$f(x) = e^{a-bx}$$

where a = 3.17, b = 0.034, and x = midpoint of the distance bin (km) ($R^2 = 0.79$; Fig. 2A). This function was used to generate the corresponding redistribution kernel, described by a Laplace distribution:

$$f(x) = \begin{cases} \frac{1}{2b}e^{x/b} & x<0 \\ \frac{1}{2b}e^{-x/b} & x\geq 0 \end{cases}$$

where b = 29.75, and x = distance flown (km) (Fig. 2B). The excess kurtosis measure was 3, indicating that the equation describing the curve that was produced is leptokurtic (Fig. 2B).

Discussion

In an outdoor screen house lacking climate control, male and female *R. vulneratus* were capable of flying considerable distances on flight mills; 42 and 66% of male and female weevils, respectively, that exhibited >1 km of flight on flight mills, flew >10 km, and of these, 18% of females flew >50 km, and one female flew 100.1 km in a 24-h period. Flight distances exceeding 50 km were not observed for male weevils, but this may have been an artifact of the low number of males used for experiments. In contrast, 20% of females and 42% of males (i.e., 27% of experimental weevils) flew <1 km in

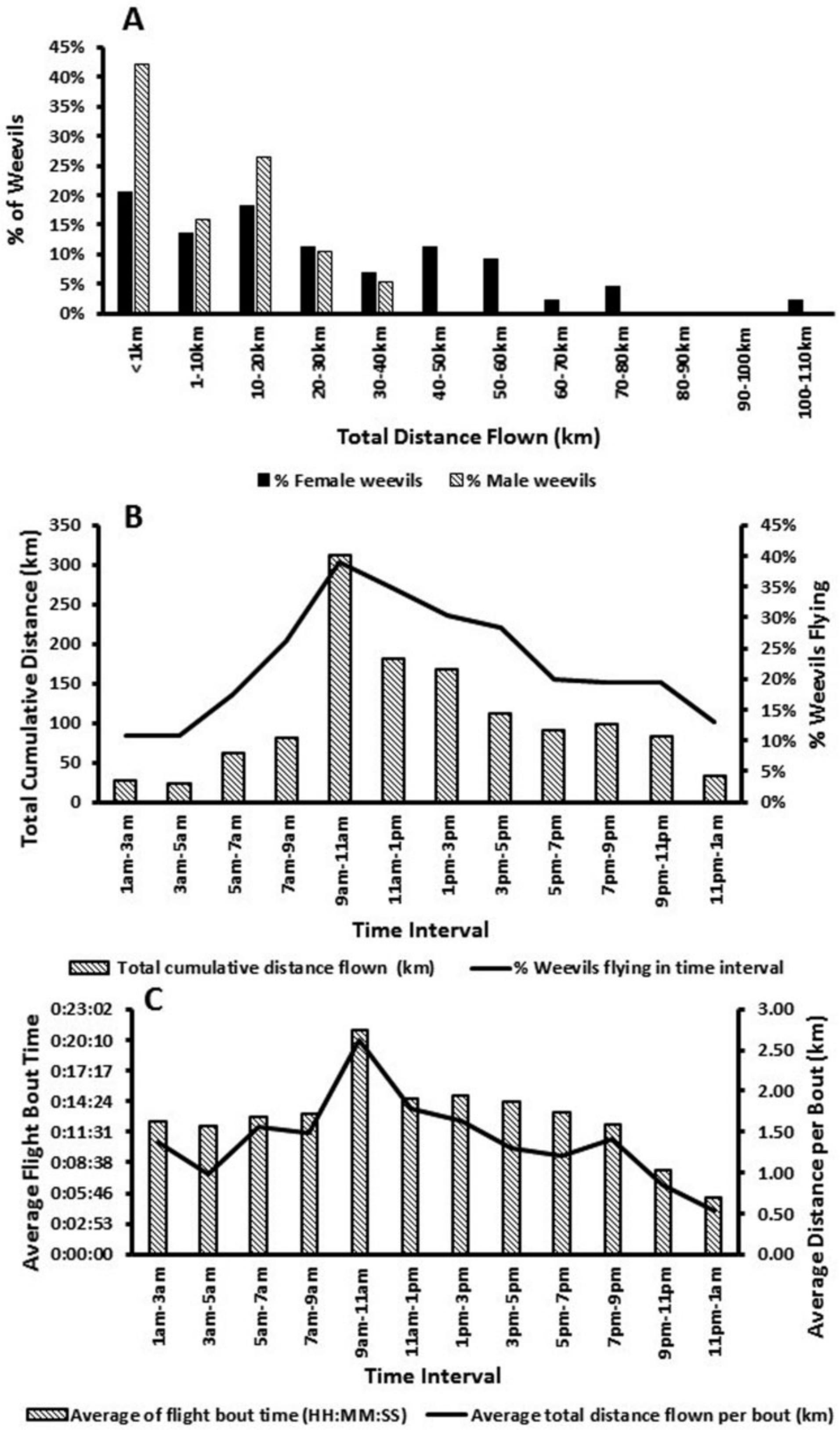

Fig. 1. Summary data for male and female *Rhynchophorus vulneratus* flown on flight mills for 24 h in an outdoor screen house. (A) Percentage of male and female *R. vulneratus* binned by total distance (km) flown. (B) Total cumulative distance (km) flown and percentage of weevils that flew binned by 2-h time intervals. (C) Average distance flown (km) per flight bout and average flight bout time (h:min:sec) binned by 2-h time intervals.

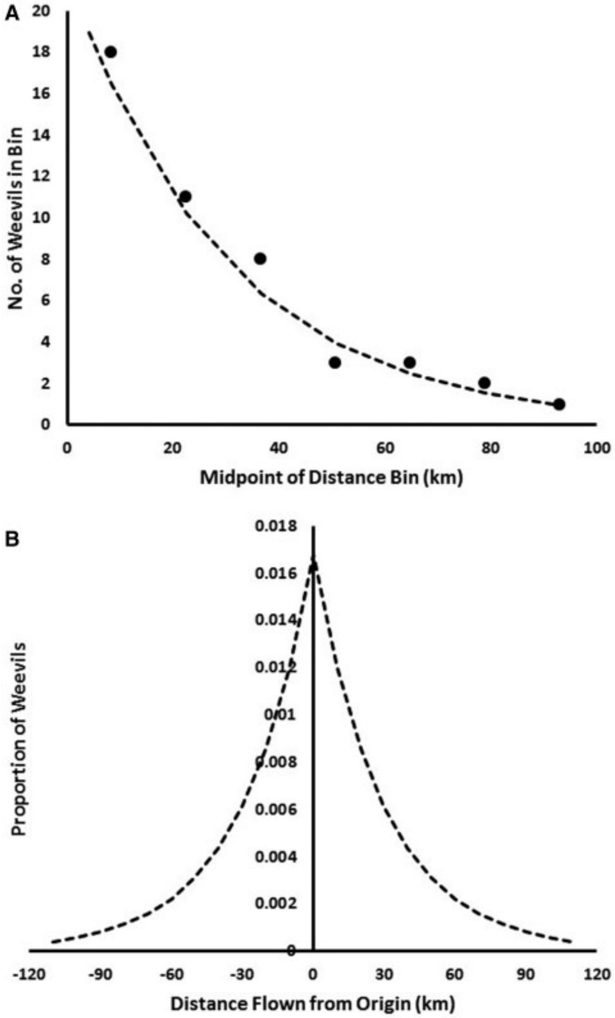

Fig. 2. (A) Dispersal curve and (B) redistribution kernel generated using flight data combined for male and female *Rhynchophorus vulneratus* flown on flight mills in an outdoor screen house for 24 h.

24 h. These weevils were considered non-fliers, but likely capable of short-distance dispersal between palm trees. Hoddle et al. (2015) reported that ~30% of field-captured *R. ferrugineus* tethered to flight mills failed to fly >1 km in 24 h, and Ávalos et al. (2014) also reported a 30% failure rate for flight by *R. ferrugineus* over a 12-h period.

Rhynchophorus vulneratus flight activity was greatest between 9 and 11:00 am in terms of cumulative distance flown, average flight bout times, average total distance flown per bout, and percentage of weevils flying. A similar result was reported for flight mills studies with *R. ferrugineus* (Hoddle et al. 2015). This periodicity should be interpreted with some caution, as it may be an experimental artifact as weevil tethering in both studies was completed by 9:00 am and experimental weevils, like other insects (Hollick 1940, Weis-Fogh 1956, Wilson 1961), tend to fly once tarsal contact with substrate was lost.

Captures of *R. ferrugineus* in "smart traps" loaded with aggregation pheromone and baited with date fruit deployed in a date palm plantation in Saudi Arabia resulted in the majority of weevils being trapped during the day, with relatively few captures occurring at night (Aldryhim and Al Ayedh 2015). Fanini et al. (2014) report a similar result for *R. ferrugineus* captured in traps in Italy and Greece, which, as with Saudi Arabia, are part of the non-native range of this palm pest. For invasive populations of *R. ferrugineus*, diurnal trap captures and activity on flight mills suggest a tendency for flight during daylight hours (Aldryhim and Al Ayedh 2015, Fanini et al. 2014, Hoddle et al. 2015). Conversely, in the oil palm orchard where *R. vulneratus* used for flight mill studies were collected, baited pheromone traps captured 61% of weevils between 3:00 pm and 7:30 am, suggesting that the majority of captures may have occurred after dark (Hoddle and Hoddle 2015). Flight mill data indicated that 11–20% of tethered *R. vulneratus* flew between 7:00 pm and 7:00 am, demonstrating that weevils fly at night. However, interpreting the significance of the timing of weevil captures in field-deployed traps with respect to flight behavior recorded on flight mills is difficult, as dispersal activity and attraction to pheromone traps may be independent of each other.

Humidity and temperature affect flight activity and mortality rates in *Rhynchophorus cruentatus* (F.) (Weissling and Giblin-Davis 1993; Weissling et al. 1994) and *R. ferrugineus* (Hoddle et al. 2015). Under low humidity conditions (<30%) and high temperatures (~27°C), about 80% of *R. ferrugineus* that exhibit >1 km of flight die over a 24-h period when tethered to a flight mill (Hoddle et al. 2015). In this study, survivorship of tethered *R. vulneratus* that flew >1 km was high, with 100% of experimental adults surviving under ambient conditions of ~27°C and ~80% RH. The strong effects of humidity and temperature on *Rhynchophorus* spp. flight and survival may result from these weevils being hygric-adapted, which results in adults favoring moist concealed harborage sites (Weissling and Giblin-Davis 1993). It is unknown how *R. vulneratus* flight activity and survivorship rates would be affected under varying temperature and humidity regimens, as weevils were not flown under conditions where these two variables were manipulated to determine their potential effects. These abiotic factors, temperature and humidity, could strongly influence flight and survival for *R. vulneratus*, especially in non-native ranges that lack a year-round tropical climate (e.g., Laguna Beach in California).

Rhynchophorus vulneratus exhibited leptokurtic dispersal and significant sex-biased differences in flight distances were observed, with female weevils flying significantly further than males. Sex-biased dispersal could affect reproductive success and subsequent establishment in non-native areas because of an inability to locate mates following long-distance flight (Miller et al. 2011). Ironically, it is possible that long-distance flight driven by environmental factors (e.g., low humidity) and sex of dispersing weevils could have contributed, in part, to the successful eradication of *R. vulneratus* in Laguna Beach, as it could have resulted in potential long-distance colonizers arriving in inhospitable habitat (e.g., the Pacific Ocean or the xeric San Joaquin Hills).

There are significant challenges to executing field studies designed to investigate the short- and long-distance dispersal of *Rhynchophorus* spp. weevils. Flight mill studies (Taylor et al. 2010) and mark–recapture studies (Yamamura et al. 2003) have well-recognized shortcomings. An improvement over these two methods of assessing dispersal capability could be through the use of very small electronic devices attached to free-ranging insects that record and transmit locality data for over time. Space-based tracking technologies (e.g., GPS satellite monitoring or near-earth orbit receivers) may be one way to measure long-distance insect movement in environments of interest (Kissling et al. 2014). However, energy supply, signal broadcast range, and equipment costs are significant obstacles that need to be overcome before the use of this technology will be possible for monitoring insect movement (Kissling et al. 2014).

In conclusion, flight mill generated data indicated that ~80 and ~58% of field-captured female and male *R. vulneratus*, respectively, flew >1 km in a 24-h period, and the average total distance flown was significantly greater for female weevils (~32 km [females] vs. ~15 km [males]). Of those female weevils flying >1 km, ~83% flew >10 km in a 24-h period, and flight distance data for female and male weevils combined exhibited a leptokurtic distribution, which can potentially result in faster than expected spread during the initial stages of an invasion into new areas (Kot et al. 1996). Incursion management plans for *R. vulneratus*, especially at the early stages of colonization, may need to consider the possibility for rapid long-distance flight from infestation foci because the likelihood of successful detection in new areas and subsequent containment and eradication is greatest when populations are small and localized (Tobin et al. 2014).

Acknowledgments

We are indebted to Stephen Nelson, Ahmed Saleh, Lisanti Cahyasiwi, Adi Sumantri, Linda Purwaninigsih, and Prima Wijayanto, Sumatra Bioscience, Bah Lias Research Station (Lonsum), for their outstanding hospitality and generous assistance with flight mill trials in Sumatra, Indonesia. Research in support of this project was supported, in part, by a CDFA Specialty Crops Grant, SCB11061, "Addressing Urgent Research Needs for Red Palm Weevil in California." Karen Huaying Xu, Department of Statistics, University of California Riverside, provided statistical assistance. We thank anonymous reviewers for their useful comments.

References Cited

Aldryhim, Y. N., and H. Y. Al-Ayedh. 2015. Diel flight activity patterns of the red palm weevil (Coleoptera: Curculionidae) as monitored by smart traps. Fla. Entomol. 98: 1019–1024.

Ávalos, J. A., A. Martí-Campoy, and A. Soto. 2014. Study of the flying ability of *Rhynchophorus ferrugineus* (Coleoptera: Dryopthoridae) adults using a computerized flight mill. Bull. Entomol. Res. 104: 462–470.

Clark, J. S., M. Lewis, J. S. McLachlan, and J. Hille Ris Lambers. 2003. Estimating population spread: What can we forecast and how well? Ecol. 84: 1979–1988.

David, G., B. Giffard, D. Piou, and H. Jactel. 2014. Dispersal capacity of *Monochamus galloprovincalis*, the European vector of the pine wood nematode, on flight mills. J. Appl. Entomol. 138: 566–576.

Fanini, L., S. Longo, R. Cervo, P. Roversi, and G. Mazza. 2014. Daily activity and non-random occurrence of captures in the Asian palm weevils. Ethol. Ecol. Evol. 26: 195–203.

Faleiro, J. R. 2006. A review of the issues and management of the red palm weevil *Rhynchophorus ferrugineus* (Coleoptera: Rhynchophoridae) in coconut and date palm during the last one hundred years. Int. J. Trop. Insect Sci. 26: 135–150.

Giblin-Davis, R., J. R. Faleiro, J. A. Jacas, J. E. Peña, and P.S.P.V. Vidyasagar. 2013. Biology and management of the red palm weevil, *Rhynchophorus ferrugineus*, pp. 1–34. *In* J. E. Peña (ed.), Potential invasive pests of agricultural crops. CABI Publishing, United Kingdom.

Hallett, R. H., G. Gries, R. Gries, and J. H. Borden. 1993. Aggregation pheromones of two Asian palm weevils, *Rhynchophorus ferrugineus* and *R. vulneratus*. Naturwissenschaften 80: 328–331.

Hallett, R. H., B. J. Crespi, and J. H. Borden. 2004. Synonymy of *Rhynchophorus ferrugineus* (Olivier), 1790 and *R. vulneratus* (Panzer), 1798 (Coleoptera, Curculionidae, Rhynchophorinae). J. Nat. Hist. 38: 2863–2882.

Hoddle, M. S. 2010. Confirmed: live red palm weevil found in US. (http://cisr.ucr.edu/blog/invasive-species/confirmed-live-red-palm-weevil-found-in-us/, last accessed 4 January 2016).

Hoddle, M. S. 2015. Red palm weevils - food or foe? Palms 59: 21–31.

Hoddle, C. D., and M. S. Hoddle. 2015. Evaluation of three trapping strategies for the palm weevil, *Rhynchophorus vulneratus* (Coleoptera: Curculionidae), in Sumatra Indonesia. Pak. Entomol. (in press).

Hoddle, M. S., C. D. Hoddle, J. R. Faleiro, H.A.F. El-Shafie, D. R. Jeske, and A. A. Sallam. 2015. How far can the red palm weevil (Coleoptera: Curculionidae) fly? Computerized flight mill studies with field captured weevils. J. Econ. Entomol. 108: 2599–2609.

Hollick, F.S.J. 1940. The flight of the dipterous fly *Muscina stabulans* Fallén. Phil. Trans. B. 230: 357–390.

Kissling, W. D., D. E. Pattemore, and M. Hagen. 2014. Challenges and prospects in the telemetry of insects. Biol. Rev. 89: 511–530.

Kot, M., M. A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. Ecol. 77: 2027–2042.

Leibhold, A. M. and P. C. Tobin. 2008. Population ecology of insect invasions and their management. Ann. Rev. Entomol. 53: 387–408.

Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2013. Modeling the geographic spread of invasive species pp. 157–188. *In* Invasion Ecology Second Edition, Blackwell Publishing Ltd., Chichester, United Kingdom.

Lopez, V. M., M. N. McClanahan, L. Graham, and M. S. Hoddle. 2014. Assessing the flight capabilities of the goldspotted oak borer (Coleoptera: Buprestidae) with computerized flight mills. J. Econ Entomol. 107: 1127–1135.

Martini, X., A. Hoyte, and L. L. Stelinski. 2014. Abdominal color of the Asian citrus psyllid (Hemiptera:Liviidae) is associated with flight capabilities. Ann. Entomol. Soc. Am. 107: 842–847.

Miller, T.E.X., A. K. Shaw, B. D. Inouye, and M. G. Neubert. 2011. Sex-biased dispersal and the speed of two-sex invasions. Am. Nat. 177: 549–561.

Murphy, S. T., and B. R. Briscoe. 1999. The red palm weevil as an alien invasive: Biology and the prospects for biological control as a component of IPM. Biocont. News Inform. 20: 35N–46N.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (http://www.R-project.org/, last accessed 4 January 2016)

Reynolds, A. M., and C. J. Rhodes. 2009. The Lévy flight paradigm: random search patterns and mechanisms. Ecology 90: 877–887.

Rugman-Jones, P. F., C. D. Hoddle, M. S. Hoddle, and R. Stouthamer. 2013. The lesser of two weevils: Molecular genetics of pest palm weevil populations confirm *Rhynchophorus vulneratus* (Panzer 1798) as a valid species distinct from *R. ferrugineus* (Olivier 1790), and reveal the global extent of both. PLoS ONE 8: e78739.

SAS Institute. 2008. SAS/STAT User's Guide 9.2, second edition. SAS Institute, Cary, NC.

Sturges, H. A. 1926. The choice of a class interval. J. Am. Stat. Assoc. 21: 65–66.

Taylor, R.A.J., L. S. Bauer, T. M. Poland, and K. N. Windell. 2010. Flight Performance of *Agrilus planipennis* (Coleoptera: Buprestidae) on a flight mill and in free flight. J. Insect Behav. 23: 128–148.

Tobin, P. C., J. M. Kean, D. M. Suckling, D. G. McCullough, D. A. Herms, and L. D. Stringer. 2014. Determinants of successful arthropod eradication programs. Biol. Invas. 16: 401–414.

Wattanapongsiri, A. 1966. A revision of the genera *Rhynchophorus* and *Dynamis* (Coleoptera: Curculionidae). Dept. Agric. Sci. Bull. 1: 1–328.

Weis-Fogh, T. 1956. Biology and physics of locust flight. II: Flight performance of the desert locust (*Schistocerca gregaria*). Phil. Trans. B 239: 459–510.

Weissling, T. J., and R. M. Giblin-Davis. 1993. Water loss dynamics and humidity preference of *Rhynchophorus cruentatus* (Coleoptera: Curculionidae) adults. Environ. Entomol. 22: 93–98.

Weissling, T. J., R. M. Giblin-Davis, B. J. Center, and T. Hiyakawa. 1994. Flight behavior and seasonal trapping of *Rhynchophorus cruentatus* (Coleoptera: Curculionidae). Ann. Entomol. Soc. Am. 87: 641–647.

Wilson, D. M. 1961. The central nervous control of flight in a locust. Exp. Biol. 38: 471–490.

Yamamura, K., K. Mitsunobu, A. Norio, K. Futoshi, and S. Yasutsune. 2003. Estimation of dispersal distance by mark recapture experiments using traps: correction of bias caused by the artificial removal by traps. Popul. Ecol. 45: 149–155.