ECOLOGY AND BEHAVIOR

Diel Flight Pattern and Flight Performance of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) Measured on a Flight Mill: Influence of Age, Gender, Mating Status, and Body Size

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ABSTRACT *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) is an invasive herbivore that poses a serious risk to *Opuntia* cacti in North America. Knowledge of the flight behavior of the cactus moth is crucial for a better understanding of natural dispersal, and for both monitoring and control. We used computer-linked flight mills to investigate diel flight activity and flight performance in relation to gender, age, mating status, and body size. Maximal flight activity for both mated and unmated moths occurred during twilight, whereas flight activity was low during photophase. The total distance flown and the number of initiated flights within a diel cycle were higher in both unmated and mated females than in males, but the longest single flight was similar in both genders. These findings suggest that pheromone trap captures of males likely indicate the simultaneous presence of females and that mated females might even be in areas where males are not detected yet. Flight performance heterogeneity was large, with a small portion of the population (both males and females) performing long unbroken flights, whereas the majority made short flights. Females had higher pupal and adult body size and shorter longevity than males. A few individuals, particularly young mated females, flying long distances may be important for active spread of a population and the colonization of new habitats. Implications of this study in the control of the cactus moth by using the sterile insect technique are discussed.

KEY WORDS cactus moth, flight, dispersal, circadian rhythm, sterile insect technique

Cactoblastis cactorum (Berg) (Lepidoptera: Pyralidae), a moth native to northern Argentina, Uruguay, Paraguay, and southern Brazil, was introduced as a biological control agent to successfully control the invasive prickly pear cacti (*Opuntia* spp.) in Australia, South Africa, Hawaii, and the Caribbean (Stiling 2002, Zimmermann et al. 2004). Larvae hollow out and destroy cactus cladodes, enabling secondary pathogens to enter the damaged cladode (Starmer et al. 1988), which may eventually lead to the death of the entire plant (Zimmermann et al. 2004). The moth was recorded from the Florida Keys in 1989, and it is now considered an invasive pest in the United States (Pemberton 1995, Stiling and Moon 2001, Hight et al. 2002). The rapid spread of this invasive moth (Hight et al. 2002) is not only a threat to rare endemic cacti (Rebman and Pinkava 2001, Stiling and Moon 2001, Hight et al. 2002), native desert ecosystems (Mahr 2001), and the ornamental prickly pear industry in the United States (Irish 2001), but it could have catastrophic effects on the *Opuntia* industry in Mexico, where prickly pear cacti are being used extensively as human food and livestock fodder (Zimmermann et al. 2004).

The moth has three, nonoverlapping generations per year in the southern United States (Zimmermann et al. 2004), and in the laboratory its life cycle can be as long as 90 d from egg to adult (J.E.C., unpublished data). Females initiate calling and copulation occurs ≈1 h before sunrise (Hight et al. 2003). Mated females produce up to three eggsticks in the next few days, generally at 24-h intervals, with 40–90 eggs in each eggstick (S.D.H., unpublished data). Moths were observed to perform erratic short flights close to the ground, which has been interpreted as the moth is not a long distance flyer (Zimmermann et al. 2004). Field monitoring of infestations in its native range in South America (Zimmermann et al. 2004) and of released moths in Australia and South Africa (Dodd 1940, Pettey 1948) indicated that cactus moth populations

typically dispersed only relatively short distances each year. However, census data from the United States (Florida) found that the infestation spread rate has been ≈50–75 km/yr (Stiling 2002). Released male cactus moths have been collected in pheromone-baited sticky traps as far as seven km from their release point between islands, including up to 1 km from a release point in 24 h (S.D.H., unpublished data). It is yet unknown to what degree such dispersal is accomplished by winged flight, by wind dispersal, or by anthropogenic activities (Stiling 2002).

Currently, there are no satisfactory methods to control this pest over a wide area (Bloem et al. 2005b). Although insecticides have been identified (Poon et al. 2003, Bloem et al. 2005b) and possible biological control agents (Pemberton and Cordo 2001), their success is questionable (Zimmermann et al. 2004). Currently, the use of the sterile insect technique (SIT) with inherited F_1 sterility (released males are only partially sterile, which allows deleterious effects of radiation to be inherited in the first filial generation) (Carpenter et al. 2001), offers the greatest potential to stop the spread of this pest (Bloem et al. 2005a, 2007). In SIT, the target insect species is reared in large numbers, sterilized by gamma radiation (Dyck et al. 2005, Klassen 2005), and released as a component of areawide integrated pest management programs (Carpenter et al. 2005) to mate with and reduce the reproductive output of the target pest population (Hight et al. 2005). SIT is being commercially used to control the codling moth *Cydia pomonella* (L.) (Bloem et al. 2006) and the efficacy of SIT was demonstrated on other Lepidoptera, including corn earworm, *Helicoverpa zea* (Boddie), by using inherited F_1 sterility (Carpenter 1993); on cabbage looper, *Trichoplusia ni* (Hübner) (North and Holt 1969); and on pink bollworm, *Pectinophora gossypiella* (Saunders) (Henneberry and Clayton 1981, Henneberry 1993, Bloem et al. 2005a). The number of irradiated and released sterile specimens must be larger than the wild population at the target location (Calkins and Parker 2005). Hight et al. (2005) showed that an overflooding ratio as low as 5:1 (irradiated released:wild) could significantly reduce wild *C. cactorum* populations in field cage trials.

One of the keys to success with SIT is understanding the activity patterns and dispersal behavior of the target pest (Bloem et al. 2006). Computer-linked flight mills (Hughes and Dorn 2002) have been successfully used in comparative studies to assess the flight performance of different insect species. In flight mills, individuals are tethered and allowed to fly in a circle of known circumference while a linked computer counts each rotation. This information is used to calculate parameters describing an individual's flight performance (Schumacher et al. 1997b, Wanner et al. 2006). Quantitative comparisons of flight on flight mills have been carried out with the lepidopteran species *Cydia pomonella* (L.) (Schumacher et al. 1997b) and *Cydia molesta* (Busck) (Hughes and Dorn 2002, Hughes et al. 2004) and with the hymenopteran *Cotesia glomerata* (L.) (Wanner et al. 2006). Under field conditions, many factors influence insect flight, including abiotic cues such as wind and biotic cues such as the presence of pheromones. Laboratory flight mill studies exclude these extrinsic stimuli (Erber 1975), focusing on intrinsic flight capacity. Studies on flight capacity can be made in relation to gender, age, and mating status (Hughes and Dorn 2002) of the adult insect and factors such as pupal weight and the impact of handling, shipping, and radiation. Furthermore, flight mill studies allow for assessment of homogeneity or heterogeneity of flight capacity within a population (Schumacher et al. 1997a, Hughes and Dorn 2002). Thus, although tethered flight studies with insects that do not carry their own weight (Schumacher et al. 1997b) cannot be used to directly estimate active dislocation distances in the field, positive correlations between moth activity patterns in the laboratory and the field have been demonstrated (Keil et al. 2001a).

The principal objectives of this study were to assess the diel pattern of flight activity in the cactus moth and to characterize flight performance in relation to gender, age, mating status, and body size by using computer-linked flight mills. Flight performance was investigated based on the total distance flown (TDF), the longest single continuous flight (LSF), and the number of flights (NOF) initiated.

Materials and Methods

Test Insects. One hundred to 200 *C. cactorum* pupae of each gender were randomly selected once a week from a laboratory colony of moths that originated from field collections in Florida and Georgia in 2002. The colony insects have been reared for 12 generations on cactus pads in Tifton, GA, at the USDA–ARS laboratory. Wild individuals collected at the same Florida and Georgia locations were added to the laboratory-reared colony annually. The silk cocoons were carefully removed by hand, the pupae were sorted by gender, and each gender was placed in separate plastic petri dishes (14 cm in diameter). Pupae were flown weekly to ETH, Institute of Plant Sciences/Applied Entomology, Zurich, Switzerland. Each shipment arrived within 4 d of departure and 7–8 d after pupation. An electronic data pod (HOBO, Onset, Bourne, MA) was included in each shipment to monitor temperature and humidity during transport. Mortality due to eclosion or physical damage during shipment was low. Upon arrival, the pupae were placed on filter paper in 30- by 30- by 30-cm emergence cages (BugDorm, Megaview Science Education Co., Taichung, Taiwan), and the two genders were kept separate in controlled environment rooms (28°C, 70% RH, and a photoperiod of 12:12 [L:D] h). Concurrent with the findings of Pettey (1948), male eclosion preceded female eclosion by 2 d, with a mean eclosion time (after arrival under the conditions of the current study) of 7.5 d in males and 9.5 d in females ($n = 100$/gender).

Survival. The survival rate of the male and female adults was measured on randomly selected female ($n = 51$) and male ($n = 50$) moths. Moths were placed

into 30 ml plastic containers (BioServ, Frenchtown, NJ) before eclosion, and they were kept at 28°C, 70% RH, and a photoperiod of 12:12 (L:D) h. The number of moths surviving was recorded every 24 h for 7 d.

Pupal and Adult Body Size. Because *C. cactorum* adults are not able to feed, their weight loss can provide essential information about the energy used for all flight- and mobility-related activities. Upon arrival, 100 male and 100 female pupae were randomly selected, and their pupal weight was measured (AB204 scale, Mettler, Küsnacht, Switzerland; range 0.1 mg–220 g). After eclosion, 51 females and 50 males were randomly selected and kept individually in 30-ml plastic containers (BioServ, Frenchtown) at 28°C, 70% RH, and a photoperiod of 12:12 (L:D) h. The size of the containers allowed movement and flight. Adult weight of each specimen was recorded every 24 h for 6 d.

Flight Mill Technique. *Tethering Technique.* Emergence cages were checked daily for adult eclosion. For experiments using unmated moths, eclosed adults were moved individually into 30-ml plastic cups within 24 h of their eclosion and weighed (AB204 scale, range 0.1 mg–220 g). Experiments with unmated moths were set to start 1 h before the start of simulated dawn; therefore, moths needed to be transferred from the emergence cages and tethered in the dark by using only a 100-W IR light (120 lux). The moths did not show any different behaviors under IR light than in the dark.

For experiments using mated moths, 15–20 males and females were collected within 24 h of eclosion (0-d-old moths) and placed in a 30-cm^3 mating arena (BugDorm, Megaview Science Education Co., Taichung, Taiwan) and allowed to mate at random. Mating in the laboratory was observed in the twilight hours before sunrise (dawn), supporting the results of previous field experiments (Hight et al. 2003). Tethering occurred in the daylight because trials with mated moths were set to start 3 h after the start of simulated dawn during the photophase to ensure undisturbed mating. The mating status of the moths was determined within 3 h after each trial. Female mating status was confirmed by observing the presence of a spermatophore in the bursa copulatrix. Mating status of male moths was identified by observing the color and the texture of the posterior simplex, as described by Marti and Carpenter (2007).

Tethering of both mated and unmated adults took place at 4°C to immobilize the moths. Because extended cooling can have detrimental physiological effects, moths were kept at this low temperature for <45 min. Using 00 size insect pins, 20- by 5-mm paper strips were fixed to a tray and a pinhead-size drop of fast drying solvent-free glue (Migros, Zurich, Switzerland) placed on the end of each paper strip. The dorsal side of the thorax and abdomen of each moth was placed on this glued surface without allowing tarsal or wing contact with the paper or the glue. The glue dried within 30–60 s at 4°C. Because the tip of the abdomen and the ovipositor were free to move, the tethered females were able to lay eggs on the paper

strips during the experiment. Moths attached to pin-held strips were moved to the flight mill room (Conviron, PGV 36, Controlled Environments Limited, Winnipeg, MB, Canada) where 24 flight mills were set up operating in tandem under 28°C and 70% RH.

Flight Mill Methodology. Flight was monitored for a 24-h time period. During scotophase (10 h) light amounted to 0.36 lux. Simulated dawn (2 h) and dusk (2 h) were composed of a sequence of 5-min steps during which light intensity gradually increased or decreased between 0.36 and 3320 lux (0.36, 0.62, 1.5, 2.6, 4.2, 6.2, 8.1, 10, 11.4, 13, 14.4, 15.8, 17.2, 35, 83, 168, 380, 720, 1,100, 1,500, 1,900, 2,200, 2,500, 2,800, 3,270, and 3,320). Photophase was maintained at 3,320 lux for 10 h. Each flight mill consisted of two magnets (20 mm in height and 5 mm in diameter) held 30 mm apart, below a small infrared transmitter/receiver (Schumacher et al. 1997b). Twenty-four of these apparatuses were affixed to an aluminum frame with five flight mills in a column and six flight mills in a row. The flight mills were inside a controlled environment walk-in chamber. Moths fixed on the paper strip (see above) were pinned to the end of a 24-cm-long flight arm with a 0.75-m revolution circumference. The other end of the arm was covered with a reflective material and a no. 4 insect pin provided the balance. The flight arm was placed between the two magnets of the flight mill with a 2-cm-long central pin pushed vertically through it, touching only one of the magnets to reduce friction to a minimum. A small infrared transmitter/receiver registered the movement of the reflective flight arm, and a computer program recorded every rotation. All flight mills were run simultaneously. Flight mills were tested before each trial and free movement of the moth wings were checked with a gentle blow of air. The few adults that remained immobile (probably due to destructive handling) were excluded from the trials. A tightly closed curtain in front of the flight mills ensured a constant microclimate during the experiments.

Flight Parameters Measured. Flight consisted of a sequence of revolutions and breaks. A specifically developed analytical program (M. Gernss, ETH) was set to eliminate all but one or two revolutions, in accordance with our behavioral observations showing that moths were not able to fly faster than two revolutions per s, or slower than half a revolutions per s. Artificially elevated counts can occur when a moth discontinues flight at a location where a constant infrared signal is elicited. Furthermore, if there was a break longer than 2 s between two consecutive revolutions, the second revolution was counted as a beginning of a new flight. All flights had to last at least 2 s. Flight activity was defined as the distance flown in meters in 60 min. Flight capacity was characterized using both the longest single flight (LSF) and the total distance flown (TDF) within a 24-h-long trial. TDF was calculated by summing all flights made by a single moth during a 24-h-long trial. Moths were assigned to five arbitrary flight classification categories according to the distance of the longest single unbroken flight made by each individual, similar to Hughes and Dorn (2002),

Table 1. Comparison of flight parameters of *C. cactorum* in respect to gender and mating status of adult moths

Flight parameter	Mating status[a]	Females			Males		
		Means ± SEM[b]	Max	n	Means ± SEM[b]	Max	n
Total distance flown (m)	Unmated	2,016.42 ± 260.88a	21,510.00	155	1,038.93 ± 142.25b	10,713.62	181
	Mated	2,364.14 ± 433.75a	11,909.45	62	808.28 ± 226.73b	5,804.25	42
Longest single flight (m)	Unmated	151.82 ± 43.18a	5,499.00	155	71.03 ± 20.62a	2,992.50	181
	Mated	125.15 ± 51.76a	3,078.00	62	65.73 ± 21.08a	679.50	42
No. of flights	Unmated	354.88 ± 41.70a	2,609	155	218.04 ± 29.51b	2,770	181
	Mated	544.03 ± 110.70a	3,677	62	144.92 ± 37.46b	1,094	42

Experiments were conducted for 24 h on the flight mills at 28°C and 70% RH, with changing photoperiod (0.36–3320 lux). The effect of mating status, gender and age was measured using generalized linear models ($\alpha = 0.05$; ANOVA) on the log-transformed data. Due to the lack of significant age effect, flight data of the four unmated and two mated moth age categories were pooled by gender and mating status. Female and male flight parameter means within the same mating status (gender effect) within the same row followed by different letters are significantly different ($P < 0.05$; Tukey–Kramer, LSMeans).

[a] Flight parameter means between unmated and mated moths were not found significantly different in either of the genders ($P < 0.05$; Tukey–Kramer, LSMeans).

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

who used three categories. Short flyers were defined to have a LSF of up to 20 m, and long flyers were defined to have a LSF of at least 100 m.

The effect of age on the flight performance of unmated and mated moths was measured for both genders. Age was determined as the number of nights after eclosion. Moths were kept individually in 30-ml plastic containers until they reached the required age for a given trial. To avoid any daily bias, testing of moths of each age category was distributed over at least 5 d. Flight performance of both male and female unmated moths was determined for the age categories of 0, 1, 2, and 3 d old. In studies with mated moths 1- and 2-d-old specimens were tested. Flight parameters of 1- and 2-d-old unmated and mated moths were also compared. Sample sizes for each category can be found in Table 1.

Flight performance in relation to body size was measured for unmated moths. Adult moths were weighed within 24 h of eclosion (0 days old). To identify the diel cycle of both mated and unmated *C. cactorum*, the distance flown by 0-d-old unmated and 1-d-old mated male and female moths was recorded for every hour for 24 h. The mean flight activity under dusk, dawn, photophase, and scotophase light conditions was measured.

Statistical Analysis. Survival rate of female and male moths was compared using log-rank and Wilcoxon tests with PROC LIFETEST command (SAS Institute 2000) from 0 to 7 d after the eclosion. The long-rank test places more weight on larger survival times, whereas the Wilcoxon test places more weight on early survival times. Survival functions were compared between 51 female and 50 male moths by using censoring on the six male and one female moth that remained alive at the seventh day of the experiment. Mean and median survival times were calculated for both genders, and the results from the comparison of survival curves were presented. The influence of gender and age after eclosion on adult *C. cactorum* body size was tested using restricted maximum likelihood models (Littell et al. 1996) with the repeated function (PROC MIXED procedure) (SAS Institute 2000). Degrees of free-

dom were calculated using the method described by Kenward and Roger (1997), and the autoregressive model was identified by the Akaike and Schwartz Information Criteria to fit the data the best (Littell et al. 1996). Flight capacity was characterized using LSF, TDF, and NOF (see Introduction for definitions). Effects of age and gender on the flight capacity of unmated and mated moths were measured, and before the statistical analysis the data were log transformed for each model to meet the assumption of normality. For graphical visualization of the data, means and their SEMs were used from the untransformed data. The data were unbalanced (not the same number of moths flew each time) and analyzed using multifactor analysis of variance (ANOVA) with PROC GLM (SAS Institute 2000). Regression analysis was carried out with PROC REG (SAS Institute 2000) to test the relationship between body size and flight performance and to test the interactions between flight parameters. If significant effects were detected by the models, pairwise comparisons were performed using LSMEANS command (SAS Institute 2000) on the least square means separated by the Tukey–Kramer procedure (Littell et al. 1996). Diel cycle of flight activity in unmated 0-d-old moths and mated 1-d-old moths were analyzed using restricted maximum likelihood models (Littell et al. 1996) with the repeated function (PROC MIXED procedure) (SAS Institute 2000). Degrees of freedom were calculated using the method detailed by Kenward and Roger (1997). The Aikaike and Schwartz Information Criteria were used to identify the appropriate covariance matrices (Littell et al. 1996) and for both mated and unmated moths the autoregressive model was chosen due to the lower criteria. Frequency distribution of the LSF of mated and unmated female and male *C. cactorum* was analyzed after the flight data were separated into five groups by the LSF (<5, 5–20, 20–100, 100–500, and >500 m). Frequencies of LSF were compared using chi-square test (SAS Institute 2000) or Fischer exact chi-square test where the sample size was below five (LSF < 500 m).
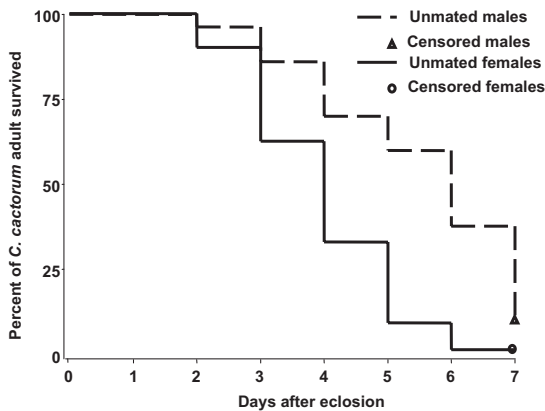
Fig. 1. Comparison of the percentage of male and female *C. cactorum* that survived after eclosion at 28°C, 70% RH, and a photoperiod of 12:12 (L:D) h. Female (*n* = 51) and male (*n* = 50) moths were observed for 7 d, and percentage of survival was recorded daily. Survival curves of female and male moth were compared using log-rank and Wilcoxon tests, and both tests indicated a significant difference between the two genders (*P* < 0.0001). The surviving six males and one female were censored in the analysis at the seventh day of the experiment.

Results

Survival. The rank tests for homogeneity indicate a significant difference in survival between the adult female and male *C. cactorum* (log-rank test: $\chi^2 = 27.14$, df = 1, *P* < 0.0001 and Wilcoxon test: $\chi^2 = 22.97$, df = 1, *P* < 0.0001), because males live significantly longer than females (Fig. 1). The percentage of unmated moths that survived during days 0, 1, and 2 after eclosion was high (>80%) regardless of the gender (Fig.

1). Median survival time was 2 d later for males than for females (fourth day and sixth day, respectively).

Pupal and Adult Body Size. Statistical comparison of the square root transformed adult weight showed a significant difference between males and females (*F* = 364.39; df = 1, 456; *P* < 0.0001). Male pupae were 20% lighter than female pupae, whereas in adults, females weighed on average 80% more than males on the same day after eclosion (Fig. 2). *C. cactorum* adults do not feed, and body size decreased in both females and males over time (*F* = 11.65; df = 1, 456; *P* < 0.0001). The interaction term between the genders and the age of the adults was not significant (*F* = 0.88; df = 1, 456; *P* = 0.4976). Female adult weight decreased by the second day after eclosion, and they decreased again by the fourth day (Fig. 2). On the fifth day, the sample size of the measured females was low (*n* = 5) due to high mortality. In males, similarly to females, the weight decreased by the second day after eclosion, but there was no further decrease measured in male weight afterward.

Diel Cycle of Flight Activity in Unmated Moths. The diel pattern of flight on the flight mill changed with changing photoperiod conditions for both genders (Fig. 3). Flight activity was high in both genders at the beginning of dawn (sunrise), and then it gradually decreased as light intensity increased. Flight activity for both genders fell to a minimum during full light conditions (photophase). Female flight started to increase again at simulated dusk when photointensity began to decrease. A second relative maximum in female flight activity was reached toward the end of the decreasing photoperiod, i.e., at the end of dusk (sunset), and females remained active during the next 5 h of the night (scotophase). Flight activity of males remained low during the night, and only increased
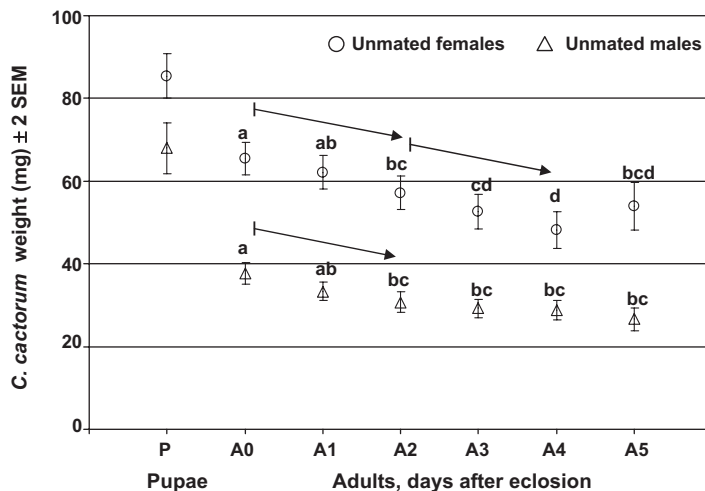

Fig. 2. Comparison of female and male body size from pupal stage until the fifth day after eclosion at 28°C, 70% RH, and a photoperiod of 12:12 (L:D) h. ANOVA was conducted on the square-root transformed weight of adult moths from day 0 to day 5 (α = 0.05; ANOVA). Means ± 2 SEM of the untransformed *C. cactorum* weight are presented. The 7–8-d-old pupae were weighed upon arrival (female, *n* = 100; male, *n* = 100), whereas adult weight was measured every day after eclosion (female, *n* = 51; male, *n* = 50). The vectors indicate the weight loss between days. Body sizes within the same gender followed by different letters are significantly different (*P* < 0.05; Tukey–Kramer LSMeans).
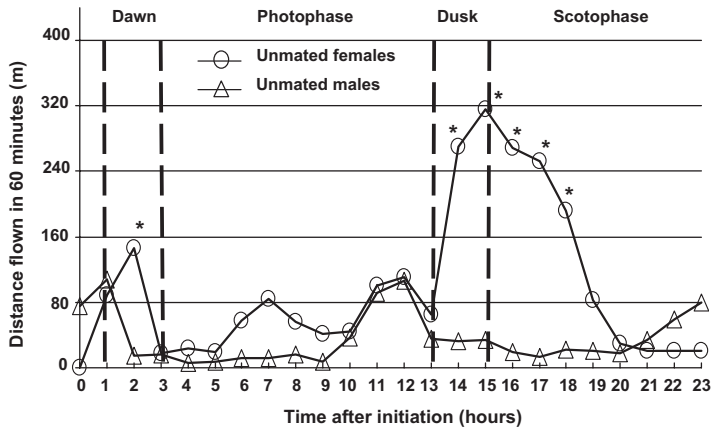
Fig. 3.   Diurnal rhythm of 0-d-old unmated male and female *C. cactorum*. Flight mill-measured mean ± SEM distance flown per hour (meters) is presented (female, $n = 30$; male, $n = 49$). Photointensity amounted to 0.36 lux during scotophase and 3,320 lux during photophase, and it gradually increased and decreased during dusk and dawn, respectively. ANOVA was conducted on the natural log transformed data ($\alpha = 0.05$; ANOVA). Distances flown per hour marked with an asterisk are significantly higher than the flight activity of the other gender in the same hour ($P < 0.05$; Tukey-Kramer LSMeans).

during the 3–4 h before dawn (Fig. 3). The statistical model showed a significant effect of both time ($F = 2.29$; df = 23, 1,438; $P = 0.0005$) and gender ($F = 6.02$; df = 1, 187; $P = 0.0150$), with a significant interaction term ($F = 2.03$, df = 23, 1,429; $P = 0.0032$). Separate analysis of the effect of the time on the two genders showed that the significant time effect in the full model was due to the significant change of female flight activity during the diel period ($F = 2.08$; df = 23, 487; $P = 0.0030$), whereas male flight activity did not change over time ($F = 1.04$; df = 23, 925; $P = 0.4140$). Pairwise comparisons of male and female diel flight activity showed that females flew significantly longer distance ($P < 0.05$) during 6 h of the diel cycle, of which all were at dawn, dusk, or scotophase (Fig. 3).

Unmated Moths: Effects of Age, gender and body size on flight performance. No differences among the age groups were found in unmated moths for any of the flight parameters (TDF: $F = 1.94$; df = 3, 328; $P = 0.1236$; LSF: $F = 1.84$; df = 3, 328; $P = 0.1396$; NOF: $F = 1.89$; df = 3, 328; $P = 0.1317$). The TDF for unmated moths was significantly different between the two genders ($F = 5.15$; df = 1, 328; $P = 0.0239$), but the interaction between age and gender was not significant ($F = 0.73$; df = 3, 328; $P = 0.5333$). The maximum total distance flown by an individual under the conditions of the test was 21.5 km for females and 10.7 km for males. Individual variations in flight performance were large (Table 1). Body size (weight) of the eclosed females did not show any significant relationship with the log transformed TDF [$r^2 = 0.02$; $P = 0.2350$; $\ln(\text{tdf}) = 2.95 - 0.0006(\text{weight})$], but there was a moderately significant positive relationship in males [$r^2 = 0.1005$; $P = 0.0434$; $\ln(\text{tdf}) = 0.9018 + 0.0035(\text{weight})$].

The values for LSF for unmated moths were not significantly different between the two genders ($F = 2.70$; df = 1, 328; $P = 0.1012$). The interaction term between age and gender also was not significant ($F =$

1.62; df = 3, 328; $P = 0.1837$). Maximum values assessed for an individual moth reached 5.5 km in females and 2.9 km in males (Table 1). A larger percentage of the tested females ($\chi^2 = 36.22$, df = 1, $P < 0.0001$) and males ($\chi^2 = 114.29$, df = 1, $P < 0.0001$) flew continuously for 20 m or less (short flyers), than 100 m or more continuous flights (long flyers) (Fig. 4). Body size (weight) of the eclosed adults did not show any significant relationship with the log transformed LSF for the females [$r^2 = 0.01$; $P = 0.4592$; $\ln(\text{lsf}) = 1.50 - 0.0003(\text{weight})$], but there was a significant positive relationship in males [$r^2 = 0.1437$; $P = 0.0145$; $\ln(\text{lsf}) = 0.0569 + 0.0027(\text{weight})$].

The NOF during a diel period trial was significantly different between the two genders ($F = 4.37$; df = 1, 328; $P = 0.0375$), but not between genders within age groups ($F = 0.64$; df = 3, 328; $P = 0.5895$). Adult unmated males had a maximum NOF (2,770 take-offs) when they were 1 d old (Table 1), whereas females initiated the most flight at age 0 (2,606 take-offs). Body size (weight) of the eclosed adults did not show any significant relationship with the NOF for females [$r^2 = 0.04$; $P = 0.1556$; $\ln(\text{nof}) = 2.39 - 0.0007(\text{weight})$] or males [$r^2 = 0.05$; $P = 0.1377$; $\ln(\text{nof}) = 0.8336 + 0.0023(\text{weight})$]. The regression analysis of TDF and the NOF showed a strong positive correlation between these two flight parameters in unmated females [$P < 0.0001$; $r^2 = 0.78$; $\ln(\text{tdf}) = 1.51 + 0.9928(\ln(\text{nof}))$] and unmated males [$P < 0.0001$; $r^2 = 0.87$; $\ln(\text{tdf}) = 1.027 + 1.0627(\ln(\text{nof}))$]. The relationship between the TDF and the LSF was weaker in unmated females [$P < 0.0001$; $r^2 = 0.54$; $\ln(\text{tdf}) = 3.04 + 0.9517(\ln(\text{lsf}))$] and in unmated males [$P < 0.0001$; $r^2 = 0.62$; $\ln(\text{tdf}) = 2.17 + 1.1582(\ln(\text{lsf}))$].

Mated Moths: Effects of Photoperiod on Diel Flight Activity and of Age and Gender on Flight Performance. For methodological reasons, measurement of diel flight activity could only be started after the time period for mating ended, which coincided in the lab-
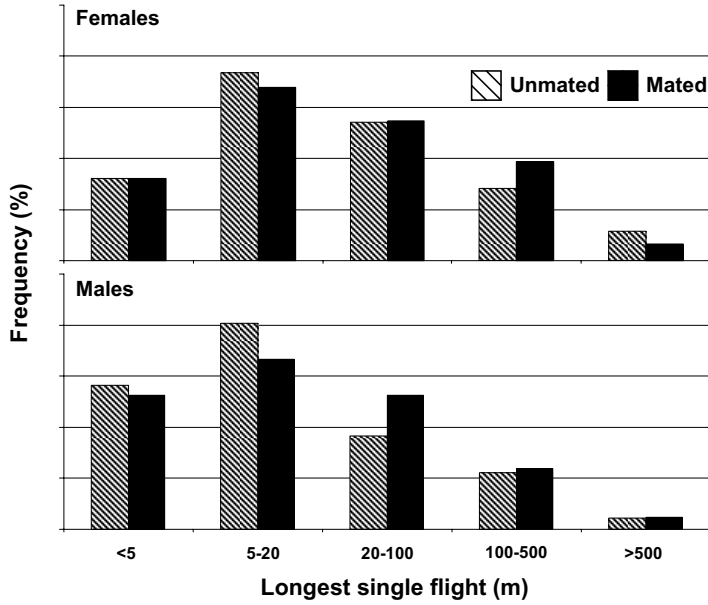
Fig. 4. Frequency distribution of the LSF assessed for every 1-d-old mated and unmated female and male cactus moths (mated females, $n = 40$; unmated females, $n = 75$; matted males, $n = 23$; unmated males, $n = 73$). Frequencies of LSF were compared between unmated and mated females and between unmated and mated males for each distance category.

oratory with simulated dawn (Fig. 5). Spontaneous flight activity in mated males and females was low during the photophase. Similarly to unmated females, flight activity reached its maximum at simulated sunset, after which flight decreased gradually to a minimum at the start of the photophase. Both mated and unmated males showed a spike in activity at the end of the scotophase shortly before dawn (Figs. 3 and 5). The full statistical model showed a significant effect of gender ($F = 5.33$; df = 1, 90.5; $P = 0.0233$) but not time ($F = 1.06$; df = 23, 1,167; $P = 0.3802$), with a nonsignificant interaction term ($F = 1.37$; df = 23, 1,167; $P = 0.1120$). Separate analyses of the effect of the time on

the two genders showed that there was a significant change in female flight activity during the diel period ($F = 1.82$; df = 23, 738; $P = 0.0.0109$), whereas male flight did not change over time ($F = 1.26$; df = 23, 428; $P = 0.1926$). Pairwise comparisons of mated male and mated female diel flight activity showed that mated females flew significantly greater distance ($P < 0.05$) during 8 h of the diel cycle, of which all were at dusk or during scotophase (Fig. 3).

In mated moths, similarly to unmated moths, age did not significantly affect any of the flight parameters (TDF: $F = 1.89$; df = 1, 100; $P = 0.1725$; LSF: $F = 2.11$; df = 1, 100; $P = 0.1492$; NOF: $F = 1.98$; df = 1, 100; $P =$
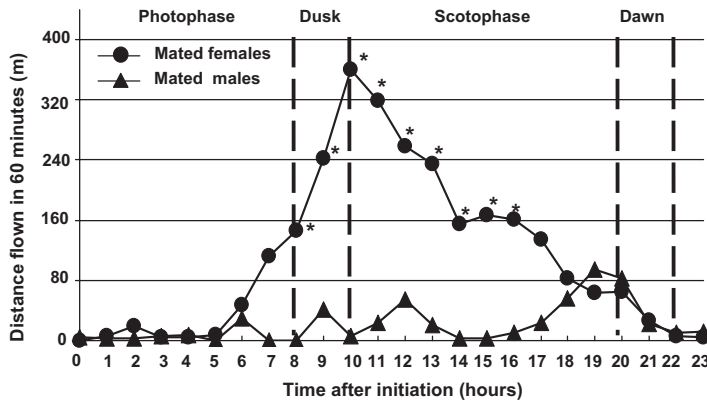

Fig. 5. Diurnal rhythm of flight mill measured average distance flown per hour (meters) by 1-d-old mated male and female *C. cactorum* (for *n*, see Fig. 4). Photointensity amounted to 0.36 lux during scotophase and 3,320 lux during photophase, and it gradually increased and decreased during dusk and dawn, respectively. ANOVA was conducted on the natural log transformed data ($\alpha = 0.05$; ANOVA). Distances flown per hour marked with an asterisk are significantly higher than the flight activity of the other gender in the same hour ($P < 0.05$; Tukey–Kramer LSMeans).

0.1620). There was a slight but significant difference in the TDF within a diel period between mated males and mated females ($F = 4.22$; df $= 1, 100$; $P = 0.0425$), but the interaction term between age and gender was not significant ($F = 3.44$; df $= 1, 100$; $P = 0.0664$). The maximum distance flown during a 24-h trial on the flight mill by an individual mated female was 11.9 km on the first day, and 5.8 km by a mated male on the second day after mating. The LSF in mated moths was not significantly different between the two genders ($F = 0.53$; df $= 1, 100$; $P = 0.4681$), and the interaction term between age and gender also was not significant ($F = 2.56$; df $= 1, 100$; $P = 0.1130$). A larger percentage of the tested mated females ($\chi^2 = 10.08$, df $= 1$, $P = 0.0015$) and males ($\chi^2 = 18.45$, df $= 1$, $P < 0.0001$) flew continuous flights of 20 m or less (short flyers) than 100 m or more (long flyers) (Fig. 4).

The gender ($F = 5.17$; df $= 1, 100$; $P = 0.0251$) of mated adults did not influence the number of take-offs within 24 h. The interaction between age and gender also was not significant ($F = 3.5$; df $= 1, 100$; $P = 0.0642$). Mated females initiated a maximum of 3677 flights at age two, whereas mated males flew the maximum NOF at age 1 d (1,094 take-offs) (Table 1). The regression analysis of TDF and the NOF showed a strong positive correlation between these two flight parameters in mated females [$P < 0.0001$; $r^2 = 0.84$; $\ln(\text{tdf}) = 1.35 + 1.0049(\ln(\text{nof}))$] and mated males [$P < 0.0001$; $r^2 = 0.86$; $\ln(\text{tdf}) = 1.03 + 1.0833(\ln(\text{nof}))$]. The relationship between the TDF and the LSF, similarly to the unmated moths, was weaker in mated females [$P < 0.0001$; $r^2 = 0.61$; $\ln(\text{tdf}) = 2.82 + 1.0490(\ln(\text{lsf}))$] and in mated males [$P < 0.0001$; $r^2 = 0.62$; $\ln(\text{tdf}) = 2.35 + 0.9849(\ln(\text{lsf}))$].

Flight Performance of Mated versus Unmated Moths. NOF, TDF, and LSF by *C. cactorum* were compared for 1-d-old and 2-d-old mated and unmated moths for both genders separately. In females, there was no significant difference between unmated and mated 1-d-old moths (TDF: $F = 1.01$; df $= 1, 113$; $P = 0.3175$; LSF: $F = 0.40$; df $= 1, 113$; $P = 0.5290$; NOF: $F = 1.79$; df $= 1, 113$; $P = 0.1877$) and 2-d-old (TDF: $F = 1.08$; df $= 1, 60$; $P = 0.3031$; LSF: $F = 1.83$; df $= 1, 60$; $P = 0.1812$; NOF: $F = 0.23$; df $= 1, 60$; $P = 0.6124$). Comparison of flight parameters in 1-d-old (TDF: $F = 0.47$; df $= 1, 94$; $P = 0.4955$; LSF: $F = 0.18$; df $= 1, 94$; $P = 0.6734$; NOF: $F = 0.81$; df $= 1, 94$; $P = 0.3714$) and 2-d old (TDF: $F = 0.36$; df $= 1, 53$; $P = 0.5512$; LSF: $F = 1.14$; df $= 1, 53$; $P = 0.2905$; NOF: $F = 0.33$; df $= 1, 53$; $P = 0.5680$) mated and unmated males showed similar results, with no significant differences in either flight parameter.

The comparison of the frequency distribution of LSF showed no difference between mated and unmated females (<5 m: $\chi^2 = 0.00$, df $= 1$, $P = 1.0$; 5–20 m: $\chi^2 = 0.16$, df $= 1$, $P = 0.6872$; 20–100 m: $\chi^2 = 0.00$, df $= 1$, $P = 0.915$; 100–500 m: $\chi^2 = 0.89$, df $= 1$, $P = 0.3447$; and >500 m: $\chi^2 = 0.61$, df $= 1$, $P = 0.7326$) or mated and unmated males (<5 m: $\chi^2 = 0.06$, df $= 1$, $P = 0.7957$; 5–20 m: $\chi^2 = 0.70$, df $= 1$, $P = 0.4022$; 20–100 m: $\chi^2 = 1.36$, df $= 1$, $P = 0.2430$; 100–500 m: $\chi^2 = 0.02$,

df $= 1$, $P = 0.7922$; and >500 m: $\chi^2 = 0.00$, df $= 1$, $P = 1.000$) (Fig. 4).

Discussion

Diel Cycle of Flight in Unmated and Mated Moths. Maximal flight activity of unmated adult males of *C. cactorum* was observed at the beginning of the simulated dawn on the flight mill, which was similar to that observed in the field (Hight et al. 2003). Gatehouse and Hackett (1980) also found close agreement between tethered flight activity and that of adults in the field in another lepidopteran species. The diel pattern of activity documents that the technique is suitable for measuring comparative flight performance in *C. cactorum.* Within the first hour, unmated adults of both genders increased their flight activity indicating that the tethering method did not bias the results after a brief equilibration period. Male moths responded to the increasing light intensity faster than females during dawn, but all moths decreased their flight to a minimum at the beginning of the photophase. Interestingly, only female flight activity continued to increase during dusk, when it was significantly higher than male flight activity. Females were more active during the beginning of the scotophase than males. In the field, male flight activity only increased during dawn when females are calling (Hight et al. 2003), indicating that the primary purpose of male flight is mate finding and it is affected by photointensity. These findings provide new empirical evidence to the yet incomplete knowledge on the diel activity pattern of this crepuscular species.

Diurnal rhythms should be similar between laboratory reared and wild populations in SIT programs. Laboratory populations of several species, such as tobacco budworm, *Heliothis virescens* (F.) (Raulston et al. 1976); olive fruit fly, *Bactrocera olea* (Gmelin) (Zervas and Economopoulos 1982); and Caribbean fruit fly, *Anastrepha suspensa* (Loew) (Calkins and Parker 2005), demonstrated assortative mating in the field after release, due to changes in the temporal mating period in the laboratory. Hence, knowledge of the diel activity of laboratory-reared populations is critical for the successful application of the SIT. Similarities in cactus moth diel activity in the flight mill chamber and in the field suggest that the risk of mating asynchrony between laboratory-reared moths released from this population and wild moths in the southern United States is low.

To understand flight behavior of the cactus moth in a broader context, we further evaluated the diel activity pattern in mated individuals and found it to be similar to that of unmated moths. After mating, female cactus moths again showed significantly higher flight activity than males at dusk and at the beginning of scotophase, males had a relative maximum in their flight activity shortly before dawn. Physiological alterations elicited by mating may explain the slightly changed response of male flight activity to changing photointensity. For example, mating activity triggers physiological changes in adult codling moths—the ju-

venile hormone titer strongly increases (Webb et al. 1999), behaviors change (Kuhrt et al. 2006), and response to exogenous factors resulted in a shift of the diel mobility pattern (Keil et al. 2001b).

Flight Performance of Unmated and Mated Moths. There was no difference in flight performance between age groups within the same gender of the tested young unmated and mated *C. cactorum.* In other lepidopteran species, it has been observed that the onset of oviposition often contributes to decline in flight performance, because there might be a trade-off with resource allocation. In *H. virescens*, oviposition in mated females causes a loss of energy source, lipids in general, which may reduce long flights by older mated females (Willers et al. 1987). In *C. pomonella*, a trade-off between flight and reproduction has been reported (Gu et al. 2006), but concurrent with our study, young mated females had similar flight capacity as the unmated females, and flight performance only decreased a few days after mating (Schumacher et al. 1997b, Dorn et al. 1999). In *C. cactorum,* both genders are able to mate multiple times (Hight et al. 2003), and the current results suggest moths in all of the tested age groups (0–3 d), regardless their mating status, may contribute to the dispersal of this species, threatening uninfested *Opuntia* habitats.

Comparative assessments of TDF and NOF by unmated and mated males and females indicated a greater flight performance by female *C. cactorum.* The LSF did not differ between the two genders in either mated or unmated moths. Total distance flown during a diel period was mainly accomplished by a high number of short distance flights rather than a long continuous flight for both mated and unmated moths in both genders. Short, erratic flights observed in the field suggested that *C. cactorum* is a weak flyer (Zimmermann et al. 2004); however, high numbers of consequent short distance flights may play an important role in the dispersal of this species, as indicated by the strong positive correlation between the TDF and the NOF. Flight mill data for the cactus moth suggest that pheromone trap captures of males likely indicate the simultaneous presence of females and that mated females might even be found in areas where males have not been detected yet. These results resemble the pattern observed in *C. molesta* with longer flights undertaken by females regardless of their mating status (Hughes and Dorn 2002, Hughes et al. 2004) and differs from the pattern observed in *C. pomonella* with similar flight performance of both genders (Schumacher et al. 1997b, Dorn et al. 1999).

Flight performance within the cactus moth population tested herein was highly variable, documenting heterogeneity of the population regarding this behavioral trait. Our results indicated that a limited proportion of the population, both males and females, had the capacity to undertake long-distance dispersal flights, which increases the potential for new habitats to be colonized. A similar pattern of dispersal has been described in three other lepidopteran species. Radiolabeled females of European pine shoot moth, *Rhyacionia buoliana* (Denis & Schiffermüller), were com-

posed of two major activity types: individuals with relatively low activity and individuals with greater activity (Green and Pointing 1962). Similarly, two previous flight mill studies found that both *C. pomonella* and *C. molesta* populations contain a small proportion of long flyers that have the capacity to cover considerable dispersal distances (Schumacher et al. 1997b, Hughes and Dorn 2002). The frequency of long flyers and short flyers was similar in both mated and unmated moths, again suggesting that mated females play an important role in colonizing new habitats.

Body Size and Survival. The current study documents that adult *C. cactorum* moths are relatively short lived. Decrease in body size is likely due to adults of this species not feeding. The first days after release of moths in an SIT program are thus decisive for its success, as has been shown for the codling moth (Bloem et al. 2006). A promising attribute for future SIT is the relatively longer survival of unmated males, which may underlie the success of low overflooding ratio required for cactus moth released in SIT (Hight et al. 2005). The body size of the cactus moths is much larger than the previously studied *Cydia* spp. (Schumacher et al. 1997a, 1997b; Dorn et al. 1999; Hughes et al. 2004); hence, for the purpose of the current study, the flight mill technique had to be adjusted. Sexual dimorphism was marked in *C. cactorum*, because newly eclosed females weighed an average 80% more than males. Starting from our measurements, future research may establish a threshold value of adult and pupal body size below which males can be effectively separated from females. Although this threshold value may be used in experiments, the current SIT protocol is to release mixed genders of sterile *C. cactorum*, because it provided a more successful control in field cage studies than did the release of males only (Hight et al. 2005). There was no correlation between adult weight and flight performance in females in contrast to males, but because the correlation between male body size and flight performance (total distance flown and longest single flight) was not very strong, further studies are required before conclusions for SIT can be drawn.

General Conclusions for SIT Programs. Several findings are of particular relevance for field applications. First, unmated males live longer than unmated females, increasing the probability of a successful mating between a released male with a wild female. Second, the capture of males, both close to and distant from established populations, likely indicates the presence of females. Because only a small percentage of females are long-distance fliers, dispersal by this mechanism will become more likely and problematic as an infestation grows and the population increases. As such, we postulate that short distance spread of an infestation mainly occurs through the accumulation of nightly short distance flights, but that longer distance dispersal such as that needed to overcome areas where host plants do not occur, is likely accomplished by long-distance flights of mated females. Future research will be needed to verify this postulate. Finally,

mating did not limit flight performance; therefore, the appearance of already mated females, as colonizers in new habitats, may indicate a new challenge in the control of the cactus moth.

Acknowledgments

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