

How Far Can the Red Palm Weevil (Coleoptera: Curculionidae) Fly?: Computerized Flight Mill Studies With Field-Captured Weevils

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ABSTRACT Adult *Rhynchophorus ferrugineus* (Olivier) captured in pheromone-baited traps in commercial date palm orchards in the Al Ahsaa Directorate, Kingdom of Saudi Arabia, were used in computerized flight mill studies to determine the flight characteristics of this highly invasive and destructive palm pest. Flight mill studies were run at three different time periods, winter (December), spring (March), and summer (May). Of the 192 weevils tethered to flight mills ~30% failed to fly > 1 km. Of those weevils flying > 1 km ($n = 139$), 55% flew > 10 km, and of these flyers 5% flew > 50 km in 24 h. Flying weevils exhibited an average weight loss of 20–30% and nonflying control weevils lost ~9–13% body weight in 24 h. Male and female weevils flying in summer (average laboratory temperature was ~27°C) flew the longest average distances (~25–35 km), exhibited highest weight reductions (~30%), and greatest mortality rates (~80%). Consequently, time of year not weevil sex or color morph had a consistent and significant effect on flight activity, weight loss, and survivorship rates. Flight activity was predominantly diurnal commencing around 5:00 a.m. and peaking between 9–11:00 a.m. before tapering off. The distribution of flight distances combined across season and sex was mesokurtic (i.e., normally distributed).

KEY WORDS color morph, dispersal, flight, kurtosis, Saudi Arabia

Invasive insect pests can be extremely damaging to agricultural, natural, and urban areas, causing significant ecological and economic damage (Kenis et al. 2009, Simberloff et al. 2013). Consequently, these unwanted species cost hundreds of millions of dollars each year in direct losses and expenses associated with management efforts that attempt to reduce populations to less damaging levels (Pimentel et al. 2005, Kovacs et al. 2010, Van Driesche et al. 2010, Simberloff et al. 2013). Therefore, when introduced insects become pestiferous in adventive areas, studies examining their dispersal capabilities can aid in determining biotic and abiotic factors that may influence rates and direction of spread, and dispersal pathways (Lopez et al. 2014). A collective understanding of factors influencing the spread of invasive pests may help with the development of detection, monitoring, containment, and control plans (David et al. 2014).

Red palm weevil, *Rhynchophorus ferrugineus* (Olivier), (Coleoptera: Curculionidae) is a pest of coconut palms, *Cocos nucifera* L. (Arecales: Arecaceae) (Giblin-Davis et al. 2013) in its native range, the northern and western regions of continental southeast Asia (i.e., northern Thailand, Vietnam, and Cambodia), Sri Lanka, and the Philippines (Rugman-Jones et al. 2013). Accidental introduction of *R. ferrugineus* into regions outside of the native range occurred via the movement of live palms infested with weevils (Giblin-Davis et al. 2013) with the first record being in the United Arab Emirates in 1985 (Faleiro et al. 2012). *R. ferrugineus* has been recorded attacking >40 palm species in 23 genera and has caused extensive mortality of Canary Island date palms (*Phoenix canariensis* Chabaud) in the Mediterranean and date palms (*Phoenix dactylifera* L.) (both Arecales: Arecaceae) in the Middle East and North Africa (Faleiro 2006, Faleiro et al. 2012, Giblin-Davis et al. 2013, Murphy and Briscoe 1999). The invasion pattern exhibited by *R. ferrugineus* is representative of a stratified dispersal process (Hengeveld 1989), which is a combination of: 1) rapid long-distance dispersal mediated by either abiotic factors (e.g., wind) or biotic factors (e.g., anthropogenic movement), and 2) short-distance localized dispersal via flying or walking within invaded habitats (Hengeveld 1989, Petit et al. 2008).

Adult *R. ferrugineus* are large insects (~2–3 cm long and ~1 cm wide; Giblin-Davis et al. 2013) exhibiting variable coloration that is commonly composed of an

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orange thorax with varying amounts of discrete black mottling, and black and orange striations on the elytra (Rugman-Jones et al. 2013). Palm mortality caused by *R. ferrugineus* results from internal feeding by larvae (mature larvae can exceed 5 cm in length), and the entire larval life cycle is concealed within the palm, making early detection of infestations difficult (Giblin-Davis et al. 2013). Internal feeding by approximately two to three generations of weevil larvae over a 1- to 2-yr period can kill infested palms which results from mortality of apical growing areas (typical for *P. canariensis*) or trunk collapse (observed for *P. dactylifera*; Fahiero 2006, Dembilio and Jacas 2011, Ll acer et al. 2012, Giblin-Davis et al. 2013). Area-wide management programs in commercial date palm plantations using bucket traps baited with a commercially available aggregation pheromone, fermenting attractants (e.g., dates), and synergists (e.g., ethyl acetate) which attract and capture flying adults, combined with insecticide applications and removal of infested palms, can significantly reduce *R. ferrugineus* populations (Hoddle et al. 2013).

Flight capacity, a measure of short- and long-distance dispersal at the landscape level of these large insects is poorly studied. Typically, two different approaches are taken to assess insect flight capacity. The first method is to release marked insects into a field environment, and these experimental insects are then recaptured over time at varying distances from the release point. Capture frequency and capture location of marked insects at predetermined points over the course of the study are used to assess dispersal rates from a release epicenter (Margaritopoulos et al. 2012). The accuracy of data from mark-recapture field studies is limited by the number of insects available for marking and releasing, the number of traps deployed to capture marked insects, the pattern of trap placement and distance traps are placed from release points, recapture rates, and the length of time of the study (Yamamura et al. 2003, Franzen and Nilsson 2007, Hassall and Thompson 2012). Mark-recapture studies can underestimate flight distances with certain trapping designs because marked insects may be trapped at distances shorter than what they are capable of covering, or conversely, insects may have flown distances greater than the distance from the release point to the trap in which they were captured (Yamamura et al. 2003).

The second approach to measuring insect flight is the use of computerized flight mills that record insect activity under controlled conditions in the laboratory (David et al. 2014, Lopez et al. 2014, Martini et al. 2014). This method has several advantages over mark-recapture studies because covariates such as color morph (Martini et al. 2014), temperature (Ferrer et al. 2014), age, size, sex, and mating status of adult insects (Taylor et al. 2010,  avalos et al. 2014, Lopez et al. 2014), endosymbiont load (Castro et al. 2014), and diet (Lopez et al. 2014, Maes et al. 2014) on flight capability can be assessed. An additional advantage of flight mill studies is that they allow the detection and quantification of leptokurtic distributions. These distributions are characterized by a high number of individuals clustered

around the mean distance flown and in the tails of the distribution of flight data than would be expected when compared to a normal distribution with a similar mean and variance (Kok et al. 1996, Chapman et al. 2007). Leptokurtic distributions may typify the spread of some invasive species (Kok et al. 1996). However, they are difficult to quantify with mark-recapture studies because of the large number of released individuals that would have to be liberated and the number of traps that would have to be deployed over very large distances relative to the release point to recapture sufficient numbers of study organisms to quantify the underlying parameters (i.e., the "kernel") that describe a leptokurtic distribution.

Despite these advantages, there are recognized shortcomings to flight mill studies. These include potential unknown behavioral effects which are difficult to define and quantify that could result from handling and attachment to the flight mill (Taylor et al. 2010). For example, tethered insects don't have to support their own weight and are forced to fly because of lack of tarsal contact with substrate (Hollick 1940, Weis-Fogh 1956, Wilson 1961). Additionally, laboratory flight mill studies may not be representative of flight performance in the field because experimental insects don't encounter environmental cues that could either stimulate (e.g., wind) or suppress flight (e.g., heat; Taylor et al. 2010). Although flight mill studies may need to be interpreted with caution (Taylor et al. 2010), they can be useful research tools for quantifying basic attributes such as flight bout frequency and duration, distance flown, flight velocity, and flight periodicity. These types of data are very difficult to collect accurately in the field from mark-recapture studies.

The work presented here used computerized flight mills to investigate the flight capabilities of *R. ferrugineus* captured in traps baited with aggregation pheromone in commercial date palm plantations in the Kingdom of Saudi Arabia. To be used in flight mill studies, weevils had to fly to traps, which meant trapped insects had demonstrated an ability and propensity for this behavior. Additional benefits to using field-captured weevils were the large numbers readily available for study, and in comparison to *R. ferrugineus* reared on artificial diet or excised pieces of palm (these are expensive labor-intensive rearing processes [Aldawood and Rasool 2011]), weevils that develop in the field on live palm hosts tend to be larger and fitter (Al-Ayedh 2011), which likely affects flight performance parameters. The work presented here investigated the effects of color morph, sex, size, and time of year on flight activity for field-captured *R. ferrugineus* in Saudi Arabia in the laboratory over a 24-h period.

Materials and Methods

Source and Preparation of *R. ferrugineus* for Flight Mill Studies. Weevils used for this study were captured in bucket traps deployed in the Al Ahsaa Directorate, in the Kingdom of Saudi Arabia. Standard 5-liter capacity bucket traps with four windows cut into the sides of the bucket baited with aggregation

pheromone (Ferrolure 700 mg, ChemTica International S.A., Costa Rica), ~200 g of fermented dates as food bait, and 1 liter of water were used to trap *R. ferrugineus*. Ethyl acetate synergist and insecticides were not added to traps. Traps were partially inserted into hollowed out date palm trunks set ~0.5 m above the ground and serviced weekly by engineers employed by the Directorate of Agriculture, Al Ahsaa. Dates and water were replaced as needed, and pheromone lures were replaced at ~6-wk intervals. Approximately 9,000 traps were deployed throughout date palm orchards in Al Ahsaa. This was equivalent to one trap per Ha dispersed amongst ~3 million date palms. The 'Khalas' date cultivar accounted for ~85% of production.

Captured weevils cleared from traps were delivered daily to the Date Palm Research Center for Excellence, King Faisal University, Al Ahsaa, Kingdom of Saudi Arabia. In the laboratory, live weevils were placed in clear plastic ventilated containers (~50 by 40 by 30 cm³) provisioned with fresh stalks of sugar cane (*Saccharum officinarum* L. [Poales: Poaceae]) that were split longitudinally. *R. ferrugineus* adults readily consume sugar cane and can be sustained for considerable periods (i.e., weeks) on this diet (Bozbuga and Hazir 2008, Li et al. 2010). Field-captured weevils used for flight mill studies were reconditioned in the laboratory for at least 14 d on sugar cane before being used for experiments. Approximately 8–10 boxes containing weevils were maintained for flight mill studies. Containerized weevils were maintained in the laboratory at 21–23°C and 26–29% relative humidity (RH).

Selection and Measurements of *R. ferrugineus* for Flight Mill Studies. For each flight mill trial, 18 adult *R. ferrugineus* of unknown age were randomly selected from boxes for use in flight mill studies. Eight weevils were used for flight experiments and 10 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. Prior to tethering on the flight mill, individual experimental and control weevils were weighed on an electronic balance (AL204 Mettler Toledo, Columbus, OH) and again postflight to determine percentage weight change. A second measure of weevil size was recorded and this consisted of measurements of thorax width and length, and body length 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). Weevils were assigned to one of eight color categories based on the number of black spots on the thorax and the intensity of maculation. The four spot categories were 2–3, 4–5, 6–7, > 8 thoracic spots and spots were assigned as being either "light" (i.e., small) or "heavy" (i.e., large). Male and female *R. ferrugineus* were frequently observed copulating in holding boxes and all experimental and control weevils were assumed to have mated.

Experimental Set Up and Description of Flight Mills. Flight mill studies were conducted at the Date Palm Research Center for Excellence, King Faisal University, over three different time periods: 6–13 December 2011 (winter), 6–19 March 2012 (spring), and 19–29 May 2012 (summer). For winter trials, only female weevils were flown. Male weevils were being used for outdoor mark-recapture flight studies. Females could not be used in these studies, as they may have initiated infestations in areas undergoing area-wide management. Eight flight mills were set up on a table (6.7 by 1.2 by 0.76 m³) inside an 8.5- by 4.5-m room. Four windows provided ambient light and there was no supplemental lighting to increase natural photoperiod. A hobo data logger (H08-007-02, Onset 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. To stimulate flight, two pheromone bucket traps which contained aggregation pheromones (Ferrolure 700 mg, ChemTica International S.A., Costa Rica), ethyl acetate, and fermenting dates submerged in water were placed on either end of the table. Experimental weevils were set up on flight mills by 9:00 a.m. each morning that experiments were run and trials lasted 24 h. Control weevils inside clear ventilated plastic containers (7.5 by 7.5 by 15 cm³) without access to food or water were placed on the table with the flight mills for the duration of the experiment. At the end of the 24-h study period, the number of live and dead weevils by treatment and sex was recorded, tethered weevils were removed from flight mills, and experimental and control weevils were weighed on a digital balance to assess weight loss in relation to treatment and sex.

Weevils were attached dorsally by their thorax to a "L"-shaped metal plate (0.59 mm diameter by 28 mm long) using high strength glue (Gorilla Glue Company, Cincinnati, OH). Once the glue was dry (30–90 s), the L-shaped metal plate with the attached weevil was connected to a standard socket crimp (model 809-043, Glenair, Glendale, CA), which was directly connected to an arm of the flight mill rotor. While each flight mill has the capability to detect flight in either direction, the rigidity of L-shaped plate only allowed for unidirectional flight. Upon attachment to the flight mill arm, visual confirmation ensured that tethered weevils could freely move their wings and legs. A counterbalance (i.e., modeling clay) of similar weight to the experimental weevil was attached to the opposite arm of the rotor. At this stage software measuring flight activity was activated and data recording began.

The flight mills used in this study were manufactured at the University of California Riverside. They were purposely designed to handle large heavy insects utilizing friction-free ball bearing technology as opposed to magnetic flotation. Customized flight mills were necessary for the size and power of *Rhynchophorus* spp., which can weigh up to ~3 g. Each flight mill was connected to a laptop computer via a USB4 Encoder Data Acquisition Device (US Digital, Vancouver, WA). The system allowed simultaneous data

collection from up to eight individual insects. Custom software was developed to record flight data and custom 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. A detailed description of this set up, including the specific methodology in which flight activity was measured and recorded, calibration accuracy of measured parameters, and schematics and photos of the flight mills with tethered insects can be found in Lopez et al. (2014).

Statistical Analyses. Prior to statistical analyses, 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: weight loss: $y^{0.25}$; thorax width: y^2 ; thorax length: y^2 ; body length: y^2 ; maximum velocity: y^2 ; total distance flown: $y^{0.5}$; maximum distance flown: not transformed; total flying time: $y^{0.5}$; number of flight bouts: $y^{0.25}$; time elapsed until first flight bout: log transformed; flight length: log transformed; and maximum flight length: $y^{0.75}$. The flight performance of *R. ferrugineus* adults by season, gender, and flight status (i.e., flyer vs. nonflying control weevils) was analyzed using a three-way analysis of variance (ANOVA). For all other flight parameters of interest by gender and season two-way ANOVA was used. Analysis of covariance (ANCOVA) was used to determine if significant relationships existed between weevil color morph and flight parameters of interest. Fisher's exact test was used to assess weevil survivorship rates at the end of flight trials. Tukey-Kramer tests were used to conduct pairwise comparisons for each significant factor in analyses. When significant interactions occurred, contrasts to determine the effects of interacting variables were conducted at the 0.05 level of significance. 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. ferrugineus* Using Flight Mill Data. Kaplan-Meier survival analyses were performed using PROC LIFETEST in SAS (SAS Institute Inc. 2008) on flight distance data for live and dead weevils. Kaplan-Meier survival curves, as a function of survival probability and distance flown in a 24-h period, were generated for each gender by season. These five survival curves were subjected to a log-rank test in PROC LIFETEST, at the 0.05 level of significance to determine if significant differences in distances flown existed between live and dead male and female weevils across seasons (i.e., winter, spring, and summer). No significant differences were detected as function of gender or season (see results); hence, all flight data by season and sex were combined and used to define dispersal curves and corresponding redistribution kernels.

Flight distance data were divided across nine bins (distance interval = 7.78 km with the maximum flight distance recorded acting as the upper bin limit)

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 ($R^2 = \text{SSE}/\text{total sums of squares [SST]}$). 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 (139) and a normalizing constant (2184.47) 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:

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

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

Results

A total of 192 tethered and 160 nontethered control *R. ferrugineus* were used in flight mill studies (Table 1). Of the weevils tethered to flight mills, 28% (33 females and 20 males) failed to fly > 1 km and were therefore considered nonfliers and were excluded from analyses. Consequently, 139 weevils (93 females and 46 males) flew > 1 km in 24 h and were classified as flyers and used for statistical analyses (Table 1).

Weevil color morph was not significantly associated with any measured flight parameters (ANCOVA results not shown). Mean body weight of weevils before experiments were initiated exhibited significant differences across seasons ($F = 52.28$, $df = 2$, $P < 0.001$), gender ($F = 9.55$, $df = 1$, $P = 0.002$), and flyer status (i.e., flyer vs. nonflying control weevils; $F = 19.37$, $df = 1$, $P < 0.001$). Female weevils tended to be heavier than males and this was consistent across seasons. Further, female weevils captured in traps over spring and summer and used for experiments were generally heavier than females captured in winter (Table 1). Average percentage weight loss over the course of a 24-h experiment was significant across seasons ($F = 41.72$, $df = 2$, $P < 0.001$), gender ($F = 5.13$, $df = 1$, $P = 0.02$), flyer status ($F = 1075$, $df = 1$, $P < 0.001$), and a significant interaction effect between season and flyer status was detected ($F = 6.76$, $df = 2$, $P = 0.001$). Flying male and female weevils lost on average >20% of their body weight in a 24-h period. In comparison, control weevils lost ~9–13% of their original body weight. For female and male weevils, both flyers and controls, mean percentage weight loss in 24 h tended to be higher in

Table 1. Average (\pm SE) body size and flight parameters by season and gender for *R. ferrugineus* 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 (\pm SE) parameter measured	Winter (6–13 Dec. 2011)				Spring (6–19 Mar. 2012)				Summer (19–29 May 2012)			
	Female		Male		Female		Male		Female		Male	
	Flyer (n = 35)	Control (n = 60)	Flyer (n = 33)	Control (n = 20)	Flyer (n = 27)	Control (n = 20)	Flyer (n = 25)	Control (n = 30)	Flyer (n = 19)	Control (n = 30)		
Weight before trial (g)	1.13 \pm 0.04de	1.05 \pm 0.02e	1.35 \pm 0.03ab	1.27 \pm 0.04bcd	1.25 \pm 0.04bcd	1.13 \pm 0.05cde	1.47 \pm 0.04a	1.32 \pm 0.04ab	1.40 \pm 0.03ab	1.29 \pm 0.04bc		
Weight after trial (g)	0.90 \pm 0.04	0.96 \pm 0.02	1.02 \pm 0.02	1.17 \pm 0.04	0.94 \pm 0.04	1.02 \pm 0.04	1.06 \pm 0.03	1.18 \pm 0.04	0.99 \pm 0.03	1.13 \pm 0.04		
% Weight loss	20.42 \pm 1.28c	9.05 \pm 0.01f	24.07 \pm 0.75b	8.30 \pm 0.01f	24.60 \pm 0.98ab	9.25 \pm 0.01ef	27.87 \pm 0.78ab	11.27 \pm 0.01de	29.39 \pm 0.81a	12.64 \pm 0.01d		
Thorax width (mm)	9.01 \pm 1.10ab	9.03 \pm 0.07ab	9.31 \pm 0.08a	9.07 \pm 0.11ab	9.21 \pm 0.16ab	8.70 \pm 0.16b	9.47 \pm 0.10a	9.25 \pm 0.12ab	9.53 \pm 0.11a	9.14 \pm 0.12ab		
Thorax length (mm)	10.60 \pm 0.14abc	10.31 \pm 0.07bc	10.64 \pm 0.08abc	10.35 \pm 0.13bc	10.50 \pm 0.17abc	10.07 \pm 0.16c	10.97 \pm 0.12a	10.71 \pm 0.10ab	10.79 \pm 0.12ab	10.44 \pm 0.10bc		
Body length (mm)	26.05 \pm 0.30bc	25.61 \pm 0.17bcd	26.67 \pm 0.16ab	26.14 \pm 0.30ab	25.53 \pm 0.34bcd	24.61 \pm 0.31d	27.32 \pm 0.24a	26.55 \pm 0.24ab	26.25 \pm 0.22abc	25.41 \pm 0.22cd		
% Survivorship	88	100	67	100	67	100	20	93	21	90		
Velocity (m/s)	1.19 \pm 0.08b	1.53 \pm 0.08ab	1.53 \pm 0.08ab	1.56 \pm 0.07ab	1.56 \pm 0.07ab	1.53 \pm 0.08ab	1.79 \pm 0.13a	1.68 \pm 0.16a	1.68 \pm 0.16a	1.68 \pm 0.16a		
Maximum velocity (m/s)	2.76 \pm 0.10c	3.08 \pm 0.11bc	3.08 \pm 0.11bc	3.20 \pm 0.13bc	3.20 \pm 0.13bc	3.08 \pm 0.11bc	3.82 \pm 0.16a	3.42 \pm 0.13ab	3.42 \pm 0.13ab	3.42 \pm 0.13ab		
Total distance flown (km)	14.95 \pm 1.89b	21.52 \pm 1.97ab	21.52 \pm 1.97ab	24.12 \pm 3.11ab	24.12 \pm 3.11ab	21.52 \pm 1.97ab	34.79 \pm 4.00a	25.28 \pm 3.66ab	25.28 \pm 3.66ab	25.28 \pm 3.66ab		
Max. distance flown (km)	9.69 \pm 1.12c	11.90 \pm 1.31bc	11.90 \pm 1.31bc	13.60 \pm 1.86abc	13.60 \pm 1.86abc	11.90 \pm 1.31bc	18.98 \pm 2.23a	18.85 \pm 2.70ab	18.85 \pm 2.70ab	18.85 \pm 2.70ab		
Total time flying (h)	3.35 \pm 0.30a	3.89 \pm 0.31ab	3.89 \pm 0.31ab	4.12 \pm 0.45ab	4.12 \pm 0.45ab	3.89 \pm 0.31ab	5.56 \pm 0.59a	4.12 \pm 0.44ab	4.12 \pm 0.44ab	4.12 \pm 0.44ab		
Total flight bouts	74 \pm 12b	92 \pm 13ab	92 \pm 13ab	100 \pm 16ab	100 \pm 16ab	92 \pm 13ab	125 \pm 20ab	147 \pm 29a	147 \pm 29a	147 \pm 29a		
Time elapsed to first flight bout (h)	0.29 \pm 0.17a	1.20 \pm 0.24b	1.20 \pm 0.24b	1.21 \pm 0.27b	1.21 \pm 0.27b	1.20 \pm 0.24b	0.31 \pm 0.06a	0.37 \pm 0.06a	0.37 \pm 0.06a	0.37 \pm 0.06a		
Flight bout length (h)	0.23 \pm 0.05a	0.19 \pm 0.04a	0.19 \pm 0.04a	0.21 \pm 0.06a	0.21 \pm 0.06a	0.19 \pm 0.04a	0.28 \pm 0.07a	0.19 \pm 0.07a	0.19 \pm 0.07a	0.19 \pm 0.07a		
Max. flight bout length (h)	1.55 \pm 0.15a	1.63 \pm 0.15a	1.63 \pm 0.15a	1.76 \pm 0.19a	1.76 \pm 0.19a	1.63 \pm 0.15a	2.02 \pm 0.20a	2.07 \pm 0.2a	2.07 \pm 0.2a	2.07 \pm 0.2a		
Room temp. ($^{\circ}$ C)	21.14 \pm 0.09a	23.75 \pm 0.07b	23.75 \pm 0.07b	26.44 \pm 0.11a	26.44 \pm 0.11a	23.75 \pm 0.07b	27.20 \pm 0.23c	27.20 \pm 0.23c	27.20 \pm 0.23c	27.20 \pm 0.23c		
% RH in room	29.06 \pm 0.16a	26.44 \pm 0.16a	26.44 \pm 0.16a	29.95 \pm 0.26a	29.95 \pm 0.26a	26.44 \pm 0.16a	29.95 \pm 0.26a	29.95 \pm 0.26a	29.95 \pm 0.26a	29.95 \pm 0.26a		

Means with different letters within rows indicate significant differences at the 0.05 level.

summer (Table 1). The percentage of male and females weevils surviving after 24 h was highest in controls (90–100% survivorship) and lower for flyers (20–88% survivorship), with mortality rates reaching ~80% for male and female flyers in summer (Table 1).

Mean thorax width varied significantly by season ($F=6.36$, $df=2$, $P=0.002$) and flyer status ($F=11.81$, $df=1$, $P=0.007$). Male and female flyers used in summer and spring trials were slightly larger than male control weevils used in spring trials (Table 1). Significant differences in average thorax length were detected across season ($F=9.84$, $df=2$, $P<0.001$), gender ($F=5.59$, $df=1$, $P=0.02$), and flyer status ($F=19.24$, $df=1$, $P<0.001$). Male control weevils in spring trials had slightly shorter thoraxes when compared to other experimental weevils (Table 1). Mean weevil body length was significantly different across season ($F=14.66$, $df=2$, $P<0.001$), gender ($F=41.46$, $df=1$, $P<0.001$), and flyer status ($F=17.88$, $df=1$, $P<0.001$). Nonflying control male weevils used in spring were on average shorter than other experimental weevils (Table 1). All body size measurements, thorax width and length, and body length indicate that male weevils used as controls for spring trials were consistently smaller than other experimental weevils (Table 1).

Average velocity of flying weevils was significant by season only ($F=10.27$, $df=2$, $P<0.001$). Male and female weevils flew faster in summer, had intermediate velocities in spring, and females (only sex flown) were slowest in winter (Table 1). Mean maximum velocity for tethered weevils was significantly different across seasons ($F=22.36$, $df=2$, $P<0.001$), and a significant season by gender effect was detected ($F=6.48$, $df=1$, $P=0.01$). Female and male weevils flying in summer exhibited a higher average maximum velocity and females flown in winter had an average maximum velocity that was significantly lower than summer weevils (Table 1).

For tethered male and female weevils combined across seasons that flew > 1 km, 18% flew 1–10 km, 15% flew 10–20 km, 18% flew 20–30 km, 11% flew 30–40 km, 6% flew 40–50 km, 4% flew 50–60 km, and three females (2%) flew >60 km in a 24-h period (Fig. 1A). Weevil flight activity (data for sexes and seasons combined) commenced around 5:00 a.m., and the highest percentage of weevils flying was observed between 9:00 a.m. to 3:00 p.m. (Fig. 1B). Cumulative total distance flown was greatest between 9–11:00 a.m. before tapering off in the afternoon. Very low levels of flight activity were recorded between 11:00 p.m. and 5:00 a.m. with < 2% of weevils flying at this time (Fig. 1B). Average total distance flown was significantly different for season only ($F=8.9$, $df=2$, $P=0.0002$). Mean flight distances were highest for females flying in summer (~35 km flown in 24 h), and lowest for females in winter (~15 km flown in 24 h; Table 1). The mean maximum distance flown in a single flight bout was also significant for season only ($F=10.96$, $df=2$, $P<0.001$). The longest distance flown in a single bout was ~19 km for male and female weevils in summer and females flying in winter flew ~10 km (Table 1).

Total average time spent flying within a 24-h period was significantly different by season only ($F=4.70$,

$df=2$, $P=0.01$; Table 1). Female weevils flew significantly longer (~40% longer) in summer (~5.6 h of flight) than female weevils flown in winter (~3.4 h of flight; Table 1). Similarly, the total number of flight bouts was significant for season only ($F=5.06$, $df=2$, $P=0.008$). Male weevils flying in summer engaged in significantly more flight bouts, ~50% more, when compared to female weevils flying in winter (Table 1). Average flight bout time and distance flown per bout (data for sex and season combined) increased steadily after 5:00 a.m., peaked between 9–11:00 a.m., before declining and stabilizing at distances of ~1 km and bout durations of ~7 min (Fig. 1C). Time elapsed to first flight bout was significantly different for season only ($F=33.98$, $df=2$, $P<0.0001$). The shortest elapsed times to the first flight bout were shortest for weevils flying in summer and winter, and longest (~4 times longer) for weevils flown in spring (Table 1). Average flight bout lengths (~0.2 h) were not significantly different across season or gender (Table 1). The average time (~1.5–2.0 h of continuous flight) of the maximum flight recorded for each weevil did not differ significantly across season or gender (Table 1).

The average room temperature at which flight mill studies were conducted varied significantly across season ($F=99.04$, $df=2$, $P<0.0001$). Temperatures were highest in summer, lowest in winter, and intermediate in spring (Table 1). No significant differences in mean percentage relative humidity were detected (Table 1).

Dispersal and Redistribution Kernel for *R. ferrugineus*. The log-rank test assessing the probability of weevil survivorship as a function of distance flown was not significant for gender by season ($\chi^2=6.35$, $df=4$, $P=0.17$), season alone ($\chi^2=3.28$, $df=2$, $P=0.19$), or sex alone ($\chi^2=0.57$, $df=1$, $P=0.45$). Therefore, all flight data by season and sex were combined and the best fitting of the five curves analyzed from Kot et al. (1996) was curve 1:

$$f(x) = e^{a-bx^2}$$

where $a=3.32$, $b=0.0005$, x = midpoint of the distance bin (km) (SSE = 86.71, $R^2=0.89$; Fig. 2A). This function was used to generate the corresponding redistribution kernel, described by the equation:

$$f(x) = ae^{-\frac{x^2}{b}}$$

where $a=0.013$, $b=1985.38$, and x = distance flown (km). The excess kurtosis measure was 0 indicating that the equation describing the curve that was produced is mesokurtic (i.e., has a normal distribution) (Fig. 2B) which is analogous to:

$$f(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{x^2}{2\sigma^2}}$$

where $\sigma=31.5$ which can be denoted as $N(0, 31.5^2)$ and x = distance flown (km).

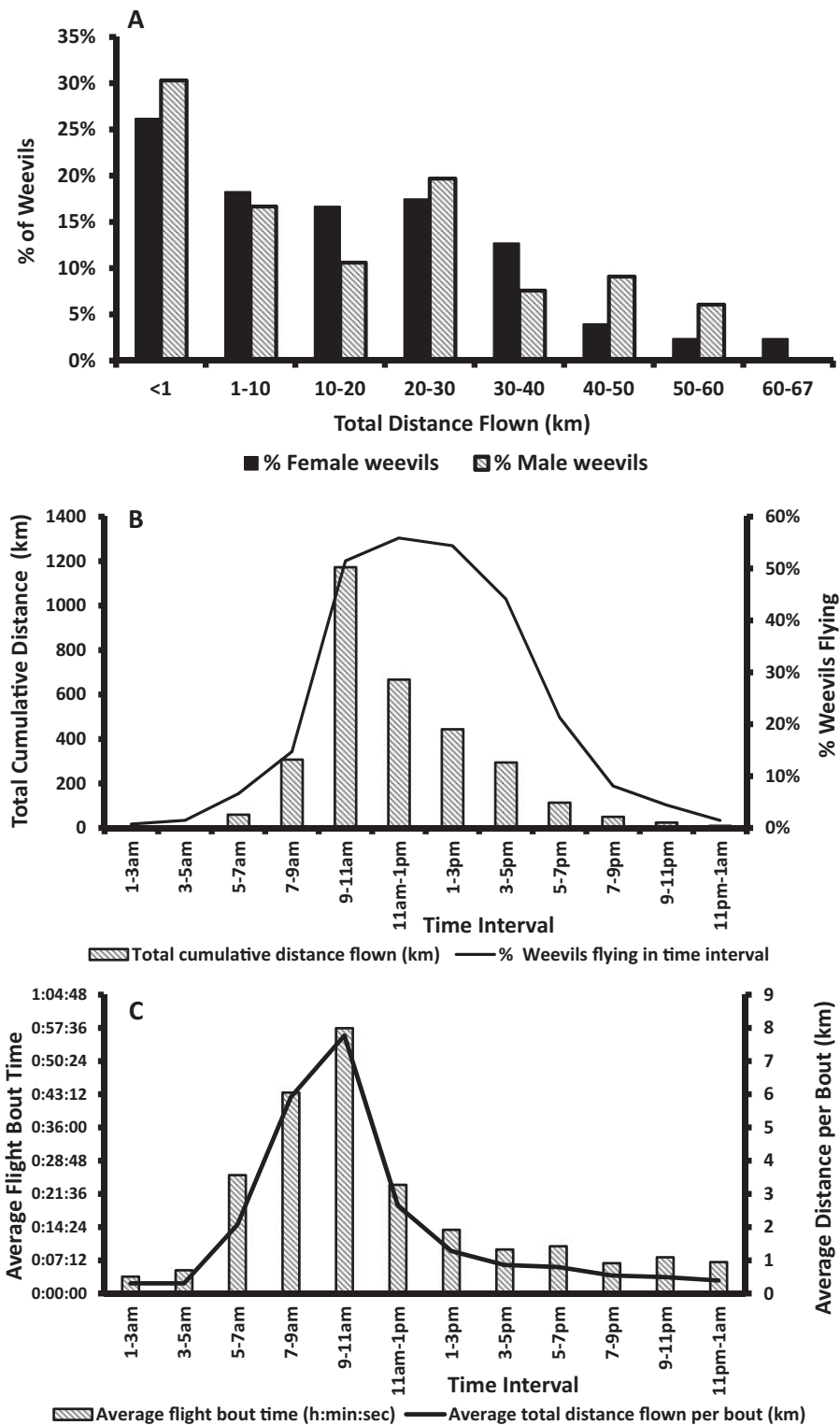


Fig. 1. Summary data combined across seasons (i.e., winter, spring, and summer) for male and female *R. ferrugineus* flown on flight mills for 24 h in the laboratory. (A) Percentage of male and female *R. ferrugineus* binned by total distance (km) flown. (B) Total cumulative distance (km) flown and percentage 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:s) binned by 2-h time intervals.

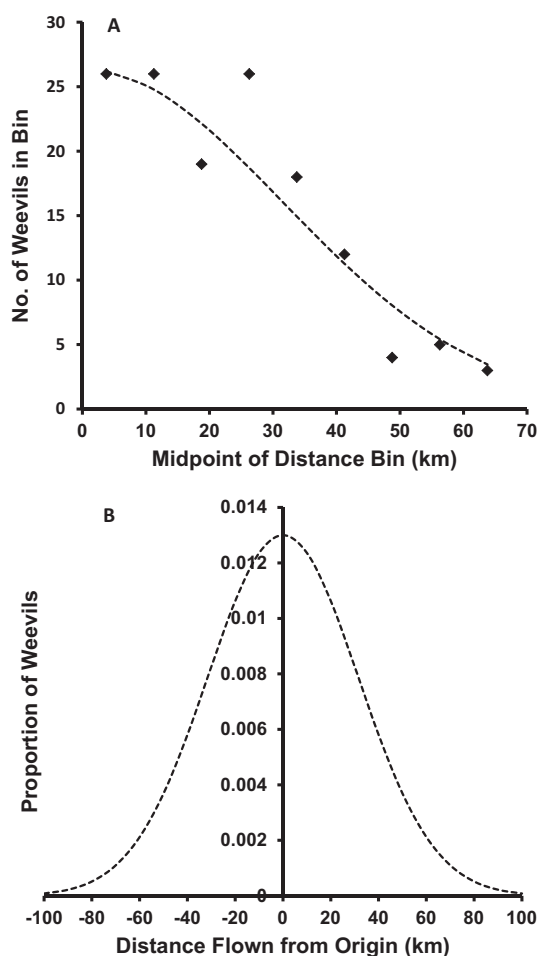


Fig. 2. (A) Dispersal curve and (B) redistribution kernel generated using flight data combined across seasons (winter, spring, and summer) for male and female *R. ferrugineus* flown on flight mills in the laboratory for 24 h.

Discussion

In the laboratory, male and female *R. ferrugineus* are capable of flying considerable distances; 55% of weevils that exhibited >1 km of flight on flight mills flew >10 km and of these 5% flew >50 km in a 24-h period. In contrast, ~30% of experimental weevils flew <1 km in 24 h and these weevils were considered nonfliers, but likely capable of short-distance dispersal within date palm orchards. Similarly, Ávalos et al. (2014) reported that ~30% of virgin *R. ferrugineus* tethered to flight mills failed to fly in 12 h (the start and stop times for these experiments were not noted) while 10% of experimental weevils flew >5 km in this time period. The longer flight distances recorded here could be a function of both weevil propensity to fly (insects were removed from field deployed pheromone traps and had to fly unknown distances to traps) and weevil age. Ávalos et al. (2014) reported that older weevils (8–14 d of age) tended to fly greater distances. The ages of all weevils used in these studies exceeded 14 d,

but exact ages of field-captured weevils was unknown. In the laboratory, adult weevils are long-lived and can survive on a date palm trunk diet for ~82–92 d (El-Shafie et al. 2013). Factorial experiments investigating flight activity of cohorts of *R. ferrugineus* as a function of age (e.g., young [< 7 d of age] or old [> 21 d]), time of year (e.g., spring vs. summer), mating status (e.g., mated vs. virgins), and gustatory satiation (e.g., starved vs. fed) would improve our understanding of the flight characteristics of these large weevils.

Additionally, temperature and humidity are important environmental variables that affect weight loss and flight propensity in *R. cruentatus* (F.), a palm weevil species congeneric to *R. ferrugineus* (Weissling and Giblin-Davis 1993, Weissling et al. 1994). Under low humidity conditions (<33%) adult *R. cruentatus* can lose ~30% body weight in 24 h (Weissling and Giblin-Davis 1993) and flight activity increases significantly as temperature increases and humidity declines (Weissling et al. 1994). It is possible that temperature and humidity affect flight initiation and cessation in *R. ferrugineus* in a similar manner, but this appears not to have been studied. The flight mill studies conducted here over winter, spring, and summer had temperatures averaging 21–27°C and low humidity (~30%). Collectively this temperature range coupled with low humidity may have had a significant effect on flight activity, especially at higher temperatures, when the combined stress of both of these factors would be expected to be greatest. This may explain, in part, why flight distances and weevil mortality were greatest when flight trials were conducted over summer when average temperatures were highest. Consequently, in humid areas with abundant food (e.g., well irrigated date palm plantations), *R. ferrugineus* may not readily undertake long-distance flights.

However, under experimental conditions reported here, results suggest that long-distance dispersal by *R. ferrugineus* is possible and in the field these large weevils, perhaps ~70% of a population greater than 14 d of age, may have the capacity to fly long distances (>10 km) in a relatively short time (24 h). A mark-recapture study in date palm plantations in the United Arab Emirates indicated that *R. ferrugineus* can fly ~1–7 km in 3–5 d to reach pheromone traps (Abbas et al. 2006). Determining the significance of these flight distance data is difficult. Data from this study and Ávalos et al. (2014) indicate that a substantial proportion (~30%) of *R. ferrugineus* exhibit short-distance flights covering distances similar to those reported by Abbas et al. (2006). It is possible that Abbas et al. (2006) only recaptured *R. ferrugineus* that engaged in short relatively localized dispersal. Alternatively, captured weevils may have flown distances exceeding 7 km before being captured in traps 3–5 d postrelease. This possibility would underestimate distances flown by *R. ferrugineus*, which is a shortcoming of field studies using mark-recapture techniques (Yamamura et al. 2003). Field studies quantifying short- and long-distance dispersal of *R. ferrugineus* need to assess the feasibility of using electronic devices that record and transmit locality data over time. However, significant challenges (e.g., energy

supply, signal broadcast range, and equipment costs) need to be overcome before these types of studies, especially technology utilizing space-based tracking technologies (i.e., GPS satellite monitoring or near-earth orbit receivers), will be possible (Kissling et al. 2014). Space-based tracking technologies may be the only way to accurately estimate the distances of flights made by *R. ferrugineus* that are > 1 km (Kissling et al. 2014).

Strong flight activity had a significant cost in terms of percent body weight lost and survivorship rates. Weevils engaging in flight over a 24-h period exhibit significant weight loss, ~20–30% (depending on sex and season) of their preflight body weight. Average percentage body weight lost during flight was highest (~30%) over summer (i.e., May) when the longest average total flight distances (~25–35 km) were recorded and ~80% of weevils died that flew within the 24-h trial period. The average laboratory temperature when flight studies were conducted was ~27°C and average outdoor summer temperatures in Al Ahsaa when experiments were run was ~35°C (Hoddle et al. 2013). The effect of temperatures > 27°C on *R. ferrugineus* flight propensity, distances flown, and survivorship rates in the field is unknown. However, flight propensity as determined from pheromone trap captures does not indicate significant changes in mean numbers of captured weevils over summer (Hoddle et al. 2013). These field data suggest that numbers of weevils flying to traps is reasonably consistent year round in Al Ahsaa (Hoddle et al. 2013). However, no inferences about average distances flown in the field throughout the year can be made from these trap data (Hoddle et al. 2013).

Strong flight capabilities exhibited by *R. ferrugineus* could facilitate rapid spread and colonization of widely separated resources. This possibility needs serious consideration when *R. ferrugineus* is detected in new areas and incursion foci are highly localized and parameterization of quarantine boundaries are under consideration. Accurate quantification of the dispersal potential of a pest species is critical during the initial stages of managing an invasion because containment and eradication success is greatest when populations are relatively small and localized (Tobin et al. 2014).

Invasive insect pests can exhibit sex-biased dispersal behavior which can have important consequences at the leading edge of an invasion because population densities tend to be lower in this zone and sex bias can affect reproductive success and subsequent establishment (i.e., Allee effects may result from an inability to locate mates [Miller et al. 2011]). Additionally, the distribution of dispersal distances significantly influences a species potential rate of spread and occasional long-distance spread by some individuals can lead to skewed dispersal distance distributions and faster than expected invasion speeds (Kot et al. 1996). In this study, flight mill data for *R. ferrugineus* indicated that season (i.e., time of year) not sex had a significant effect on total distance flown (and average flight velocity) by male and female weevils. Ávalos et al. (2014) also reported that sex was not significantly correlated with

flight distance. Additionally, the distance distribution kernel derived from flight distance data (for both sexes and all seasons combined) was mesokurtic (i.e., normally distributed) and lacked the fat-tailed characteristics of a leptokurtic distribution exhibited by some invasive species that demonstrate rapid and expansive spread (Kot et al. 1996).

The majority of flight activity in the laboratory was diurnal, with an average ~54% of weevils exhibiting varying levels of activity between 9:00 a.m. and 3:00 p.m. Flight propensity increased after 5:00 a.m. and peaked between 9–11:00 a.m. Low levels of flight activity were observed between 7:00 p.m. and 5:00 a.m. (on average ~4% of weevils flew in this time interval). Fanini et al. (2014) determined that the outdoor flight activity of *R. ferrugineus* as monitored by attraction to pheromone traps in Italy and Greece (part of the invaded range in the Mediterranean) and Vietnam (part of the native range) was diurnal. In contrast, flight activity recorded by captures in baited pheromone traps in Goa, India (part of the native range), was greatest between midnight and 6:00 a.m. (Faleiro and Satar-kar 2003), and in Sri Lanka (part of the native range) captures were only recorded between 6:00–8:00 p.m. and 6:00–8:00 a.m. (Faleiro 2006). Trap captures of *R. ferrugineus* in the Philippines were highest between 5:00 p.m. and 6:00 a.m., with 78% of weevils being caught in this time interval (Hoddle and Hoddle 2011). These different trap capture times could support the putative suggestion by Rugman-Jones et al. (2013) that *R. ferrugineus* in its home range may consist of cryptic species that could potentially exhibit different temporal responses to aggregation pheromone rather than a single species exhibiting response plasticity due to environmental conditions (Faleiro 2006).

In conclusion, flight mill-generated data indicated that a considerable proportion (~70%) of field-captured *R. ferrugineus* exhibited an ability to fly > 1 km in a 24-h period. Of those weevils flying > 1 km 55% flew > 10 km in a 24-h period. Time of year influenced both average total flight distance and mortality rates in a 24-h period, with both being elevated in summer (i.e., May) when temperatures were significantly higher than winter (December) and spring (March). Incursion management for this pest, especially at the early stages of an invasion, need to consider the possibility for rapid long-distance flight by mated male and female weevils. Use of dispersal data from flight mill studies could assist with the design and implementation of monitoring boundaries, which may maximize the likelihood of detecting weevils capable of long-distance dispersal, which would assist with the development of containment and eradication programs when new infestations are detected.

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