Bulletin of Entomological Research (2014) **104**, 462–470
doi:10.1017/S0007485314000121

Study of the flying ability of *Rhynchophorus ferrugineus* (Coleoptera: Dryophthoridae) adults using a computer-monitored flight mill

J.A. Ávalos[1], A. Martí-Campoy[2] and A. Soto[1]*

[1]Instituto Agroforestal Mediterráneo (IAM), Universitat Politècnica de València, Camino de Vera s/n, 46022, Valencia, Spain: [2]Departamento de Informática de Sistemas y Computadores (DISCA), Universitat Politècnica de València, Camino de Vera s/n, 46022, Valencia, Spain

Abstract

The red palm weevil, *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Dryophthoridae), native to tropical Asian regions, has become a serious threat to palm trees all over the world. Knowledge of its flight potential is vital to improving the preventive and curative measures currently used to manage this pest. As *R. ferrugineus* is a quarantine pest, it is difficult to study its flight potential in the field. A computer-monitored flight mill was adapted to analyse the flying ability of *R. ferrugineus* through the study of different flight parameters (number of flights, total distance flown, longest single flight, flight duration, and average and maximum speed) and the influence of the weevil's sex, age, and body size on these flight parameters. Despite significant differences in the adult body size (body weight and length) of males and females, the sex of *R. ferrugineus* adults did not have an influence on their flight potential. Neither adult body size nor age was found to affect the weevil's flying abilities, although there was a significantly higher percentage of individuals flying that were 8–23 days old than 1–7 days old. Compared to the longest single flight, 54% of the insects were classified as short-distance flyers (covering <100 m) and 36 and 10% were classified as medium- (100–5000 m) and long-distance (>5000 m), respectively. The results are compared with similar studies on different insect species under laboratory and field conditions.

Keywords: Red palm weevil, flight potential, tethered, dispersal, behaviour, *Arecaceae*

(Accepted 17 January 2014; First published online 17 April 2014)

Introduction

The red palm weevil, *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Dryophthoridae), is a key pest of palm trees (Arecaceae), native to tropical Asia (Wattanapongsiri, 1966) and introduced worldwide (OEPP/EPPO, 2008). It has a broad host range and is able to breed in a wide variety of climates (Murphy & Briscoe, 1999). In the last 20 years, the weevil has invaded the Middle East and the Mediterranean Basin and in 2009 reached the island of Curaçao, in the Caribbean (OEPP/EPPO, 2009). The pest has killed thousands of palms in the newly invaded areas, especially *Phoenix canariensis* (Hort. ex Chabaud) (Arecales: Arecaceae) and *Phoenix dactylifera* (Linnaeus), causing serious financial losses.

*Author for correspondence
Phone: (+34) 963 879 252
Fax: (+34) 963 877 331
E-mail: asoto@eaf.upv.es

In the Persian Gulf, the estimated cost of pest management and eradication in a 5% infested *P. dactylifera* plantation was around US$26 million (El-Sabea *et al.*, 2009). *R. ferrugineus* is also a threat to world heritage areas such as the largest palm plantation in Europe, in Elche in the Valencia Region of Spain, a UNESCO World Heritage Site (OEPP/EPPO, 2008). The weevil's expansion has been largely due to the widespread practice of shipping palm trees between different territories (Abraham *et al.*, 1998). Besides human activity, the insects usually spread by flying in search of new habitats, food sources and oviposition sites (Cooter, 1993).

Information on the insect's flight performance under different environmental and physiological conditions is essential for the efficient development of forecasting and control strategies (Cooter & Armes, 1993). Despite the wide range of measures currently used to prevent and control *R. ferrugineus* infestations, new management strategies will have to be developed, based on a better understanding of the flying abilities and dispersion capacity of *R. ferrugineus* adults. The insect's flight range and dispersion capabilities can be analysed under field conditions using methods such as the mark–release–recapture (MRR) method. Abbas *et al.* (2006) analysed the distances covered by *R. ferrugineus* by this method; however in some regions, it is difficult to study its flight potential and behaviour outdoors as it is considered a quarantine pest. Chinchilla *et al.* (1993) also analysed the migration of *R. palmarum* (Linnaeus) adults by MRR. In order to overcome the problems inherent in field conditions, a number of laboratory techniques have been developed to quantify insect flying abilities, including static tethering, flight mills, and flight balances and pendulums, which can be used to analyse the influence of different factors under laboratory conditions (Cooter, 1993). These techniques can be used to measure an insect's flying abilities without interference from external stimuli such as pheromones or abiotic factors like wind (Sarvary *et al.*, 2008). The flight mill method is considered a model system for the laboratory analysis of insects' flight behaviour (Schumacher *et al.*, 1997) and has been used successfully to study flight performance of a large number of economically important agricultural species belonging to different orders, such as *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae) (Hughes & Dorn, 2002), *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae) (Wu *et al.*, 2006), *Aphis glycines* (Matsumura) (Hemiptera: Aphididae) (Zhang *et al.*, 2008), *Cylas formicarius* (Fabricius) (Coleoptera: Brentidae) (Moriya & Hiroyoshi, 1998), and *Conotrachelus nenuphar* (Herbst) (Coleoptera: Curculionidae) (Chen *et al.*, 2006).

As far as we know, no laboratory study using a tethered technique had been carried out to date to determine the flight potential of *R. ferrugineus*. A basic flight mill was used by Kloft *et al.* (1986) to test whether sterilization with radio-isotopes affects the flight ability of *R. ferrugineus*, but this work did not provide any data on its flight performance. Also under laboratory conditions, Weissling *et al.* (1994*a*) studied the sequence of events leading to flight and the influence of different climatic factors on the flying behaviour of *R. cruentatus* (Fabricius).

The experiments conducted in this study were designed to obtain useful information on the flight abilities of *R. ferrugineus* with the aim of improving pest management strategies. An *R. ferrugineus*-adapted computer-monitored flight mill was built to analyse the influence of different biotic factors, such as sex, age, and body size on different flight parameters (number of flights (NOF), total distance flown (TDF), longest single flight (LSF), flight duration (FD), and average and maximum flying speed).

Materials and methods

Experimental insects

A total of 206 *R. ferrugineus* unmated adults (115 males and 91 females) were used for the experiments, obtained from cocoons collected from infested *P. canariensis* palms in the town of Sueca, in Eastern Spain (latitude 39°12′N; longitude 00°18′W; altitude 7 m), between January and December 2012. The cocoons were held in individual sterilized 100 ml plastic containers with perforated lids and maintained in a climatic chamber at 25 ± 2°C and 65 ± 5% relative humidity (RH). Adult emergence was checked once a day to determine their exact age and sex, after which the newly emerged weevils were returned to the containers. A piece of apple, replaced twice a week, was provided as a food source (Llácer *et al.*, 2012). Immediately before taking part in the flight mill tests, the weevils were weighed with a precision scale (Acculab, ALC-210.4, Bradford, US) and measured longitudinally with a digital calliper (Comecta Corp., Barcelona, Spain), from the beginning of the rostrum to the end of the last abdominal segment. The adults were kept in the same climatic cabinet until the tests.

Flight mill design

A flight mill as described in the work of Dubois *et al.* (2009), designed to test the flight potential of *Osmoderma eremita* (Scopoli) (Coleoptera: Cetoniidae), was adapted to *R. ferrugineus* with the addition of a computer-monitored system (fig. 1). In order to minimize friction on the pivot caused by the lever effect of the arm, a key component of the device was a miniature ball bearing (internal Ø = 4 mm, external Ø = 8 mm, thickness = 3 mm) (Minebea Co., Japan) (fig. 1A) with a precision rate number ABEC 5 (Annular Bearing Engineering Committee scale system). The pivot (fig. 1B) was an iron rod (length = 160 mm, Ø = 15 mm) inserted into a heavy iron base (fig. 1C) (Ø = 200 mm) supported on a foam cushion to reduce any vibrations produced during the flying tests. Another finer rod (Ø = 4 mm) containing the miniature ball bearing was inserted on the pivot. The arm (fig. 1D) fastened to the ball bearing, was a 64 cm carbon fibre rod (Ø = 2 mm), giving a flight path of 2.01 m per revolution. As *R. ferrugineus* is smaller than *O. eremita*, using a lighter material in the arm allowed the weevils to turn the arm without difficulty. There were two pins (fig. 1E) at the end of the arm to which the insect was attached. The weevils were tethered at the pronotum with cyanoacrylate glue (Super Glue-3, Henkel Ibérica, Barcelona, Spain) to lengths of polyethylene foam (30 × 4 × 4 mm) fixed to the two aforementioned pins. A counterweight of adhesive paste was placed on the opposite end of the arm (fig. 1F). Two reflectors on the flight arm (fig. 1G) and a pair of infrared sensors (transmitter/receiver) (Honeywell International Inc., Mexico DF, Mexico) mounted in the frame, detected every half revolution of the flight mill arm and transferred the signal to a computer, allowing the different flight parameters to be measured easily and accurately. Five flight mills ran simultaneously in a climatic chamber, maintained at 25 ± 2°C, 65 ± 5% RH, and constantly lit by non-flickering 58W

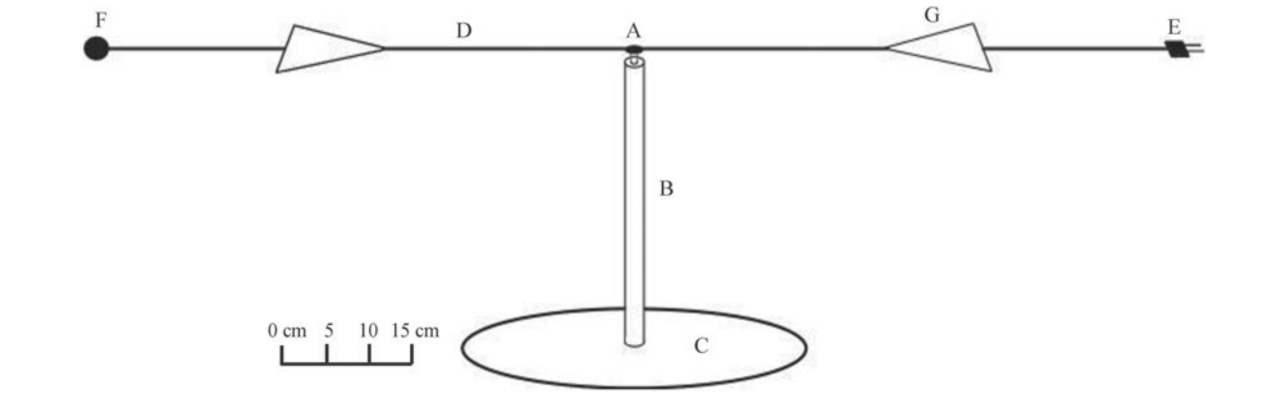

Fig. 1. Schematic representation of a flight mill unit: (A) miniature ball bearing; (B) flight mill pivot; (C) flight mill base; (D) carbon fibre arm; (E) pins to attach the insect; (F) counterweight; (G) reflector.

fluorescent (Philips Ibérica, Madrid, Spain) and Grolux lamps (Osram Sylvania Inc, Danvers, USA).

Flight parameters measured

The flight mill data were logged by a specially developed computer program which recorded each revolution and the time of its occurrence. The sequence of revolutions was interpreted in terms of single flights and breaks. A break was defined as a period of time longer than 2000 ms in which the arm did not revolve, and a single flight as the period between two breaks. In accordance with our behavioural observations (20 insects tested for 12 h $insect^{-1}$), the flight time of the weevil was quantified between 400 and 2000 ms, and so the program was set to eliminate any turns with values outside this time range. The flights were monitored over a 12-h period, measuring the duration, number of turns, and number of single flights, and then computing the distance covered and speed. The flight ability of *R. ferrugineus* adults was characterized using the following flight parameters: NOF, TDF, LSF, FD, average flight speed (AS), and maximum flight speed (MAXS) in a 12-h trial. Only unmated males and females were tested from four age groups: from 1 to 3 days old, from 4 to 7 days old, from 8 to 14 days old, and from 15 to 23 days old. To analyse the effect of adult body size, the insects were classified by body length into three different ranges: less than 30 mm, between 31 and 34 mm, and more than 35 mm. Each flight mill was checked before each trial to ensure proper functioning.

Statistical analysis

Adults which did not fly were classified as 'non-flyers' and were excluded from the data analysis, except for the analysis of body weight and body length. A one-way analysis of variance (ANOVA) was used to analyse the influence of sex on adult body weight and length. Regression analysis was carried out to test the relationship between body weight and length. The percentage of flyers by sex and established age ranges was compared using the χ^2 test. The effect of sex, age, and body length and their interactions on each of the flight parameters were analysed using a multifactor ANOVA. Means were separated using Tukey's Honest Significant Difference (HSD) test with a 95% confidence level. As the flight parameters were

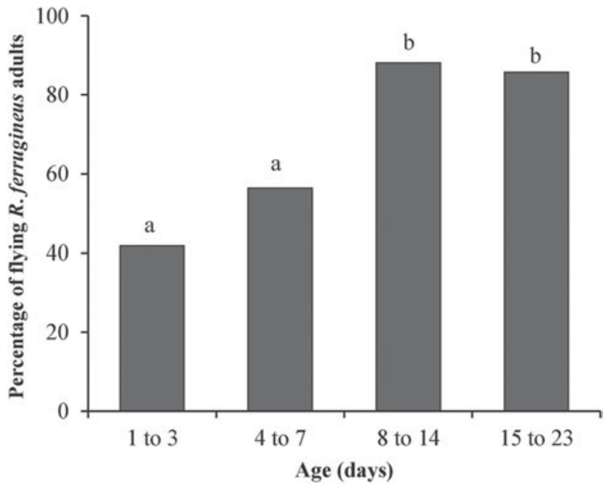

Fig. 2. Percentage of flying *Rhynchophorus ferrugineus* unmated adults ($n = 206$), for different age ranges (from 1 to 3 days old, 4 to 7 days old, 8 to 14 days old, and 15 to 23 days old). Different letters above the columns denote statistically significant differences at $P < 0.05$ (χ^2 test).

not normally distributed, the data were transformed by $\ln(x)$ before the analysis. The untransformed means and their standard errors (SE) were used for graphical visualization of the data. Taking distance as the essential parameter, a regression analysis was performed to test the relationship between the TDF and the remaining flight parameters (NOF, LSF, FD, AS, and MAXS). All the analyses were performed using Statgraphics Plus 5.1 (Statgraphics Plus, 2000).

Results

Body size

The statistical comparison of *R. ferrugineus* adult body weight showed a significant difference between males (1.04 ± 0.02 g) and females (1.18 ± 0.03 g) (one-way ANOVA: $F = 15.99$; df = 1, 205; $P = 0.0001$). Males reached a maximum and minimum of 1.62 and 0.53 g respectively, whereas females had a maximum weight of 1.68 g and a minimum of 0.40 g.

Table 1. Summary of flight performance parameters (mean ± SE) of *Rhynchophorus ferrugineus* unmated adults, during 12-h tethered flight assays (25°C and 65% RH).

Flight parameter	Total (n = 132)		Males (n = 72)	Females (n = 60)
	Mean ± SE[1]	Max[1]	Mean ± SE[1]	Mean ± SE[1]
No. of flights [NOF]	14.9 ± 2.3	233	18 ± 4.1	11.1 ± 1.5
Total distance flown [TDF] (m)	2615.4 ± 381	19659.6	3037 ± 549	2138.5 ± 527.6
Longest single flight [LSF] (m)	1312.5 ± 213	11244.9	1559 ± 300.6	1048.2 ± 304.4
Flight duration [FD] (min.)	30.7 ± 4.5	260.6	36.63 ± 6.52	24.08 ± 6.12
Average speed [AS] (km h^{-1})	3.7 ± 0.07	7.05	3.73 ± 0.1	3.66 ± 0.1
Maximum speed [MAXS] (km h^{-1})	6 ± 0.11	9.29	5.95 ± 0.16	6.07 ± 0.16

[1] Means and their standard errors and maximum single values measured were obtained from the untransformed data set.

Table 2. Effect of sex, age, and body length on flight parameters of *Rhynchophorus ferrugineus* unmated adults tested (n = 132) by multifactor analysis of variance (ANOVA).

Flight parameter	Factor											
	Sex (A)			Age (B)			Body length (C)			Interaction ABC		
	F	df	P	F	df	P	F	df	P	F	df	P
No. of flights [NOF]	0.00	1,120	0.9860	0.00	1,120	0.9482	0.54	2,120	0.5870	0.69	2,120	0.5023
Total distance flown [TDF] (m)	0.50	1,120	0.4824	1.73	1,120	0.1905	0.14	2,120	0.8688	1.26	2,120	0.2883
Longest single flight [LSF] (m)	1.20	1,120	0.2749	3.11	1,120	0.0804	0.13	2,120	0.8741	1.26	2,120	0.2880
Flight duration [FD] (min.)	0.51	1,120	0.4745	1.81	1,120	0.1813	0.03	2,120	0.9678	1.50	2,120	0.2282
Average speed [AS] (km h^{-1})	3.72	1,120	0.0562	0.21	1,120	0.6464	2.01	2,120	0.1384	0.32	2,120	0.7283
Maximum speed [MAXS] (km h^{-1})	2.07	1,120	0.1526	0.13	1,120	0.7201	4.34	2,120	0.0151[1]	0.14	2,120	0.8676

[1] This value shows statistical significant differences (multifactor ANOVA).

The body length of the insects also showed significant differences between sexes (males: 31.17 ± 0.22 mm; females: 33.9 ± 0.27 mm) (one-way ANOVA: F = 65.53; df = 1, 205; P < 0.0001). The maximum body length values were 38 and 39 mm in males and females, respectively, whereas the minimum were 24 mm in males and 26 mm in females. Adult weight showed a strong significant positive relationship with body length in males [linear regression: R^2 = 0.7994; F = 455.18; df = 1, 113; P < 0.0001; body length = 21.5017 + 9.2989 (weight)], and females [linear regression: R^2 = 0.7348; F = 250.38; df = 1, 89; P < 0.0001; body length = 23.961 + 8.505 (weight)]. The insect body length is a less variable parameter than body weight; therefore, the former was used instead of the latter for the subsequent analysis.

Effect of age and sex on the percentage of flying insects

Overall, 64.08% of the *R. ferrugineus* adults tested were inside the established flight thresholds. The percentage of flying insects differed significantly between age groups. No significant differences were observed between the percentage of flying adults of 1–3-day-old versus 4–7-day-old insects (χ^2 test: χ^2 = 2.57; df = 1; P = 0.1090). Nor were there any significant differences between 8 and 14-day-old and 15–23-day-old adults (χ^2 test: χ^2 = 0.10; df = 1; P = 0.7064). However, the percentage of flying *R. ferrugineus* adults differed significantly between 4 and 7-day-old and 8–14-day-old insects (χ^2 test: χ^2 = 11.44; df = 1; P = 0.0007), increasing substantially from 56.4% in the former to 88.1% in the latter case (fig. 2). Based on the previous results, we tested the effect of sex on the percentage of flying insects in the 1–7-day-old and 8–23-day-old categories. In neither case did sex affect the percentage of flying *R. ferrugineus* (χ^2 test: χ^2 = 0.78; df = 1; P = 0.3767, and χ^2 = 0.09; df = 1; P = 0.7656, respectively).

Effect of sex, age, and body length on flight performance

The data for the different flight parameters are shown in table 1. In all the established flight parameters, except in MAXS, the mean was higher in *R. ferrugineus* males than in females. It is important to highlight that the maximum values registered for the parameters examined were very high compared with the mean, especially for TDF and LSF, due to the high flight potential of some of the adults. LSF accounted for approximately 50% of TDF by *R. ferrugineus* adults. On the other hand, AS and MAXS were less variable.

Based on the results of the percentage of flying insects, two age ranges were used for the analysis of the influence of age on the flight parameters: 1–7 days old and 8–23 days old. The data for weevil body length was classified into three categories: under 30 mm, between 30 and 35 mm, and over 35 mm. There were no significant differences in the defined flight parameters (NOF, TDF, LSF, FD, AS, and MAXS) for the three analysed factors (sex, age, and body length) and their interaction (table 2). Only MAXS was significantly influenced by body length, being higher in insects longer than 35 mm, but the interaction between body length, sex, and age was not significant (table 2).

We detected a significant positive relationship between TDF and NOF (linear regression: R^2 = 0.5468; F = 156.75; df = 1, 131; P < 0.0001; fig. 3A). Likewise, TDF and LSF showed a strongly positive relationship (linear regression: R^2 = 0.9509; F = 2502.55; df = 1, 131; P < 0.0001; fig. 3B). TDF and FD were strongly correlated (linear regression: R^2 = 0.9687; F = 3920.32; df = 1, 131; P < 0.0001; fig. 3C). Finally, the speed values

https://doi.org/10.1017/S0007485314000121 Published online by Cambridge University Press

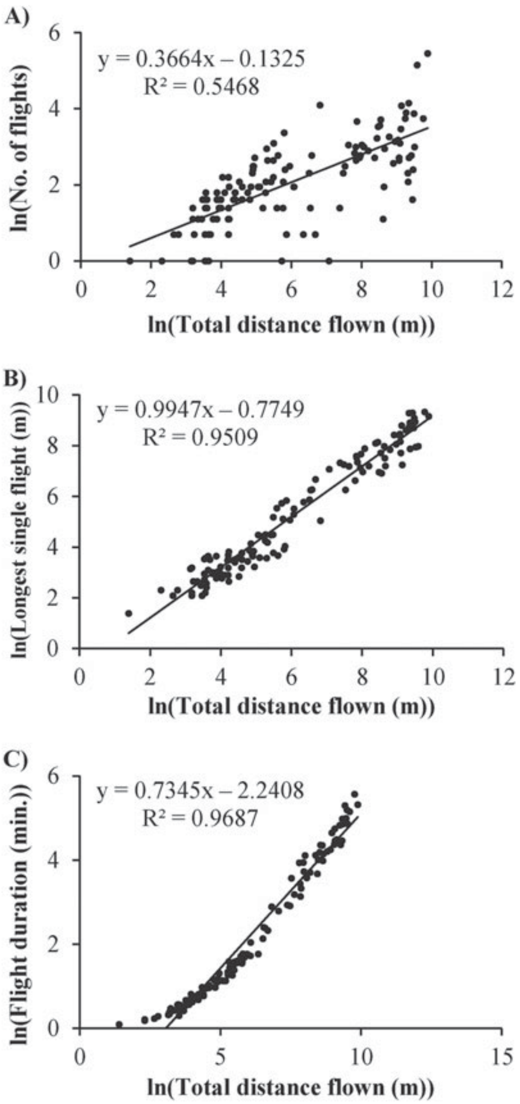

Fig. 3. Relationship between flight parameters for *Rhynchophorus ferrugineus* unmated adults ($n=132$): (A) total distance flown (TDF) and number of flights (NOF); (B) TDF and longest single flight (LSF); (C) TDF and flight duration (FD).

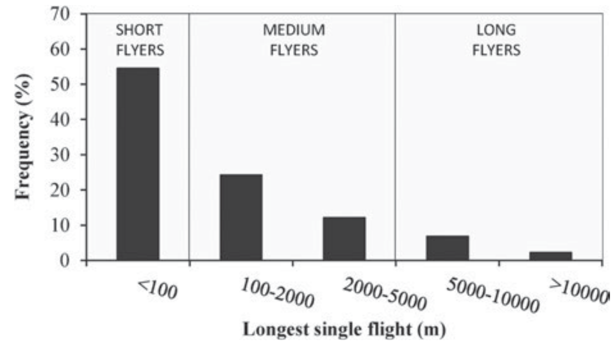

Fig. 4. Frequency distribution of the longest single flight (LSF) for *Rhynchophorus ferrugineus* unmated adults tested in flight mill ($n=132$) and arbitrary flight classification categories.

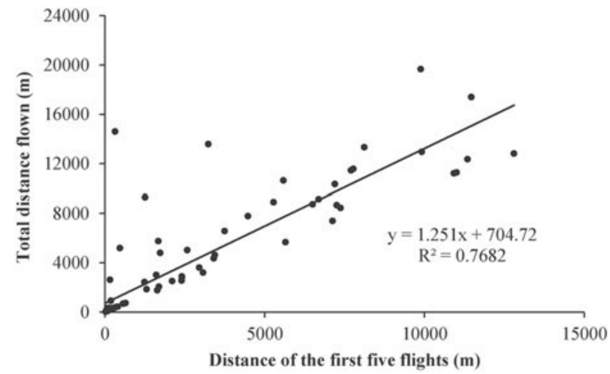

Fig. 5. Relationship between the total distance flown (TDF) and the distance covered during the first five flights, by *Rhynchophorus ferrugineus* unmated adults ($n=91$).

(AS and MAXS) showed no correlation with TDF (AS linear regression: $R^2=0.2646$; $F=46.79$; df = 1, 131; $P<0.0001$; MAXS linear regression: $R^2=0.4420$; $F=103.01$; df = 1, 131; $P<0.0001$).

Flight classification

In accordance with the individual LSF distances flown, we assigned *R. ferrugineus* adults to three arbitrary flight categories: short-distance (less than 100 m), medium-distance (between 100 and 5000 m), and long-distance flyers (more than 5000 m). Up to 54% of the tested insects performed a LSF of less than 100 m (short-distance flyers). The percentage of medium-distance flyers was 36%, whereas 10% of the tested *R. ferrugineus* adults flew a distance greater than 5000 m (long-distance flyers) (fig. 4).

The first flight of the insects tested on the flight mill was the LSF in 61.4% of cases and 71.9% of the weevils achieved their MAXS during the LSF. In fact, the first five flights explained 77% of the variability observed in the TDF (linear regression: $R^2=0.7682$; $F=294.90$; df = 1, 89; $P<0.0001$) (fig. 5).

Fig. 6 shows the mean distance travelled and the average speed in relation to the elapsed time of LSF for the insects considered as long-distance flyers (LSF > 5 km). We only considered those insects which flew the longest distances without interruption, whose exhaustion was greater and therefore made a change in flying speed easier to detect. *R. ferrugineus* adults initially increased their average speed by approximately 0.5 km h^{-1}, reaching a maximum speed at the midpoint of the flight.

Discussion

According to the findings *R. ferrugineus* adults have a great potential for dispersal, since, although most adults make short flights (<100 m), 46% of adults are able to perform medium- or long-distance flights (from 100 to 5000 m, and more than 5000 m, respectively). The flight potential of adults was not influenced by sex, age, or body size.

The flight mill technique is one of the best methods of analysing the flight performance of an insect under laboratory conditions (Schumacher *et al.*, 1997). However, a certain

https://doi.org/10.1017/S0007485314000121 Published online by Cambridge University Press

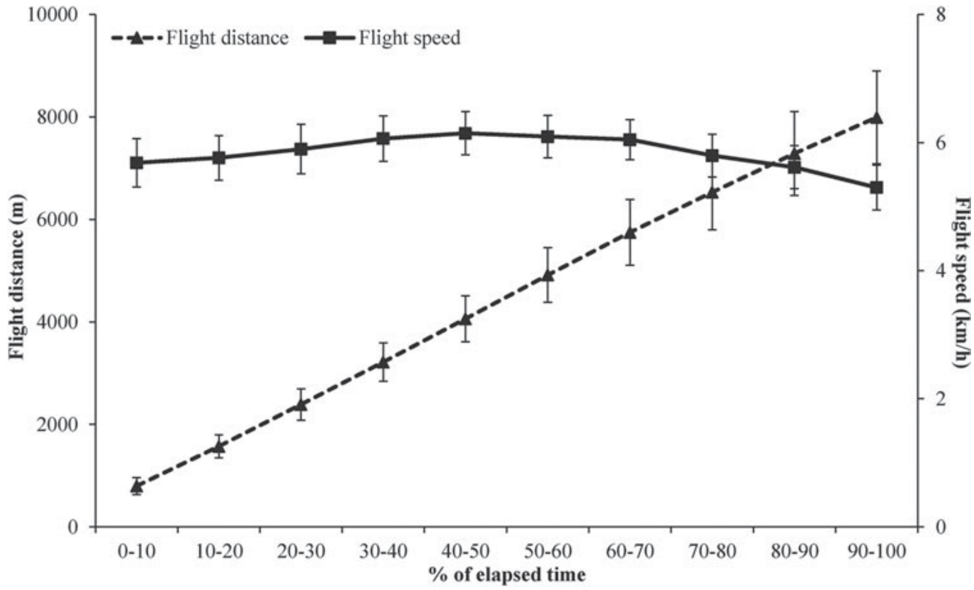

Fig. 6. Distance flown (*m*) and average speed ($km\,h^{-1}$) throughout the flight duration for the *Rhynchophorus ferrugineus* unmated adults whose longest single flights (LSF) were more than 5 km (*n* = 12). Data are presented as mean ± SE.

percentage of the insects do not fly at all, which in the case of *R. ferrugineus*, accounted for 35.42% of the adults tested. In studies carried out with other insect species, such as *Ips sexdentatus*, the percentage of non-flyers was similar: 31.7 ± 16.2% of the tested insects (Jactel, 1993). The percentage of non-flying insects could be a consequence of the tethered flight test method, possible morphological deficiencies that prevent them from flying, or because a portion of the individuals are not capable of flight.

The mean body size of *R. ferrugineus* (body weight and body length) differed significantly by sex. Other studies have also found sex differences in *R. ferrugineus* for these two morphological parameters (Longo, 2007; Prabhu & Patil, 2009). Although differences in male and female body weight and length were observed, sex did not influence the flight potential of *R. ferrugineus* unmated adults. This could possibly be due to the sexual status of the tested insects (unmated adults), since in this work mated males and females were not compared. Another possibility is that olfactory signals used by the insects for communicating with individuals of the same species would have an impact. *R. ferrugineus* adults produce a male aggregation pheromone (Hallet *et al.*, 1993) in the same way as other *Rhynchophorus* species, for example *R. palmarum* (Rochat *et al.*, 1991), *R. phoenicis* (Fabricius) (Gries & Gries, 1993), and *R. cruentatus* (Weissling *et al.*, 1994*b*). The release of an aggregation pheromone causes an increase in the density of conspecifics near the pheromone source, attracting individuals of both sexes (Wyatt, 2003). For this reason it is not necessary for an individual to seek the opposite sex in order to mate, and therefore both sexes have similar flight potentials. This flight behaviour can also be observed in other coleopteran species which produce male aggregation pheromones and in which sex does not influence flight potential, for example the six-toothed pine bark beetle, *I. sexdentatus* (Börner) (Coleoptera: Scolytidae) (Vité *et al.*, 1974; Jactel, 1993), or the plum curculio, *C. nenuphar* (Eller & Bartelt, 1996; Chen *et al.*, 2006). On the other hand, in species which do produce sex pheromones, such as *O. eremita*, males produce the pheromone (Larsson *et al.*, 2003) and females have greater flight potential (Dubois *et al.*, 2010). In the sweet potato weevil, *C. formicarius*, females produce the sex pheromone (Heath *et al.*, 1986) and males have greater flight ability (Moriya & Hiroyoshi, 1998).

R. ferrugineus body size did not influence its flight ability, except for adults (males and females) with a body length greater than 35 mm, which had a significantly higher MAXS. This may be because they are equipped with better musculature to reach maximum speeds at peak times. Some studies also found an absence of correlation between the flight potential and the parameters used to determine the body size of *Ips typographus* and *I. sexdentatus* (Botterweg, 1982; Jactel, 1993; respectively).

The age of *R. ferrugineus* adults affected the percentage of flying insects but had no influence on their flight potential. The current results therefore suggest that *R. ferrugineus* adults of all ages may contribute to a greater or lesser extent to the dispersal of the pest. The percentage of flying weevils in adults from 1 to 7 days old was significantly lower than in 8–23 days old. *R. ferrugineus* adults remain inside the cocoon an average of 8 days after emergence from the pupal case (Menon & Pandalai, 1960). Probably the high percentage of non-flying 1–7-day-old insects could be a consequence of incomplete development of the muscles needed for flight. In agreement with our findings, Tanaka & Yamanaka (2009) pointed out that the percentage of *Ophraella communa* (LeSage) (Coleoptera: Chrysomelidae) flyers increased with age, from days 1 to 5 and thereafter remained at a high level. The life average span of *R. ferrugineus* adults is 1.5–3 months (Esteban-Durán *et al.*, 1998), but we cannot say what would have happened if we had tested weevils more than 23 days old.

The flight capability data obtained in the study indicate that *R. ferrugineus* tends to fly short distances. Most of the tested adults were classified as short-distance flyers (54%), covering less than 100 m. A high number of consecutive short flights may play an important role in the dispersal of *R. ferrugineus*, as demonstrated by the strong positive correlation between the TDF and the NOF. Oehlschlager *et al.* (1992) pointed out in their MRR study with *R. palmarum* that the highest percentage of recaptures occurred at 500 m from the release point, the shortest of the distances tested. In other studies carried out with migratory insects such as the beet armyworm, *Spodoptera exigua* (Hübner), more than 60% of the moths tested flew more than 10 km and 5 h during a tethered flight of 12-hours (Jiang *et al.*, 1999). Kennedy (1985) defines 'migratory flight' as an active process: persistent, straight, and undistracted movement. We believe that according to this definition, the behaviour of *R. ferrugineus* adults during its dispersion does not correspond to a migratory flight, but rather to a 'trivial flight' (Southwood, 1962). In the study carried out by Abbas *et al.* (2006) under field conditions using MRR, some *R. ferrugineus* adults were recaptured at 7 km from the release point. In our laboratory study, unmated weevil adults flew a mean total distance of around 2.5 km and were able to cover distances of about 20 km. In addition, the fact that 10% of the adults were able to fly more than 5000 m corroborates that some *R. ferrugineus* have the ability to fly considerable distances, which would heighten the pest's dispersal despite not exhibiting migratory behaviour.

Another indicator of the high flight potential of *R. ferrugineus* is its flying speed, with a mean around 4 km h^{-1}, similar to studies on other coleopteran species, e.g. *I. sexdentatus* and *O. eremita*, whose average speed was between 4 and 5 km h^{-1} (Jactel & Gaillard, 1991; Dubois *et al.*, 2010). Interestingly, the speed of *R. ferrugineus* was fairly constant, even when it travelled more than 5 km non-stop, which meant that the distance travelled also increased progressively, contrary to the findings of Lu *et al.* (2007), in which the *Lygus lucorum* (Heteroptera: Miridae) flying speed decreased gradually, so that the increase in the covered distance was also reduced.

In the Mediterranean Basin *P. canariensis* and *P. dactylifera*, the main hosts of *R. ferrugineus*, are the two major palm species used as ornamental plants (Ferry & Gómez, 2002). Palm tree distribution densities vary from residential areas, nurseries, avenues, and promenades, with dense uniform distributions, to natural areas where palm trees grow wild and scattered, with light distributions. The ability of *R. ferrugineus* to adapt to different environmental conditions, the trade and transport of infested plant material, the abundance of palm trees in most southern European countries in which the pest is present, and the high dispersal potential of the pest itself, as confirmed by the results of the present study, could explain its rapid and widespread dispersion in the last 20 years.

The flight ability of *R. ferrugineus* was not found to be influenced by sex, age, or body size in the conditions tested. Although weevil adults do not have a potential for long-range migratory flights, they are capable of covering long distances in a series of short flights, which contributes significantly to their potential for spreading. Although the data obtained on their flying ability under laboratory conditions should not be interpreted as an exact reflection of the performance of an insect in its natural environment, we believe this information could be useful for improving strategies currently in place for the management of this pest, such as olfactory trapping. It will also allow us to better define critical areas around pest outbreaks, to intensify inspections, and improve the phytosanitary treatment of palm trees.

Acknowledgements

The authors wish to thank researcher Daniel Sauvard (INRA – Unité de Zoologie Forestière – Orléans) for helping in the knowledge of the flight mill technique. For the help in the design and construction of the flight mill device, we thank Anna Comes and Iñaki Moratal. For the reviews on the previous versions of this manuscript, we thank Ferràn García-Marí (Universitat Politècnica de València – Instituto Agroforestal del Mediterráneo) and Apostolos Pekas (Biobest Belgium N. V.). This research was partially funded by the Foundation of the Comunidad Valencia for the Agroalimentary Research, Agroalimed, within the project named: *Study of the flight behaviour and chromatic attraction in Rhynchophorus ferrugineus adults (Coleoptera: Curculionidae).*

References

Abbas, M.S.T., Hanounik, S.B., Shahdad, A.S. & Al-Bagham, S.A. (2006) Aggregation pheromone traps, a major component of IPM strategy for the red palm weevil, *Rhynchophorus ferrugineus* in date palms (Coleoptera: Curculionidae). *Journal of Pest Science* **79**, 69–73.

Abraham, V.A., Al-Shuaibi, M., Faleiro, J.R., Abozuhairah, R.A. & Vidyasagar, P.S.P.V. (1998) An integrated management approach for red palm weevil *Rhynchophorus ferrugineus* Oliv. – a key pest to date palm in the Middle East. *Sultan Qaboos University Journal for Scientific Research Agricultural Science* **3**, 77–83.

Botterweg, F.P. (1982) Dispersal and flight behaviour of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. *Journal of Applied Entomology* **94**, 466–489.

Chen, H., Kaufmann, C. & Scherm, H. (2006) Laboratory evaluation of flight performance of the plum curculio (Coleoptera: Curculionidae). *Journal of Economic Entomology* **99**, 2065–2071.

Chinchilla, C.M., Oehlschlager, A.C. & Gonzales, L.M. (1993) On the management of red ring disease in oil palm through pheromone based trapping of *Rhynchophorus palmarum*. in *Pipoc Porim International Palm Oil Congress "Update and vision", Kuala Lumpur*, Kuala Lumpur, Malaysia, 20–25 September 1993.

Cooter, R.J. (1993) *The Flight Potential of Insect Pests and its Estimation in the Laboratory: Techniques, Limitations and Insights*. South Benfleet, Central Association of Bee-keepers, Thorpe Bay, United Kingdom, 24 pp.

Cooter, R.J. & Armes, N.J. (1993) Tethered flight technique for monitoring the flight performance of *Helicoverpa armigera* (Lepidoptera: Noctuidae). *Environmental Entomology* **22**, 339–345.

Dubois, G.F., Vernon, P. & Brustel, H. (2009) A flight mill for large beetles such as *Osmoderma eremita* (Coleoptera: Cetoniidae). pp. 219–224 *in* Buse, J. (*Ed.*) *Saproxylic Beetles – Their Role and Diversity in European Woodland and Tree Habitats*. Lüneberg, Germany, Pensoft Publishers.

Dubois, G.F., Le Gouar, P.J., Delettre, Y.R., Brustel, H. & Vernon, P. (2010) Sex-biased and body condition dependent dispersal capacity in the endangered saproxylic beetle *Osmoderma eremita* (Coleoptera: Cetoniidae). *Journal of Insect Conservation* **14**, 679–687.

Eller, F.J. & Bartelt, R.J. (1996) Grandisoic acid, a male-produced aggregation pheromone from the plum curculio, *Conotrachelus nenuphar*. *Journal of Natural Products* **59**, 451–453.

El-Sabea, A.M.R., Faleiro, J.R. & Abo-El-Saad, M.M. (2009) The threat of red palm weevil *Rhynchophorus ferrugineus* to date plantations of the Gulf region in the Middle-East: an economic perspective. *Outlooks on Pest Management* **20**, 131–134.

Esteban-Durán, J., Yela, J.L., Beitia-Crespo, F. & Jiménez-Alvarez, A. (1998) Biología del curculiónido ferruginoso de las palmeras *Rhynchophorus ferrugineus* (Olivier) en laboratorio y campo: ciclo en cautividad, peculiaridades biológicas en su zona de introducción en España y métodos biológicos de detección y posible control (Coleoptera: *Curculionidae: Rhynchophorinae*). *Boletín Sanidad Vegetal de Plagas* **24**, 737–748.

Ferry, M. & Gómez, S. (2002) The red palm weevil in the Mediterranean area. *Palms* **46**, 172–178.

Gries, G. & Gries, R. (1993) Aggregation pheromone of the African palm weevil, *Rhynchophorus phoenicis* F. *Naturwissenschaften* **80**, 90–91.

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

Heath, R.R., Coffelt, J.A., Sonnet, P.E., Proshold, F.I., Dueben, B. & Tumlinson, J.H. (1986) Sex pheromone produced by female sweetpotato weevil, *Cylas formicarius elegantulus* (Summers). *Journal of Chemical Ecology* **12**, 1489–1503.

Hughes, J. & Dorn, S. (2002) Sexual differences in the flight performance of the oriental fruit moth, *Cydia molesta*. *Entomologia Experimentalis et Applicata* **103**, 171–182.

Jactel, H. (1993) Individual variability of the flight potential of *Ips sexdentatus* Boern. (Coleoptera: Scolytidae) in relation to day emergence, sex, size, and lipid content. *The Canadian Entomologist* **125**, 919–930.

Jactel, J. & Gaillard, J. (1991) A preliminary study of the dispersal potential of *Ips sexdentatus* (Boern) (Col., Scolytidae) with an automatically recordings flight mill. *Journal of Applied Entomology* **112**, 138–145.

Jiang, X., Luo, L. & Hu, Y. (1999) Influence of larval diets on development, fecundity and flight capacity of the beet armyworm, *Spodoptera exigua*. *Acta Entomologica Sinica* **42**, 150–158.

Kennedy, J.S. (1985) Migration, behavioural and ecological. pp. 7–26 *in* M. A. Rankin (*Ed.*). *Migration: Mechanisms and Adaptive Significance*. Texas, USA, University of Texas Marine Science Institute.

Kloft, W.J., Kloft, E.S., Kanagaratnam, P. & Pinto, J.L.J.G. (1986) Studies on the use of radioisotopes for the control of the red palm weevil, *Rhynchophorus ferrugineus* F. by the sterile insect technique. *Cocos* **4**, 11–17.

Larsson, M.C., Hedin, J., Svensson, G.P., Tolasch, T. & Francke, W. (2003) Characteristic odor of *Osmoderma eremita* identified as a male-released pheromone. *Journal of Chemical Ecology* **29**, 575–587.

Llácer, E., Jacas, J.A. & Álvarez, S. (2012) Could sterile males be used to vector a microbiological control agent? The case of *Rhynchophorus ferrugineus* and *Beauveria bassiana*. *Bulletin of Entomological Research* **103**, 241–250.

Longo, S. (2007) Dimorfismo sessuale degli adulti di *Rhynchophorus ferrugineus* e *Scyphophorus acupunctatus* (Coleoptera Curculionidae) in Sicilia. *Bolletino di Zoologia Agraria e di Bachicoltura* **39**, 45–50.

Lu, Y., Wu, K. & Guo, Y. (2007) Flight potential of *Lygus lucorum* (Meyer-Dür) (Heteroptera: Miridae). *Environmental Entomology* **36**, 1007–1013.

Menon, K.P.V. & Pandalai, K.M. (1960) Pests. pp. 261–265 *in* Indian Central Coconut Committee (*Ed.*) *The Coconut Palm: A Monograph*. Ermakulam, India, Indian Central Coconut Committee.

Moriya, S. & Hiroyoshi, S. (1998) Flight and locomotion activity of the sweetpotato weevil (Coleoptera: Brentidae) in relation to adult age, mating status and starvation. *Journal of Economic Entomology* **91**, 439–443.

Murphy, S.T. & Briscoe, B.R. (1999) The red palm weevil as an alien invasive: biology and the prospects for biological control as a component of IPM. *BioControl* **20**, 35–45.

Oehlschlager, A.C., Chinchilla, C.M. & González, L.M. (1992) Manejo del picudo de la palma (*Rhynchophorus palmarum*) y la enfermedad del anillo rojo mediante un sistema de trampeo basado en la feromona de agregación. *ASD Oil Palm Papers* **5**, 24–31.

OEPP/EPPO (2008). *Rhynchophorus ferrugineus*. Data sheets on quarantine pests. Available online at http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2338.2008.01195.x/pdf.

OEPP/EPPO (2009) First record of *Rhynchophorus ferrugineus* in: Morocco and Curaçao, Netherland Antilles. *EPPO Reporting Service, Pest & Diseases* 2009: No. 1.

Prabhu, S.T. & Patil, R.S. (2009) Studies on the biological aspects of red palm weevil, *Rhynchophorus ferrugineus* (Oliv.). *Karnataka Journal of Agricultural Sciences* **22**, 732–733.

Rochat, D., Malosse, C., Lettere, M., Ducrot, P., Zagatti, P., Renou, M. & Descoins, C. (1991) Male-produced aggregation pheromone of the American palm weevil, *Rhynchophorus palmarum* (L.) (Coleoptera: Curculionidae): collection, identification, electrophysiological activity, and laboratory bioassay. *Journal of Chemical Ecology* **17**, 2127–2141.

Sarvary, M.A., Hight, S.D., Carpenter, J.E., Bloem, S., Bloem, K.A. & Dorn, S. (2008) Identification of factors influencing flight performance of field-collected and laboratory-reared, overwintered, and non overwintered cactus moths fed with field-collected host plants. *Environmental Entomology* **37**, 1291–1299.

Schumacher, P., Weyeneth, A., Weber, D.C. & Dorn, S. (1997) Long flights in C*ydia pomonella* L. (Lepidoptera: Tortricidae) measured by a flight mill: influence of sex, mated status and age. *Physiological Entomology* **22**, 149–160.

Southwood, T.R.E. (1962) Migration of terrestrial arthropods in relation to habitat. *Biological Reviews* **37**, 171–211.

Tanaka, K. & Yamanaka, T. (2009) Factors affecting flight activity of *Ophraella communa* (Coleoptera: Chrysomelidae), an exotic insect in Japan. *Environmental Entomology* **38**, 235–241.

Vité, J.P., Bakke, A. & Huges, B.A. (1974) Sex attractant of bark beetles, *Ips sexdentatus*. *Naturwissenschaften* **61**, 365–366.

Wattanapongsiri, A. (1966) A revision of the genera *Rhynchophorus* and *Dynamis* (Coleoptera: Curculionidae). PhD thesis, Oregon State University, Corvallis, OR, USA.

Weissling, T.J., Giblin-Davis, R.M., Center, B.J. & Hiyakawa, T. (1994*a*) Flight behavior and seasonal trapping of *Rhynchophorus cruentatus* (Coleoptera: Curculionidae). *Annals of the Entomological Society of America* **87**, 641–647.

Weissling, T.J., Giblin-Davis, R.M., Gries, G., Gries, R., Perez, A.L., Pierce, H.D. & Oehlschlager, A.C. (1994*b*) Aggregation pheromone of the palmetto weevil, *Rhynchophorus cruentatus* (F.) (Coleoptera: Curculionidae). *Journal of Chemical Ecology* **20**, 505–515.

https://doi.org/10.1017/S0007485314000121 Published online by Cambridge University Press

Wu, H., Wu, K., Wang, D. & Guo, Y. (2006) Flight potential of pink bollworm, *Pectinophora gossypiella* Saunders (Lepidoptera: Gelechiidae). *Environmental Entomology* **35**, 887–893.

Wyatt, T.D. (2003) Coming together and keeping apart: aggregation and host-marking pheromones. pp. 74–86 *in* Cambridge University Press (*Ed.*) *Pheromones and Animal Behaviour: Communication by Smell and Taste*. Cambridge, Cambridge University Press.

Zhang, Y., Wang, L., Wu, K., Wyckhuys, K.A.G. & Heimpel, G.E. (2008) Flight performance of the soybean aphid, *Aphis glycines* (Hemiptera: Aphididae) under different temperatures and humidity regimens. *Environmental Entomology* **37**, 301–306.