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How Far Can *Rhynchophorus palmarum* (Coleoptera: Curculionidae) Fly?

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Abstract

The palm weevil, *Rhynchophorus palmarum* (L.), was first recorded in San Diego County, CA in 2011 and breeding populations were recovered from infested Canary Islands date palms, *Phoenix canariensis*, in San Ysidro, San Diego County, in 2015. This palm pest presents a significant threat to California's edible date industry as *Phoenix dactylifera* is a recorded host for this weevil. The flight capabilities of *R. palmarum* are unknown which limits understanding of rates of natural dispersal. In response to this knowledge deficit, 24-h flight mill trials were conducted with field-collected male and female weevils. A total of 87 weevils (49 females and 38 males) were used in experiments, ~6% failed to fly >1 km in 24 h and were excluded from analyses. Of those 82 weevils flying >1 km in 24 h, the average distance flown by males and females was ~41 and ~53 km, respectively. Approximately 10% of females flew >100 km in 24 h, with two (~4%) females flying >140 km. The maximum recorded distance flown by a male weevil was 95 km. Flight activity was predominantly diurnal and flying weevils exhibited an average weight loss of ~18% while non-flying control weevils lost ~13% body weight in 24 h. The combined flight distances for male and female weevils exhibited a heavy-tailed platykurtic distribution. Flight mill data for *R. palmarum* are compared to similarly collected flight mill data for two other species of invasive palm weevil, *Rhynchophorus ferrugineus* (Olivier) and *Rhynchophorus vulneratus* (Panzer).

Key words: body size, dispersal, flight assay, flight mill, kurtosis

Rhynchophorus palmarum (L.), also referred to as the American or black palm weevil (Löhr et al. 2015), is a notorious palm pest in its native range, which includes parts of South (e.g., Brazil) and Central (e.g., Costa Rica) America, Mexico, and the Caribbean (e.g., Trinidad and Tobago) (EPPO 2005). *Rhynchophorus* spp. have a pan tropical distribution, adults are large (>25 mm depending on the species) (Wattanapongsiri 1966), and weevil larvae feeding in the apical meristematic region of palms cause mortality (Milosavljević et al. 2019). *Rhynchophorus palmarum* breeding is primarily restricted to Arecaceae (Arecales) and its known hosts include *Cocos nucifera* L. (coconut), *Elaeis guineensis* Jacq. (African oil palm), *Euterpe edulis* Mart. (juçara, grown for hearts of palm), *Metroxylon sagu* Rottb. (true sago palm), *Phoenix canariensis* Chaub. (Canary Islands date palm), *Phoenix dactylifera* L. (edible date palm), and *Saccharum officinarum* L. (sugar cane [Poales: Poaceae]) (EPPO 2005). Adult *R. palmarum* feed on a variety of ripe fruit, including avocado (*Persea americana* Mill. [Laurales: Lauraceae]), banana (*Musa* spp. [Zingiberales: Musaceae]), *Citrus* spp. (Sapindales: Rutaceae), mango (*Mangifera indica* L. [Sapindales: Anacardiaceae]), and papaya (*Carica papaya* L. [Brassicales: Caricaceae]) (EPPO 2005).

Infestations of palm weevils can quickly kill palm trees. For example, as few as 24 feeding larvae of the palmetto weevil, *Rhynchophorus cruentatus* (F.), a palm pest native to Florida, can kill a mature *P. canariensis*. Visually healthy *P. canariensis* can die in as little as 49 d from internal *R. cruentatus* infestation once external damage symptoms become obvious (Hunsberger et al. 2000). With respect to *R. palmarum*, the pestiferousness of this weevil is amplified by its ability to acquire and vector a plant pathogenic nematode, *Bursphelenchus cocophilus* (Cobb) (Aphelenchida: Parasitaphelenchidae), the causative agent of a lethal palm malady, red ring disease (Griffith 1987, Gerber and Giblin-Davis 1990, Giblin-Davis et al. 2013, Oehlschlager 2016). No other species of *Rhynchophorus* vector plant pathogenic nematodes.

In December 2010, reports of *P. canariensis* mortality in Tijuana, Baja California, Mexico resulted in the discovery of *R. palmarum* as the causative agent (Hoddle 2011, Hoddle and Hoddle 2017). In the United States, adult *R. palmarum* were trapped in San Ysidro, CA (~5 km north of Tijuana) in May 2011 (Bech 2011), Alamo, TX in March and May 2012 (El-Lissy 2012, Esparza-Díaz et al. 2013), and Yuma, AZ in May 2015 (El-Lissy 2015). Established populations in San Ysidro were confirmed in 2015 (it is likely populations had

established earlier, perhaps in 2013–2014) and weevils have now established throughout large areas of San Diego County (Hoddle 2016, 2018; Hodel et al. 2016). There are no reports of established populations of *R. palmarum* in Arizona and Texas or palm mortality caused by this weevil. *Bursphelenchus cocophilus* has not been detected in association with weevils captured in Texas (Esparza-Díaz et al. 2013), California (Hoddle and Hoddle 2017), and presumably Arizona.

The natural dispersal capabilities of an invasive pest can play an important role in population growth and phenology which in turn influences understanding of factors affecting aspects of pest invasion biology (e.g., rates of spread) and development of management plans (e.g., establishment of quarantine boundaries) (Naranjo 2019). Laboratory-based systems, such as computerized flight mills, which measure the flight activity of tethered insects, can provide useful insight into dispersal potential and assessment of experimental co-factors influencing flight capacity (Minter et al. 2018, Naranjo 2019). Factors of interest affecting flight propensity may include effects of sex, size, and time of year (Hoddle et al. 2015, Hoddle and Hoddle 2016), age and diet (Lopez et al. 2014, 2017), phenotype (Martini et al. 2014, Wiman et al. 2015), geographic origin of test populations (Yang et al. 2017), cold storage treatments (Matveev et al. 2017), resource dispersion (Venkateswaran et al. 2018), and the influence of heritable genetic factors (Dällenbach et al. 2018).

The spread of invasive insect pests may be characterized by long-range movement which can occur with considerable frequency and result in faster than expected rates of range expansion as long-distance dispersants may establish incipient infestation foci from which new populations develop and coalesce (Muirhead et al. 2006, Liebhold and Tobin 2008). The distribution of dispersal distances exhibited by an invasive pest may follow a leptokurtic pattern whereby dispersal distance curves have 'heavy' or 'fat' tails because they have numerous long-distance events sitting within the extremities of curves (i.e., the tails). Consequently, these dispersal distributions are skewed towards distances that are greater than would be predicted by a normal distribution which have fewer long-distance dispersers in distribution tails (Kot et al. 1996, Liebhold and Tobin 2008, Lockwood et al. 2013). This long-distance spread is typically part of stratified dispersal where continuous short-distance movements are occasionally punctuated by long-distance steps, and more rarely, by extremely long-distance steps (Lockwood et al. 2013). This dispersal pattern characterized by occasional continuous long-distance steps is referred to as Lévy walks or Lévy flights which can result in 'fat-tailed' leptokurtic dispersal distributions (Reynolds and Rhodes 2009, Lockwood et al. 2013).

Human activities, such as trade and tourism, can result in intentional or accidental long-distance spread of organisms. For example, flight mill studies indicated that introduction of an invasive wood-boring forest pest, the gold spotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), into California, likely resulted from unintentional human-assisted movement of infested firewood from Arizona, into previously uninfested areas ~550 km from source populations (Lopez et al. 2014). Conversely, some insect species, for example, may have the natural capacity to engage in long-distance movement (i.e., Lévy-type dispersal), and such occurrences, should they exist, would be difficult to document and quantify in the field. However, flight mill studies are well suited to determine if this possibility exists for a species of interest, such as a newly established invasive pest.

Flight mill studies by Taylor et al. (2010) indicated that ~1% of emerald ash borers, *Agrilus planipennis* Fairmaire (an invasive wood-boring buprestid), could fly >20 km in 24 h. This potential for long-distance spread could explain the ~23% of established *A. planipennis* populations that had 'fat-tail' dispersal kernels in Michigan for which human-assisted dispersal could not be accounted for (Muirhead et al. 2006). The brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), is an invasive and highly destructive agricultural pest that has spread rapidly in the United States (Leskey et al. 2012). Flight mill studies indicated that ~1% of females can fly ~75 km in 24 h (Wiman et al. 2015) which hints at possible capacity for Lévy-type dispersal. Red palm weevil, *Rhynchophorus ferrugineus* (Olivier), and the palm weevil, *Rhynchophorus vulneratus* (Panzer), are invasive palm pests (Milosavljević et al. 2019). Flight mill studies indicated that ~2% of *R. ferrugineus* females could fly >60 km in 24 h (Hoddle et al. 2015), and ~16% of *R. vulneratus* females flew 50–80 km in 24 h with one female flying ~100 km in this time period (Hoddle and Hoddle 2016). These flight mill examples suggest that populations of some invasive insect species have a small percentage of individuals that are capable of engaging in long-distance flights (i.e., Lévy-type dispersal) should they elect to do so. Factors motivating long-distance flights for a minority of individuals are unknown but the evolutionary significance of such behavior is likely important (Venkateswaran et al. 2018), especially with respect to resource location (Reynolds and Rhodes 2009). Consequently, a small subset of an invasive pest population could be responsible for naturally occurring (i.e., non-human assisted) Lévy-type (i.e., leptokurtic) dispersal, resulting in subsequent rapid spread over large areas.

At the time the work reported here was conducted, the flight capabilities of *R. palmarum* were unknown. An understanding of the natural dispersal potential of *R. palmarum* is of high importance as this information will inform assessment of the risk likelihood of short- and long-distance natural spread from infested urban areas in San Diego County. The possibility of some individuals engaging in long-distance dispersal is of particular concern as it may result in natural pest spread towards edible date production areas of the Coachella Valley in California, a linear distance of ~150 km from current *R. palmarum* infestations in San Diego County. The edible date (i.e., *P. dactylifera*, a known host for *R. palmarum*) industry in California is valued at $100 million per year and this iconic desert-growing specialty crop is farmed on around 4,000 ha (USDA-NASS 2018). To quantify the flight capacity of *R. palmarum*, work presented here used flight mills to measure flight distances for male and female *R. palmarum* over a 24-h period. In addition to quantifying flight metrics of weevils, a question of particular interest was whether resulting aggregate flight data for experimental weevils conformed to a leptokurtic distribution.

Materials and Methods

Source and Maintenance of *R. palmarum* Used for Flight Mill Studies

A total of 87 *R. palmarum* (i.e., 50 females and 37 males) were used for flight mill studies. For females and males attached to flight mills, 36 and 25, respectively, were of unknown age, assumed to be mated, and were captured alive in four bucket traps set at the Sweetwater Reserve, in Bonita San Diego County, California, an area with hundreds of naturalized *P. canariensis*, many of which are infested with *R. palmarum*. Traps were constructed from white 7.5-liter paint buckets wrapped in burlap with four evenly spaced 5-cm circular holes cut into the sides of the bucket. Buckets were suspended on metal stakes approximately 1.5 m above the ground and were separated by ~25 m. Traps were loaded with commercially available

R. palmarum aggregation pheromone (ISCALure IT192, 700 mg, ISCA Technologies, Riverside, CA) and baited with cut pieces of sugar cane, bananas, and apples which provided food and refuge for weevils that entered traps. Traps were inspected every 7 d, live weevils were removed, traps were rebaited, and lures were replaced monthly. In addition to field-captured weevils, virgin females (14) and males (12) were excised from cocoons collected from three weevil-infested *P. canariensis* that were taken down in Chula Vista, San Diego County over the same time period the weevils were field captured in bucket traps (23 February–28 April 2017).

Live field-collected weevils were moved under California Department of Food and Agriculture Permit 3289 to the Insectary and Quarantine Facility (IQF) at the University of California, Riverside and maintained in a temperature (23.26°C ± 0.84) and humidity (% RH 39.38 ± 0.15%) controlled room with a light:dark cycle set at 14:10 (lights on at 6:00 a.m. and off at 8:00 p.m.). All adult weevils were maintained individually in labeled clear ventilated plastic containers (height 18 cm, width 13 cm, depth 13 cm) which were provisioned with pieces of cut apple, longitudinally split sugar cane, and sections of banana with skin left on (weevils burrowed into banana pulp enclosed by skin to feed and hide). These foods were readily consumed and changed every 2–3 d when containers were cleaned to remove condensation and decomposing foods. After a 7- to 10-d period of feeding on this mixed fruit diet, weevils were used for flight mill trials.

Brief Description of Flight Mills and Experimental Set Up

Flight mills used in the experiments were custom made from aluminum blocks at the University of California, Riverside. Robust construction was necessary to accommodate heavy (~2–3 g) flying insects. 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 for Microsoft Excel analyzed raw data from each individual flight mill and provided summary metrics of interest such as total distance flown, average velocity, total time spent flying, total number of flight bouts (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 duration of the experiment. Weevils used in experiments were attached dorsally by their thorax to an 'L' shaped metal plate (~0.59 mm diameter by 28 mm long) flattened at one end for insect adhesion. A small drop of hot glue was applied to the thorax of the experimental weevil and the flattened end of the harness was submersed in the glue. Once glue dried, harnesses with attached weevils were affixed to 30.5-cm flight mill arms made of 0.5-mm carbon steel via a socket crimp (model 809-043, Glenair, Glendale, CA). Once attached, weevils were inspected to make sure they could open their elytra and move their legs. Modeling clay of the same weight as tethered weevils was then placed on the opposite end of the flight mill arm to counterbalance the weight of the adult beetle. Lopez et al. (2014) and Hoddle et al. (2015) provide additional details on procedures to attach weevils to flight mill arms, flight mill manufacture and calibration, data recording, and data file management.

Eight flight mills were set up in the same IQF room that weevils were maintained in. For each flight mill trial, eight randomly selected weevils were randomly assigned to flight mills and weevils were tethered to flight mills in the morning, with set up occurring between 8:00 a.m. to 9:30 a.m. An additional three to five randomly selected weevils were removed from maintenance containers and transferred to ventilated containers that lacked food. These weevils acted as controls to measure rates of naturally occurring mortality and weight loss in the absence of food and flight activity over the 24-h experimental period. Prior to the commencement of experiments, the weight of each weevil was recorded on a digital balance (GF600, A & D Instruments, Elk Grove, IL). Weevils were weighed again at the completion of experiments. 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).

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): total distance flown: $y^{0.5}$; maximum bout distance flown: $y^{0.25}$; total flying time: $y^{0.5}$; total number of flight bouts: $y^{0.25}$; time elapsed until first flight bout: $y^{0.75}$; flight bout length: log transformed; maximum bout length: log transformed. The body size (i.e., weight before and after trial, pronotum width and length, and body length) of *R. palmarum* adults by gender, mating status (i.e., virgin vs. unknown), and flight status (i.e., flyer vs. control weevils) was analyzed using a three-way analysis of variance (PROC GLM) in SAS (version 9.4; SAS 2013). The procedure GENMOD with binomial distribution and logit link function was used to test if percentage weight loss over the course of a 24-h experiment was influenced by gender, mating status (i.e., virgin vs. unknown), and flight status (i.e., flyer vs. control weevils). For all other flight parameters of interest by gender and mating status, a two-way analysis of variance was used to make comparisons (PROC GLM; SAS 2013). Tukey tests at the 0.05 level of significance were conducted to separate means when significant effects were detected.

Quantification of a Dispersal and Redistribution Kernal for *R. palmarum* Using Flight Mill Data

Kaplan–Meier analyses were performed using PROC LIFETEST in SAS (version 9.4; SAS 2013) on flight distance data for weevils. Kaplan–Meier curves, as a function of probability of distance flown in a 24-h period, were generated for each gender by mating status. These 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 mated and unmated male and female weevils. No significant differences were detected as a function of gender or mating status (see Results). Consequently, all flight data by mating status and sex were combined and used to define dispersal curves and corresponding redistribution kernels.

Flight distance data were divided across nine bins (distance interval 17.56 km with the maximum flight distance recorded acting as the upper bin limit [159.58 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 midpoints, 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 ($R^2 = 1 - SSE$/total sums of squares [SST]). Curve equation parameters were determined using the PROC NLIN

procedure in SAS (2013) and the best (determined by size of SSE [nonlinear model with the smallest value of RSS indicated the best fit to the data]) parameterized equation standardized by multiplying by bin width (2), number of weevils used (82 fliers; see Results), and a normalizing constant (3062.31; see Kot et al. [1996] for normalizing constant calculations) was fitted to binned flight data. This dispersal curve equation was parameterized and normalized to provide an area under the curve equal to 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:

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

which was solved using the option vardef = n in PROC MEANS (SAS 2013). Values of $k > 0$, $k = 0$, and $k < 0$ indicate leptokurtosis, mesokurtosis, and platykurtosis, respectively.

Comparison of Morphometrics, Weight, Distances Flown, and Flight Distance Kurtoses for *R. ferrugineus*, *R. vulneratus*, and *R. palmarum*

Flight mill study data for male and female *R. ferrugineus* (Hoddle et al. 2015), *R. vulneratus* (Hoddle and Hoddle 2016), and *R. palmarum* (this study) were used to compare morphometrics (i.e., average body size measurements), average weights before flight, percentage weight loss, and average total distance flown in 24 h. For *R. ferrugineus*, data by sex for flight and control weevils across seasons (i.e., winter, spring, and summer) were pooled. Similarly, data by sex for flight and control weevils for *R. vulneratus* and *R. palmarum* were pooled for analyses (there were no studies by season for these two species). 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): pronotum width: $y^{0.25}$; pronotum length: $y^{0.25}$; weight before trial: $y^{0.25}$; and total distance flown: $y^{0.5}$. The body size and flight performance of *R. ferrugineus*, *R. vulneratus*, and *R. palmarum* adults by species and gender was analyzed using a two-way analysis of variance (i.e., PROC GLM in SAS [2013]). The procedure GENMOD in SAS (2013) with binomial distribution and logit link function was used to test if the percentage weight loss over the course of a 24-h experiment was influenced by gender and species. Tukey tests at the 0.05 level of significance were conducted to separate means when significant effects were detected. All statistical analyses were performed using SAS (PROC GLM; SAS 2013) and only significant results are presented. Kurtoses (i.e., determination of tail extremities [Westfall 2014]) of flight distance data for *R. ferrugineus* (mesokurtic [Hoddle et. al. 2015]), *R. vulneratus* (leptokurtic [Hoddle and Hoddle 2016]), and *R. palmarum* (platykurtic [this study], see Results]) were compared by plotting model outputs on one graph.

Results

A total of 87 tethered and 41 control *R. palmarum* were used in flight mill studies (Table 1). Of the weevils tethered to flight mills, ~6% (one female [unknown] and four males [two virgins and two unknowns]) failed to fly >1 km and were considered non-fliers and excluded from analyses. Consequently, 82 weevils (49 females and 33 males, ~94% of tethered weevils) flew >1 km in 24 h and were classified as flyers and used for statistical analyses (Table 1).

No significant differences in pre-trial weevil weights were detected for control and experimental weevils tethered to flight mills (Table 1). Significant differences in average percentage weight loss over the course of a 24-h experiment were observed with non-flying control weevils generally loosing less weight than flying weevils ($\chi^2 = 6.09$, df = 1, $P = 0.0001$) (Table 1). Flying male and female weevils, both virgin and of unknown mating status, lost on average, ~18% of their body weight in a 24-h period. In comparison, non-flying control weevils lost on average ~13% of their original body weight. No significant differences in average body size measurements (i.e., thorax width and length and body length) were observed for experimental weevils (Table 1).

No significant differences in average velocity and mean maximum velocity were detected for experimental weevils based on sex and mating status (Table 1). Total average time spent flying within a 24-h period was significantly different for gender by mating status only ($F = 9.42$, df = 1,78, $P = 0.003$), being shortest for virgin males that flew, on average, less than 3.5 h (Table 1). Other variables were not significant, including average total distance flown in 24 h which ranged from ~23 to ~57 km (Table 1).

For females flying >1 km in a 24-h period, 37% ($n = 30$ out of 82 female and male weevils combined) flew 1–50 km, 16% ($n = 13$) flew 51–100 km, and 6% ($n = 5$) of females exhibited 'super-dispersive' flight and flew >100 km on flight mills (Fig. 1A and B). Of these super-dispersive females, two (~4%) flew >140 km. For males that flew >1 km in a 24-h interval, 28% ($n = 23$) flew 1–50 km, 13% ($n = 11$) flew 51–100 km, the farthest flying male flew 95 km (Fig. 1A and B). Weevil flight activity (data for males and females combined) was recorded over a 24-h period (Fig. 2A). Approximately 94% of total cumulative distance flown was recorded between 6:00 a.m. (lights on) and 8:00 p.m. (lights off), ~88% of flying activity was recorded during this 'lights on' period. Both cumulative distance flown and percentage weevils flying peaked between 11:00 a.m. and 1:00 p.m. (Fig. 2A). Average flight bout times and distances flown (data for both sexes combined) increased steadily after 5:00 a.m., with average flight bout time and distance flown per bout peaking between 11:00 a.m. and 1:00 p.m., with an average bout distance of around 17 km and average bout time of approximately 2 h (Fig. 2B). A decline in average flight bout times and distances was observed after this peak with mean flight bout times ranging approximately from 1 to 1.5 h with average distances of around ~6–8 km (Fig. 2B).

Dispersal and Redistribution Kernel for *R. palmarum*

The log-rank test assessing the probability of distance flown by adult weevils was not significant for gender by mating status ($\chi^2 = 5.17$, df = 3, $P = 0.16$), mating status ($\chi^2 = 3.17$, df = 1, $P = 0.09$), or sex ($\chi^2 = 1.41$, df = 1, $P = 0.23$). Therefore, all flight data by mating status and sex were combined and the best fitting of the five curves analyzed from Kot et al. (1996) was determined to be curve 1:

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

where $a = 2.96$, $b = 0.00013$, x = midpoint of the distance bin (km) (SSE = 39.63, $R^2 = 0.93$; Fig. 3A). This function was used to generate the corresponding redistribution kernel, described by the equation:

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

where $a = 0.0064$, $b = 7936.51$, x = distance flown (km). The excess kurtosis measure, k, was −1.46, indicating that the equation describing the curve that was produced is platykurtic (Fig. 3B).

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Table 1. Average (±SE) weight, weight loss, body size, and flight parameters by mating status for *Rhynchophorus palmarum* males and females that flew >1 km on flight mills (flyer) and control weevils maintained individually in the same room in ventilated containers without food for 24 h

Mean (±SE) parameter measured	Female				Male			
	Virgin		Unknown		Virgin		Unknown	
	Flyer (*n* = 14)	Control (*n* = 6)	Flyer (*n* = 35)	Control (*n* = 22)	Flyer (*n* = 10)	Control (*n* = 4)	Flyer (*n* = 23)	Control (*n* = 9)
Weight before trial (g)	2.28 ± 0.10a	2.29 ± 0.27a	2.28 ± 0.07a	2.22 ± 0.06a	2.27 ± 0.12a	2.19 ± 0.10a	2.27 ± 0.06a	2.38 ± 0.05a
Weight after trial (g)	1.88 ± 0.08a	2.05 ± 0.27a	1.82 ± 0.06a	1.91 ± 0.07a	1.93 ± 0.11a	1.91 ± 0.09a	1.81 ± 0.05a	2.08 ± 0.04a
% Weight loss	17.20 ± 0.77ab	11.28± 1.60c	20.33 ± 0.79a	14.40 ± 0.97bc	14.88 ± 1.06b	12.50 ± 0.53c	20.00 ± 0.73a	12.44 ± 1.02c
Pronotum width (mm)	10.60 ± 0.16a	10.38 ± 0.40a	11.01 ± 0.16a	11.03 ± 0.20a	10.44 ± 0.25a	10.55 ± 0.27a	11.06 ± 0.11a	11.20 ± 0.12a
Pronotum length (mm)	12.56 ± 0.26a	12.29 ± 0.51a	13.37 ± 0.21a	13.35 ± 0.25a	13.03 ± 0.33a	12.09 ± 0.61a	13.25 ± 0.18a	13.48 ± 0.28a
Body length (mm)	31.07 ± 0.58a	31.39 ± 1.15a	32.15 ± 0.36a	31.79 ± 0.37a	31.18 ± 0.56a	30.69 ± 0.98a	31.36 ± 0.26a	31.70 ± 0.32a
% Survivorship	100%	83%	100%	100%	100%	100%	100%	100%
Velocity (m/s)	1.64 ± 0.17a		1.89 ± 0.09a		1.94 ± 0.18a		1.99 ± 0.11a	
Maximum velocity (m/s)	3.29 ± 0.21a		3.80 ± 0.12a		3.43 ± 0.15a		3.69 ± 0.11a	
Total distance flown (km)	43.28 ± 9.79a		57.16 ± 5.51a		22.67 ± 93.76a		48.31 ± 4.93a	
Total time flying (h)	7.38 ± 1.48ab		8.85 ± 0.73a		3.45 ± 0.65b		7.41 ± 0.88a	
Total flight bouts	105 ± 29.46a		144 ± 24.21a		59 ± 10.93a		102 ± 16.31a	
Time elapsed to first flight bout (h)	0.17 ± 0.01a		0.15 ± 0.02a		0.17 ± 0.01a		0.14 ± 0.02a	
Flight bout length (h)	0.69 ± 0.24a		1.04 ± 0.32a		0.18 ± 0.10a		0.58 ± 0.19a	
Maximum flight bout length (h)	4.95 ± 1.36a		4.55 ± 0.71a		1.66 ± 0.31a		4.02 ± 0.67a	
Maximum flight bout distance (km)	34.36 ± 9.58a		37.82 ± 5.60a		14.77 ± 2.60a		31.21 ± 3.96a	

Means with different letters within rows indicate significant differences at 0.005 level.
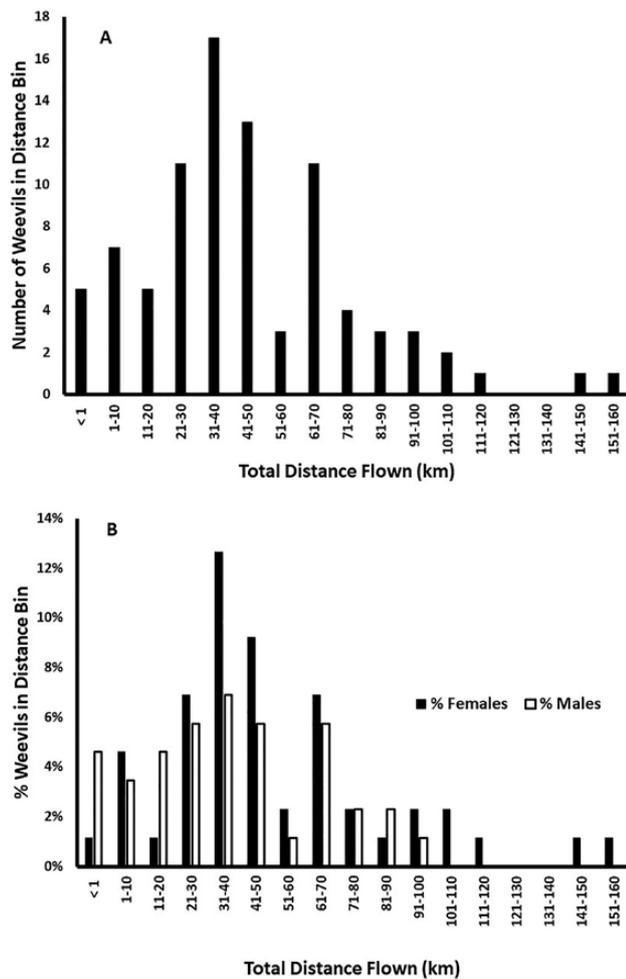
Fig. 1. (A) Number of male and female *Rhynchophorus palmarum* binned by total distance (km) flown and (B) percentage of male and female weevils in distance bin.

Fig. 2. (A) Total cumulative distance (km) flown over 24 h and percentage of weevils flying in time interval and (B) average flight bout time (h:min:s) and average distance flown (km) per bout in time interval. Lights on at 6:00 a.m. and off at 8:00 p.m.

Comparison of Morphometrics, Weight, Distances Flown, and Flight Distance Kurtoses for *R. ferrugineus*, *R. vulneratus*, and *R. palmarum*

Average body size, weight, and distances flown were significant by species only and no significant differences between sexes within species were observed (Table 2). *Rhynchophorus ferrugineus* weighed significantly less ($F = 452.49$, df = 2,478, $P < 0.0001$) than *R. vulneratus* and *R. palmarum*, both of which weighed approximately the same (Table 2). Flying weevils, regardless of species or sex, exhibited similar percentage weight loss over 24 h, which, on average, ranged ~13–18% (Table 2). Pronotum size differed significantly with male and female *R. ferrugineus* having an average pronotum width ($F = 323.95$, df = 2,484, $P < 0.0001$) and length ($F = 406.73$, df = 2,484, $P < 0.0001$) that were smaller than *R. vulneratus* and *R. palmarum*, with the latter two species being approximately equivalent in size (Table 2). *Rhynchophorus vulneratus* and *R. palmarum* exhibited approximately similar body lengths and were significantly longer that *R. ferrugineus* ($F = 250.01$, df = 2,484, $P < 0.0001$) (Table 2). The average total distance flown in 24 h was significantly higher for *R. palmarum* ($F = 24.43$, df = 2,261, $P < 0.0001$) and statistically equal for *R. vulneratus* and *R. ferrugineus* (Table 2).

The distributions of flight mill-generated flight distance data differ substantially between weevil species (Fig. 4). With respect
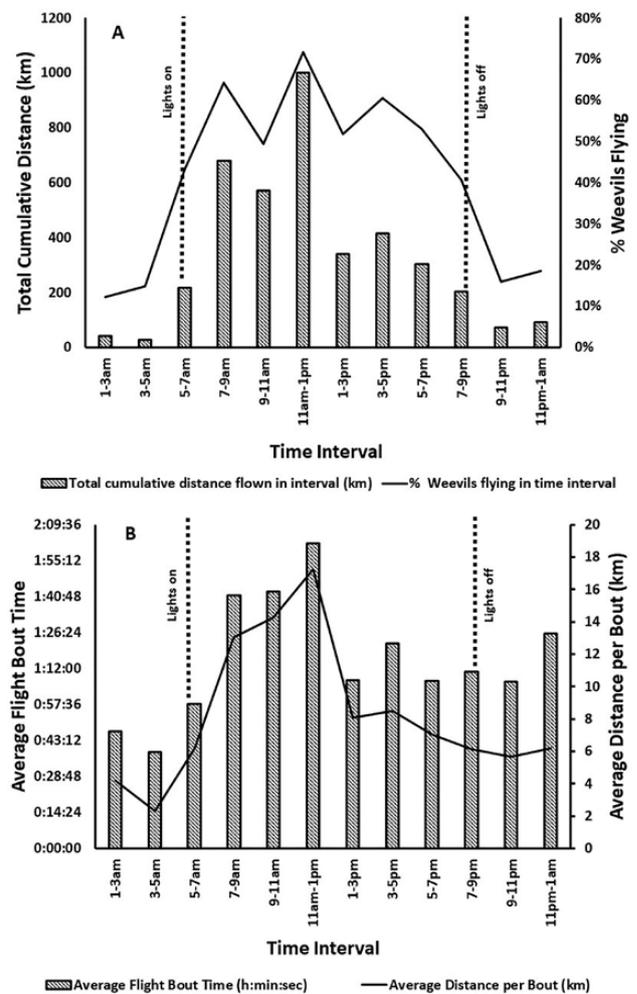
to *R. ferrugineus* (mesokurtic distribution of flight distance data [$k = 0$]), the tails of the distance dispersal graphs are longer and fatter for *R. vulneratus* (leptokurtic distribution characterized by a very high central peak and fat tails [$k = 3$]) and *R. palmarum* (platykurtic distribution with a flat central peak and very heavy tails [$k = -1.46$]). The distribution tails for *R. palmarum* are considerably fatter than either *R. ferrugineus* or *R. vulneratus* suggesting that *R. palmarum* has a greater proportion of individuals capable of engaging in long-distance flights (Fig. 4).

Discussion

Over a 24-h period in the laboratory, field-captured male and female *R. palmarum* demonstrated strong capacity for flight when tethered to flight mills. For weevils that exhibited >1 km of flight, 90 and 82% of females and males, respectively, flew >10 km, and of these, 37 and 29% of females and males, respectively, flew >50 km, and 10% of females flew more than 100 km in 24 h (no male flights exceeded 100 km, the farthest flying male reached 95 km in 24 h). The percentage of *R. palmarum* flying <1 km was relatively low at ~6% when compared to *R. ferrugineus* and *R. vulneratus*, which had ~30 and 27% of field-collected individuals, respectively, failing to cross
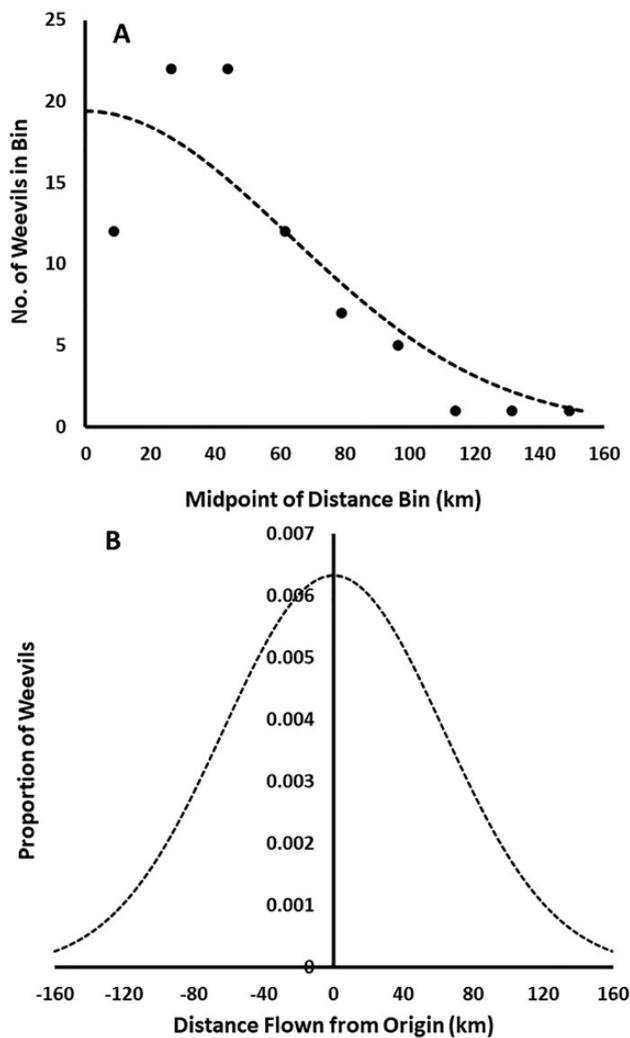
Fig. 3. (A) Dispersal curve and (B) redistribution kernel generated using flight data combined for male and female *Rhynchophorus palmarum* flown on flight mills for 24 h.

Fig. 4. Comparison of redistribution kernels generated from flight mill data for *Rhynchophorus ferrugineus* (mesokurtic distribution; $k = 0$ [Hoddle et al. 2015]), *R. vulneratus* (leptokurtic distribution; $k = 3$ [Hoddle and Hoddle 2016]), and *R. palmarum* (platykurtic distribution; $k = -1.46$ [this study]).

this minimum dispersal threshold (Hoddle et al. 2015; Hoddle and Hoddle 2016).

Rhynchophorus palmarum was first reported from infested *Washingtonia robusta* Wendl. in Todos los Santos in Baja California Sur, Mexico in November 2000 (Garcia-Hernandez et al. 2003). In December 2010, *R. palmarum* was found infesting *P. canariensis* in Tijuana, Baja California Norte, Mexico ~1,500 km north of Todos los Santos, and less than 3 km from the U.S. border with San Diego County, CA (Hoddle 2016; Hoddle and Hoddle 2017). Assuming there was no human-mediated long-distance transport, natural movement of *R. palmarum* over this ~10-y period would, on average, have required northward dispersal of ~12 km per month or about 150 km per year to reach Tijuana from Todos los Santos. Flight mill data presented here suggest that these averaged dispersal distances are within the potential flight capacity of *R. palmarum*.

Rhynchophorus palmarum flight activity on flight mills was greatest between 11:00 a.m. and 1:00 p.m., and ~88% of flight activity was recorded between lights on (6:00 a.m.) and lights off (8:00 p.m.), suggesting that flight may be largely diurnal. Hagley (1965) reported that *R. palmarum* flight activity in the field is bimodal with highest activity observed between 9 and 11:00 a.m. and between 5:00 p.m. and sunset. Flying weevils were, however,
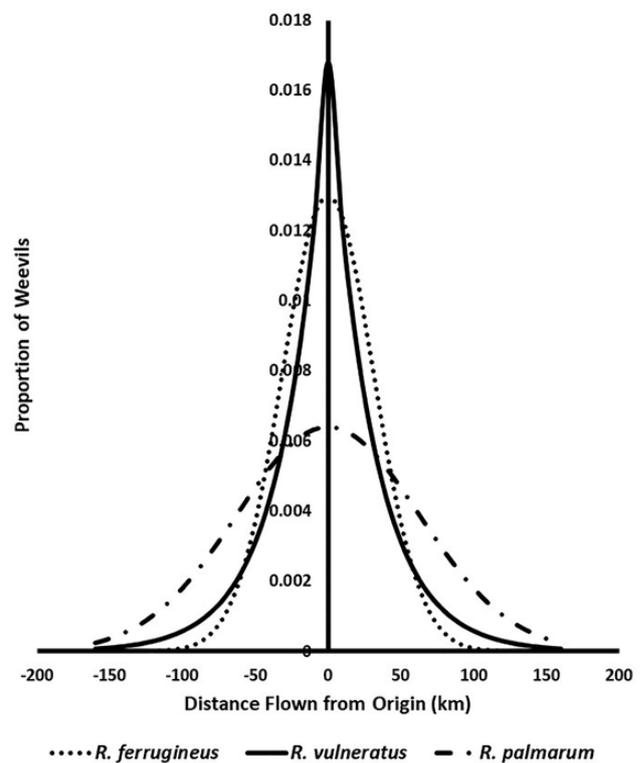
recorded with varying frequency across all daylight hours that observations were made (Hagley 1965). Hoddle et al. (2015) and Hoddle and Hoddle (2016) suggest that flight periodicity on flight mills should be viewed with caution as tethered palm weevils are unable to initiate tarsal contact with a substrate which, if possible, could terminate flight and result in flight periodicity data different to what is reported. Further, flight mill studies with *R. palmarum* (and *R. ferrugineus* [Hoddle et al. 2015] and *R. vulneratus* [Hoddle and Hoddle 2016]) were initiated in the morning (often before 9:00 a.m.) and weevils quickly engaged in flight once tethered to flight mills and tarsal contact with substrate was lost. This experimental design could be another source of bias supporting the conclusion that flight activity is predominantly diurnal. Similarly, Hagley's (1965) field observations for flying *R. palmarum* were only made between 6:00 a.m. and 6:00 p.m. probably because it is extremely difficult to visually observe fast-flying large black weevils at night. Use of 'smart traps' loaded with aggregation pheromone and fermenting bait could resolve questions over *R. palmarum* flight periodicity. Studies using 'smart traps' to investigate the periodicity of flight for *R. ferrugineus* in Saudi Arabia concluded that the majority of *R. ferrugineus* arrive at traps during daylight hours (Aldryhim and Al-Ayedh 2015). Visual inspections of bucket traps deployed for the capture of *R. ferrugineus* in Italy, Greece, and Vietnam, and *R. vulneratus* in Malaysia concluded that weevil flight was diurnal (Fanini et al. 2014). Similar field studies could be run to confirm that *R. palmarum* is a predominantly diurnal flyer.

Two abiotic factors, temperature and humidity, affect flight activity of *Rhynchophorus* spp. In the laboratory, *R. cruentatus* flight activity increases with increasing temperature and decreasing humidity (Weissling et al. 1994). Laboratory studies indicated that

Table 2. Average (±SE) body size (combined by sex and flying status) and total distance flown for weevils flying >1 km for *Rhynchophorus ferrugineus*, *R. vulneratus*, and *R. palmarum*

Mean (±SE) parameter measured	*Rhynchophorus ferrugineus*[a]		*Rhynchophorus vulneratus*[b]		*Rhynchophorus palmarum*[c]	
	Female	Male	Female	Male	Female	Male
Weight before trial (g)	1.23 ± 0.02b (*n* = 197)	1.27 ± 0.03b (*n* = 96)	2.04 ± 0.08a (*n* = 47)	2.28 ± 0.09a (*n* = 21)	2.26 ± 0.05a (*n* = 77)	2.28 ± 0.04a (*n* = 46)
% Weight loss	15.89 ± 0.60a (*n* = 197)	18.22 ± 0.88a (*n* = 96)	15.77 ± 0.92a (*n* = 47)	12.77 ± 1.32a (*n* = 21)	17.36 ± 0.60a (*n* = 77)	16.76 ± 0.68a (*n* = 46)
Pronotum width (mm)	9.17 ± 0.05b (*n* = 203)	9.15 ± 0.08b (*n* = 96)	11.23 ± 0.18a (*n* = 47)	11.67 ± 0.20a (*n* = 21)	10.89 ± 0.10a (*n* = 77)	10.91 ± 0.09a (*n* = 46)
Pronotum length (mm)	10.56 ± 0.05b (*n* = 203)	10.45 ± 0.07b (*n* = 96)	12.73 ± 0.20a (*n* = 47)	13.18 ± 0.24a (*n* = 21)	13.13 ± 0.14a (*n* = 77)	13.15 ± 0.14a (*n* = 46)
Body length (mm)	26.26 ± 0.10b (*n* = 203)	25.44 ± 0.15b (*n* = 96)	30.76 ± 0.47a (*n* = 47)	31.37 ± 0.44a (*n* = 21)	31.80 ± 0.24a (*n* = 77)	31.33 ± 0.20a (*n* = 46)
Total distance flown (km)	22.61 ± 1.67b (*n* = 93)	24.59 ± 2.35b (*n* = 46)	32.48 ± 3.97b (*n* = 35)	14.80 ± 3.16b (*n* = 11)	53.19 ± 4.86a (*n* = 49)	40.54 ± 4.15a (*n* = 33)

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

[a]Hoddle et al. (2015).

[b]Hoddle and Hoddle (2016).

[c]Work presented in this article.

R. cruentatus flight initiation was greatest at 35°C and flights were initiated twice as frequently when humidity was low (i.e., ~33% [low] vs. 77% RH [high]) (Weissling et al. 1994). The motivation to fly under low humidity conditions especially at high temperatures (e.g., 35°C) may be due to desiccation stress and flight may result in location of favorable habitat that reduces stress by stabilizing or reversing water loss (Weissling and Giblin-Davis 1993). Field mark–release–recapture studies with *R. ferrugineus* indicated that flight initiation probabilities for *R. ferrugineus* were greatest at temperatures between 17 and 25°C (~90%) and declined to ~70% at 35°C, and increasing levels of atmospheric humidity resulted in faster flight and subsequently shorter flight times were needed to cover similar distances (Ávalos et al. 2016). Dispersal and infestation severity of *R. ferrugineus* in date palm plantations in the Middle East is correlated with high humidity levels which result from flood irrigation and high-density plantings that result in closed canopies which provide shade and reduced evaporation (Aldryhim and Al-Bukiri 2003, Al-Dosary et al. 2016). Dry conditions and low humidity levels may not favor *R. ferrugineus* dispersal (Aldryhim and Al-Bukiri 2003). The effects of temperature and humidity on flight activity of *R. palmarum* are not well studied. Given the importance of these abiotic factors on other *Rhynchophorus* spp., it is likely they will exert considerable influence on the invasion dynamics of this pest as its spreads from California coastal areas with relatively high humidity and moderate summer temperatures (e.g., San Diego, CA, average monthly high temperature range from June to August: ~22–25°C; average RH ~74% [weather-us.com 2020a]) to interior desert areas with commercial date plantations with relatively high average summer temperatures and humidity (e.g., Thermal, CA, average monthly high temperature from June to August: ~40°C; average RH ~85%; weather-us.com [2020b]).

Flight dispersal data for *R. palmarum* tethered to flight mills in controlled laboratory conditions was platykurtic (*k* = −1.46). In comparison to *R. ferrugineus* (mesokurtic; *k* = 0 [Hoddle et al. 2015]) and *R. vulneratus* (leptokurtic; *k* = 3 [Hoddle and Hoddle 2016]), the tails of these platykurtically distributed flight data are very heavy indicating that they were populated with relatively higher proportions of weevils that fly very long distances (Fig. 4). Interestingly, this platykurtic spread of data suggests that

R. palmarum may have the potential to spread more rapidly (i.e., engage in Lévy-type dispersal) when compared to similarly generated flight mill data that are mesokurtically (i.e., *R. ferrugineus*) or leptokurtically (i.e., *R. vulneratus*) distributed. Curiously, fat-tailed platykurtic dispersal data do not appear to have been considered as possible explanations for Lévy-type dispersal which seems to be solely characterized by leptokurtic spread (Kot et al. 1996, Liebhold and Tobin 2008, Reynolds and Rhodes 2009, Lockwood et al. 2013).

The extreme artificiality of flight mills for quantifying flight activity in the laboratory is well acknowledged (Taylor et al. 2010, Minter et al. 2018, Naranjo 2019). However, more 'realistic' field-based approaches for quantifying flight activity also have recognized shortcomings. Tracking flying insects in the field is problematic as study organisms tend to be small, flight may occur at high altitudes making observations difficult, and long distances flown by quick moving species can rapidly result in loss of contact (Minter et al. 2018). Field-based studies, such as mark–recapture experiments to quantify dispersal capabilities, are hampered by very low recapture rates, which necessitates the need for releases of very high numbers of test insects (Ávalos et al. 2016). Poor recapture rates are affected by decreasing trap densities at increasing distances from release points which contributes to lower captures at greater distances from sources. Resources that act as competing sinks that are equally or more attractive to test insects than monitoring traps may also contribute to difficulties with this approach.

Miniaturized electronic trackers such as passive (i.e., no battery) radio frequency identification (RFID) tags and non-functional 'sham' radio-transmitters with antennae attached to the thorax of *R. ferrugineus* have been assessed for their effects on flight activity (Hamidi et al. 2017). RFID tags did not hinder weevil flight, however, the weight of sham radio-transmitters and antenna length compromised flight (Hamidi et al. 2017). Detection distances for electronic trackers are a significant issue for highly vagile insects especially if motility is many hundreds of meters over short periods of time as tagged insects may quickly fly beyond the range of receivers (Liégeois et al. 2016, Moore et al. 2017). However, some studies have managed to track cerambycid beetles (Drag and Cizek 2018) and birdwing butterflies (Papilionidae) (Wang et al. 2019) over

distances exceeding 4 km across several days. A potential advance in the use of radio tags for tracking insects in the field over very large distances could be the deployment of receivers in low earth orbit (~320 km above earth). However, 'small' transmitters weigh around 1 g and use will be constrained to 'large' insects and low earth orbit tracking may only be possible for species that occupy open habitats like deserts (Daniel Kissling et al. 2014). As outlined above, attempting to answer a seemingly simple question like 'how far can the *R. palmarum* fly?' is technically challenging. Of the tools available for measuring flight capacity and assessing the importance of covariates (e.g., sex, age, and mating status) that may influence dispersal, flight mill data provide useful insights into factors affecting insect flight behavior.

Acknowledgments

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