

# Identification of Factors Influencing Flight Performance of Field-Collected and Laboratory-Reared, Overwintered, and Nonoverwintered Cactus Moths Fed with Field-Collected Host Plants

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**ABSTRACT** Environmental conditions during egg and larval development may influence the dispersal ability of insect pests, thus requiring seasonal adjustment of control strategies. We studied the longest single flight, total distance flown, and the number of flights initiated by wild *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) to determine whether the flight performance of overwintered cactus moths with a prolonged feeding phase during development differs from nonoverwintered cactus moths. Pupae of field-collected and laboratory-reared moths were transported together from the United States to Switzerland, and flight mills were used to characterize the flight capacity of 24- to 48-h-old adults during their most active period of the diel cycle. The lack of seasonal variation in flight performance of those moths that developed under controlled environment but were fed with field-collected *Opuntia* cacti showed that seasonal changes in host plant quality did not affect flight. This consistent flight performance in the mass-reared laboratory population throughout the year is beneficial for sterile insect technique programs, which aim to limit the dispersal of this pest. For field-collected *C. cactorum*, the larger overwintered females performed similarly to nonoverwintered females, indicating that longer feeding time at lower temperature increases body size but does not influence female flight capacity. Young mated females had a similar flight capacity to unmated ones, suggesting that gravid females may play an important role in invading new habitats. For males, overwintering increased the proportion of long-distance flyers, suggesting that they are well-adapted to locate the more sparsely dispersed females in the spring.

**KEY WORDS** *Cactoblastis cactorum*, dispersal, flight, overwintering, seasonality

Environmental conditions to which Lepidoptera eggs and larvae are exposed during development are known to affect flight performance and fitness for some species in the adult stage (Willers et al. 1987, Hughes et al. 2004). Wild populations are exposed to seasonal changes and may be able to modify their behavior, including dispersal, by responding to changing biotic and abiotic cues. The primary abiotic indicators of seasonal time for the preimaginal phase of Lepidoptera are the changes in photoperiod (Han and Gatehouse 1991, Masaki and Kimura 2001) and tem-

perature (Beck 1980, Denlinger et al. 2001). Seasonal variation of adult morphology has been observed in 10 Lepidoptera species (Fric and Konvicka 2002, Van Dyck and Wiklund 2002, Fric et al. 2006), suggesting that moths developing as larvae during winter may differ in flight performance from those that develop later in the season. For example, overwintering increased the size and the flight distance of the diamondback moth, *Plutella xylostella* L. (Shirai 1991), whereas temperature and length of photoperiod during development strongly influenced the migratory potential of the oriental armyworm, *Mythimna separata* (Walker) (Lepidoptera: Noctuidae) (Han and Gatehouse 1991). In addition to abiotic cues, biotic factors such as differences in food quality during larval development caused by host plant choice (Carriere 1992, Mafokoane et al. 2007) or seasonal fluctuation of nutritional values (Scheermeyer et al. 1990) can affect fitness in Lepidoptera. Availability and quality of food sources can be crucial for insect flight performance (Willers et al. 1987, Wanner et al. 2006).

*Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), a native insect to northern Argentina, Uruguay, Paraguay, and southern Brazil (Carpenter et al. 2001,

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Bloem et al. 2005), became an invasive pest in the United States in the 1990s (Pemberton 1995, Stiling and Moon 2001, Hight et al. 2002). Depending on climatic conditions, *C. cactorum* can complete two or three generations per year (Zimmermann et al. 2004). The rapid geographical expansion of the cactus moth is a threat to endemic prickly pear cacti (*Opuntia* spp.) (Rebman and Pinkava 2001, Stiling and Moon 2001, Hight et al. 2002). In Mexico, where *Opuntia* cacti are important as human food, livestock fodder, and as keystone species in many ecosystems, *C. cactorum* will have serious economic and ecological impacts if left untreated (Zimmermann et al. 2004). The majority of adult moths perform many short flights in both the field (Zimmermann et al. 2004) and in the laboratory, whereas only few laboratory-reared cactus moths perform long single flights (Sarvary et al. 2008).

Use of the sterile insect technique (SIT) to limit further geographical expansion of this moth has shown much promise (Bloem et al. 2007). SIT is a pest management tactic that has great potential in the control of many economically important Lepidoptera such as the cabbage looper *Trichoplusia ni* (Hübner) (North and Holt 1969), pink bollworm *Pectinophora gossypiella* (Saunders) (Henneberry and Clayton 1981, Henneberry 1993), codling moth *Cydia pomonella* L. (Proverbs et al. 1982, Bloem et al. 1999), and corn earworm *Helicoverpa zea* (Boddie) (Mannion et al. 1995). Current SIT programs rely on rearing large numbers of target pest species, on sterilizing them with gamma radiation, and on releasing them into the target population (Carpenter et al. 2005, Klassen 2005). Success of the SIT can be influenced by whether or not both wild and released pest populations have similar dispersal characteristics (Lance and McInnis 2005, Vreysen 2005, Bloem et al. 2006a, b). In the field, the characterization and comparison of flight behavior of wild Lepidoptera populations is difficult, because external stimuli such as pheromones can affect flight behavior (Knight 2000). Computer-linked flight mills (Hughes and Dorn 2002, Sarvary et al. 2008) have been successfully used in comparative studies to assess the flight performance of different insect species with the exclusion of extrinsic stimuli, measuring only the intrinsic flight capacity (Bradley and Altizer 2005, Shirai 2006, Wu et al. 2006). In flight mills, individuals are tethered and allowed to fly in a circle of known circumference while a linked computer records each rotation. This information is used to calculate parameters describing an individual's flight performance (Schumacher et al. 1997, Wanner et al. 2006). Quantitative comparisons of flight on flight mills have been carried out with many economically important Lepidoptera, such as the codling moth, *C. pomonella* (Schumacher et al. 1997), the oriental fruit moth, *Cydia (Grapholita) molesta* (Busck) (Hughes and Dorn 2002, Hughes et al. 2004), the pink bollworm, *Pectinophora gossypiella* (Wu et al. 2006), the monarch butterfly, *Danaus plexippus* L. (Bradley and Altizer 2005), the corn earworm, *H. zea* (Beerwinkle et al. 1995), the cotton bollworm, *Helicoverpa armigera* Hübner (Cooter and Armes 1993),

the fall webworm, *Hyphantria cunea* (Drury) (Yamanaka et al. 2001), as well as laboratory-reared cactus moth (Sarvary et al. 2008). Flight performance was investigated based on the total distance flown (TDF), the longest single continuous flight (LSF), and the number of flights initiated (NOF). These parameters have been previously used to describe flight performance of tethered *Cotesia glomerata* L. (Wanner et al. 2006), *C. pomonella* (Schumacher et al. 1997, Dorn et al. 1999), *C. molesta* (Hughes and Dorn 2002, Hughes et al. 2004), and laboratory-reared *C. cactorum* (Sarvary et al. 2008).

Temperature regimens experienced by *C. cactorum* during its preimaginal phase were recently shown to influence adult fitness and survivorship under laboratory conditions (Legaspi and Legaspi 2007). In particular, pupal weight and adult female longevity declined with increasing temperature. Along coastal northern Florida, where this insect is abundant, overwintering eggs and larvae are exposed to average temperatures of 10–15°C, whereas temperatures prevalent during subsequent generations typically fluctuate between 18 and 26°C (National Climatic Data Center, Tallahassee, FL). In laboratory life-table studies, development (from egg to pupae) lasted 130 d at 18°C, and this period was reduced to 90 d at 22°C and to 55 d at temperatures between 26 and 34°C (Legaspi and Legaspi 2007). These data suggest that differences in abiotic conditions under which overwintering and nonoverwintering immature stages develop in the field could influence adult fitness and perhaps flight performance. As larvae continue to feed in winter, we cannot exclude that changing host plant quality may further influence adult flight performance. Seasonal variation in *Opuntia* quality has been shown previously (Koch and Kennedy 1980, Retamal et al. 1986, Inglese et al. 1999, Pimienta-Barrios et al. 2000, Orona-Castillo et al. 2004) and seems to be affected by photoperiod, availability of water (Sutton et al. 1981, Lerdau et al. 1992), and fluctuations in temperature (Littlejohn and Williams 1983).

The main objective of this study was to determine whether overwintered cactus moths, which likely experienced a prolonged feeding phase during larval development, differ in flight performance from those measured for nonoverwintered moths collected in the same field area. Laboratory-reared cactus moths fed with field-collected *Opuntia ficus-indica* L. Mill. (i.e., the host plant that was subject to seasonal change) were used as a control and tested simultaneously in these experiments. Adult body size was measured, the diel pattern of flight activity was assessed, and flight performance was characterized in relation to age, gender, and mating status using computer-linked flight mills. Body size, mating status, age, and gender were factors used to explain the variability in flight behavior.

## Materials and Methods

**Test Insects.** A laboratory colony of *C. cactorum* that originated from field collections in Florida and Geor-

gia in 2002 has been maintained at the USDA-ARS rearing facility in Tifton, GA, for 12–13 generations. Eggsticks were incubated in growth chambers (26°C, 70% RH), and neonates were placed on excised cactus pads (26°C, <20% RH) collected from an *Opuntia* plantation adjacent to the insect rearing facility. These *O. ficus-indica* plants were exposed to naturally changing environmental conditions. For this experiment, 200 *C. cactorum* pupae of each gender were randomly selected once per week from the laboratory colony (spring: 30 March–5 May; summer: 9 July–3 August). Wild insects used in this experiment were collected at Okaloosa Island, FL. For the overwintering population, pads of *O. ficus-indica* containing late-instar larvae were harvested between 27 February and 21 March 2007. The nonoverwintered larval population was collected at the same location from 14 to 27 June 2007. Collected larvae were transferred to screened boxes (1.2 by 0.9 by 0.3 m) and provided with excised *O. ficus-indica* pads and kept under ambient outdoor temperature at St. Marks National Wildlife Refuge near Tallahassee, FL, until all larvae pupated. Infested pads were periodically transferred to new boxes, but pupae remained behind to fully sclerotize before they were removed. Pupae hardened within 2–7 d. The silk cocoons of both laboratory and wild pupae were carefully removed by hand, the pupae were sorted by gender, and each gender was placed in a separate plastic petri dish (14 cm diameter). Field-collected and laboratory-reared pupae were flown to ETH, Institute of Plant Sciences/Applied Entomology, Zurich, Switzerland. Each shipment (nine total shipments) arrived within 2 d of departure. To ensure that flight performance differences measured in the laboratory were not confounded by the effects of conditions experienced during transport, temperature and humidity were measured by an electronic data logger (HOBO, Onset Bourne, MA) included with each shipment. Within 12 h of their arrival in Switzerland, the pupae were placed on filter paper inside 30 by 30 by 30-cm emergence cages (BugDorm; Megaview Science Education, Taichung, Taiwan) in a controlled environment room (28°C, 70% RH, 12 L:12 D). Pupae and adults were maintained in separate cages by colony (field-collected or laboratory-reared), shipment, and gender (male or female). Shipments 1–5 included laboratory-reared moths (laboratory 1) and overwintered field-collected moths, whereas shipments 6–9 contained laboratory-reared moths (laboratory 2) and nonoverwintered moths. This terminology will be used herewith to describe the moths of the two shipment groups.

**Adult Body Size.** Within 24 h of their eclosion 20–25 male and female laboratory-reared and field-collected *C. cactorum* adults were randomly selected from each shipment. After recording their individual weights (AB204 scale [range: 0.1 mg to 220 g]; Mettler, Küssnacht, Switzerland), they were returned to their emergence cages and used in the flight experiments.

**Flight Mill Techniques.** Emergence cages of both genders were checked daily for adult eclosion. Moths were collected within 24 h of eclosion, and all newly

emerged moths were placed into one cage and allowed to mate at random for 24–48 h. Cross-breeding between wild and laboratory colonies or between different shipments of the same colony was not allowed.

**Tethering.** Tethering took place at 4°C to immobilize the moths. Moths were kept at this low temperature for <45 min. Using 00 size insect pins, 20 by 5-mm paper strips were pinned to a polystyrene tray, and a pinhead-size drop of fast drying solvent-free glue (Migros, Zurich, Switzerland) was placed on the end of each paper strip. The dorsal side of the thorax and abdomen of each moth was placed on this glued surfaced of a paper strip without allowing tarsal or wing contact with the paper or the glue. The glue dried within 30–60 s at 4°C. Moths attached to pin-held strips were moved to the flight mill room (Conviron, PGV 36; Controlled Environments, Winnipeg, Manitoba, Canada) where 24 flight mills were set up operating in tandem under 28°C and 70% RH.

**Flight Mill Mechanics.** Moth flight was monitored individually over a diel cycle. During scotophase (10 h) light was maintained at 0 lux. Simulated dawn was composed of a 2-h long linear increase of light intensity between 0 and 4,000 lux. Photophase was maintained at 4000 lux for 10 h. Simulated dusk (2 h), similarly to dawn, was a linear change of light intensity from 4000 to 0 lux. The set-up and the mechanics of the flight mills were identical to those described in Sarvary et al. (2008).

**Data Analysis.** In the flight mills, artificially elevated counts can occur when the reflective surface of the flight arm rests in the path of the transmitter/receiver. If recorded signals occurred more than twice within the same second, they were eliminated by a specifically developed analytical program (M. Gernss, ETH). Flight consisted of a sequence of revolutions and breaks. A new flight was started if the break between two consecutive revolutions was 2 s or higher. These settings were based on the observations that cactus moths on the flight mill fly a minimum of one revolution per 2 s and a maximum of two revolutions per second. All flights had to last at least 2 s; therefore, a single revolution was considered a break, unless another revolution followed it within 2 s. To decrease the size of the data set, analysis was limited to the 14 h (dusk, scotophase, dawn) that included the periods with major flight activity, i.e., deleting the 10-h period with full light conditions where minimal activity was previously measured (Sarvary et al. 2008).

Flight capacity was characterized using LSF, TDF, and NOF. The effect of age on the flight performance of unmated and mated moths was measured on 24- to 48-h-old moths. Before statistical analysis, the data were log transformed for each model to meet the assumption of normality. The data were unbalanced (not the same number of moths from each category flew each time) and thus were analyzed using restricted maximum likelihood models (Littell et al. 1996) with PROC MIXED procedure in SAS (SAS Institute 2000). Degrees of freedom were calculated using the method described by Kenward and Roger (1997). Differences between adult weights were

**Table 1.** Body size (mean  $\pm$  SEM) in milligrams of overwintered and nonoverwintered newly emerged *C. cactorum*

Gender	Origin	Weight (mg) <sup>a</sup>			
		Overwintered <sup>b</sup>	n	Nonoverwintered <sup>b</sup>	n
Females	Field-collected	130.6 $\pm$ 3.8a	76	91.5 $\pm$ 3.1b	81
	Laboratory-reared	65.2 $\pm$ 1.5c	70	66.5 $\pm$ 2.1c	75
Males	Field-collected	67.9 $\pm$ 1.6c	76	43.6 $\pm$ 1.4d	71
	Laboratory-reared	39.5 $\pm$ 0.9d	44	39.2 $\pm$ 1.1d	75

<sup>a</sup> Weight of adults was measured within 24 h from eclosion. Means and their SEs were obtained from the untransformed dataset.

<sup>b</sup> Means followed by different letters are significantly different (Tukey-Kramer LS means,  $P < 0.05$ ).

tested using analysis of variance (ANOVA) with the PROC GLM procedure in SAS (SAS Institute 2000). If significant main effects were detected by the models, pairwise comparisons were performed between treatments using least square means separated by the Tukey-Kramer procedure with the LSMEANS command (Littell et al. 1996). Because means and their SEs calculated from the log-transformed data are not meaningful in data visualization, the actual means and their SEs calculated from untransformed data using the PROC MEANS statement (SAS Institute 2000) are presented (Tables 1 and 2). Frequency distribution of the LSF of overwintered ( $n = 70$ ) and nonoverwintered ( $n = 48$ ) 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 the  $\chi^2$  test (SAS Institute 2000).

## Results

**Adult Body Size.** Overwintered field-collected moths were significantly larger than nonoverwintered moths ( $F = 13.09$ ;  $df = 1,303$ ;  $P < 0.0001$ ), irrespective of gender ( $F = 182.12$ ;  $df = 1,303$ ;  $P = 0.13$ ; Table 1). In contrast, laboratory-reared moths from the categories tested in parallel with overwintered (laboratory 1) and nonoverwintered (laboratory 2) moths did not differ significantly in body size ( $F = 0.13$ ;  $df = 1,263$ ;

$P = 0.72$ ) in females or in males ( $F = 13.09$ ;  $df = 1,263$ ;  $P = 0.58$ ; Table 1). Field-collected insects tended to be larger than laboratory-reared insects (except for nonoverwintered males). Females were always larger than males from the same origin (Table 1).

**Pooling Data: Influence of Mating Status on Flight Capacity in Categories of Moths.** Data were analyzed separately for overwintered and nonoverwintered males and females, as well as for the categories laboratory 1 and laboratory 2. Data from the two mating status groups were pooled for field-collected nonoverwintered males because differences between mated and unmated moths were not significant (TDF:  $F = 1.38$ ;  $df = 1,45$ ;  $P = 0.24$ ; LSF:  $F = 0.87$ ;  $df = 1,45$ ;  $P = 0.35$ ; NOF:  $F = 0.52$ ;  $df = 1,36.1$ ;  $P = 0.47$ ). In nonoverwintered, field-collected, female moths the mating status also did not significantly affect any of the flight parameters tested (TDF:  $F = 0.13$ ;  $df = 1,105$ ;  $P = 0.71$ ; LSF:  $F = 0.07$ ;  $df = 1,105$ ;  $P = 0.74$ ; NOF:  $F = 0.38$ ;  $df = 1,105$ ;  $P = 0.53$ ).

In field-collected overwintered males, the data did not differ by mating status (TDF:  $F = 0.23$ ;  $df = 1,63.6$ ;  $P = 0.63$ ; LSF:  $F = 0.08$ ;  $df = 1,62.1$ ;  $P = 0.78$ ; NOF:  $F = 0.11$ ;  $df = 1,67$ ;  $P = 0.74$ ). Similarly, the flight performance of overwintered females was not different for mated and unmated individuals (TDF:  $F = 0.37$ ;  $df = 1,77.7$ ;  $P = 0.54$ ; LSF:  $F = 0.02$ ;  $df = 1,77.5$ ;  $P = 0.89$ ; NOF:  $F = 1.59$ ;  $df = 1,77.1$   $P = 0.21$ ).

**Table 2.** Flight capacity parameters (mean  $\pm$  SEM) of *C. cactorum* in respect to origin and gender of adult moths

Flight parameter	Origin	Female <sup>a</sup>	n	Male <sup>a</sup>	n
<i>Overwintered C. cactorum</i>					
Total distance flown (m)	Field-collected	2,648.6 $\pm$ 495.2ab	81	1,488.8 $\pm$ 287.0bc	70
	Laboratory 1	2,495.1 $\pm$ 454.4a	64	1,227.6 $\pm$ 380.6c	57
Longest single flight (m)	Field-collected	375.8 $\pm$ 137.0ab	81	196.1 $\pm$ 76.8bc	70
	Laboratory 1	143.8 $\pm$ 30.1a	64	285.3 $\pm$ 170.3c	57
No. flights	Field-collected	315.5 $\pm$ 54.3ab	81	217.8 $\pm$ 47.1bc	70
	Laboratory 1	341.5 $\pm$ 59.2a	64	134.2 $\pm$ 27.1c	57
<i>Nonoverwintered C. cactorum</i>					
Total distance flown (m)	Field-collected	3,301.0 $\pm$ 496.2a	108	770.6 $\pm$ 175.2b	48
	Laboratory 2	1,864.4 $\pm$ 335.5ab	49	1,426.2 $\pm$ 646.2c	37
Longest single flight (m)	Field-collected	219.9 $\pm$ 50.8a	108	31.3 $\pm$ 13.5bc	48
	Laboratory 2	114.2 $\pm$ 32.8ab	49	71.7 $\pm$ 30.2c	37
No. flights	Field-collected	489.8 $\pm$ 69.0a	108	218.7 $\pm$ 52.7ab	48
	Laboratory 2	421.5 $\pm$ 80.3a	49	157.2 $\pm$ 61.4b	37

Field-collected overwintered and nonoverwintered moths are compared with laboratory 1 and laboratory 2 moths, respectively, fed with host plants from the field (grown at the same time as the food for overwintered and nonoverwintered moths).

Effects were measured using mixed models (ANOVA,  $\alpha = 0.05$ ) on the log-transformed data.

<sup>a</sup> Means and their SEs were obtained from the untransformed dataset. Means followed by different letters within each flight parameter are significantly different (Tukey-Kramer LS means,  $P < 0.05$ ).

**Table 3.** Flight capacity parameters (mean ± SEM) of field-collected overwintered compared with nonoverwintered *C. cactorum* moths and of laboratory 1 compared with laboratory 2 moths fed with host plants from the field (grown at the same time as the food for overwintered and non-overwintered moths, respectively)

Origin	Gender	Total distance flown (m)		Longest single flight (m)		No. flights	
		Overwintered <sup>a</sup>	Nonoverwintered <sup>a</sup>	Overwintered <sup>a</sup>	Nonoverwintered <sup>a</sup>	Overwintered <sup>a</sup>	Nonoverwintered <sup>a</sup>
Field collected	Female	2648.6 ± 495.6a	3,301.0 ± 496.7a	375.8 ± 137.1a	219.9 ± 51.1a	315.5 ± 54.0a	489.8 ± 69.6a
	Male	1488.8 ± 287.2a	770.6 ± 175.4a	196.1 ± 76.1a	31.3 ± 14.0b	217.8 ± 47.5a	218.7 ± 53.5a
		Laboratory 1 <sup>a</sup>	Laboratory 2 <sup>a</sup>	Laboratory 1 <sup>a</sup>	Laboratory 2 <sup>a</sup>	Laboratory 1 <sup>a</sup>	Laboratory 2 <sup>a</sup>
Laboratory reared	Female	2495.1 ± 454.3a	1,864.4 ± 336.0a	143.8 ± 29.3a	114.2 ± 33.4a	341.5 ± 59.1a	421.5 ± 80.1a
	Male	1227.6 ± 380.1a	1,426.2 ± 646.2a	285.3 ± 170.2a	71.7 ± 30.0a	134.2 ± 27.8a	157.2 ± 61.6a

Effects were measured using mixed models (ANOVA,  $\alpha = 0.05$ ) on the log-transformed data. Comparisons were made within genders, within each origin.

<sup>a</sup> Means and their SEs were obtained from the untransformed dataset. Means followed by different letters within rows of each flight parameter column are significantly different (Tukey-Kramer LS means,  $P < 0.05$ ). For *n*, see Table 2.

In laboratory-reared males (laboratory 1), which were tested in parallel to overwintered moths, the effect of mating status could not be analyzed separately, because sample sizes of mated males were too low ( $n = 5$ ). In laboratory 1 females, mating status did not influence TDF and NOF (TDF:  $F = 0.17$ ;  $df = 1,60.1$ ;  $P = 0.67$ ; NOF:  $F = 0.22$ ;  $df = 1,60.6$ ;  $P = 0.63$ ). The LSF in mated females was higher than in unmated females ( $F = 4.15$ ;  $df = 1,58.8$ ;  $P = 0.046$ ), but this difference was minimal, with the significance being very close to the  $P = 0.05$  cut-off point.

Data collected from laboratory-reared males (laboratory 2) that were tested in parallel to nonoverwintered moths were also pooled by mating status (TDF:  $F = 0.01$ ;  $df = 1,32.7$ ;  $P = 0.97$ ; LSF:  $F = 0.09$ ;  $df = 1,32.6$ ;  $P = 0.76$ ; NOF:  $F = 0.11$ ;  $df = 1,34$ ;  $P = 0.74$ ), because differences were not significant. In the laboratory 2 category, there were no differences in TDF ( $F = 3.71$ ;  $df = 1,45.5$ ;  $P = 0.06$ ) and LSF between mated and unmated females ( $F = 0.17$ ;  $df = 1,4.77$ ;  $P = 0.66$ ); however, mating status had a significant effect on the NOF by these females ( $F = 5.06$ ;  $df = 1,45.8$ ;  $P = 0.029$ ). Because two of the three parameters were not significantly different, the data were again pooled in further comparisons.

**Comparison of Field-collected Versus Laboratory-reared Moths.** Field-collected overwintered moths did not differ significantly from laboratory 1 moths in any of the three flight parameters (TDF:  $F = 0.02$ ;  $df = 1,259$ ;  $P = 0.88$ ; LSF:  $F = 0.03$ ;  $df = 1,264$ ;  $P = 0.86$ ; NOF:  $F = 0.01$ ;  $df = 1,224$ ;  $P = 0.94$ ). This was true for both females and males (Table 2). In addition, field-collected nonoverwintered moths performed similarly to the laboratory 2 moths in the three flight parameters (TDF:  $F = 3.55$ ;  $df = 1,72.8$ ;  $P = 0.063$ ; LSF:  $F = 1.5$ ;  $df = 1,75.5$ ;  $P = 0.22$ ; NOF:  $F = 2.16$ ;  $df = 1,20.3$ ;  $P = 0.15$ ) in both genders, except for a difference ( $P = 0.0311$ ) between nonoverwintered field-collected and laboratory-reared males in TDF (Table 2).

Female moths originating from the nonoverwintered field collected and the laboratory 1 and laboratory 2 categories outperformed male moths within their origin under the conditions of the experiment (Tables 2), with one exception in the NOF in non-overwintered field-collected moths ( $t = 1.75$ ;  $df =$

1,235;  $P = 0.081$ ). Overwintered field-collected females numerically outperformed overwintered males in all flight parameters, but these differences were not significant (Table 2).

**Comparison of Laboratory 1 Versus Laboratory 2 Moths.** The two categories of laboratory-reared moths tested in parallel with the field-collected moths did not differ in any of the three flight parameters in females (TDF:  $F = 0.97$ ;  $df = 1,111$ ;  $P = 0.32$ ; LSF:  $F = 1.53$ ;  $df = 1,111$ ;  $P = 0.21$ ; NOF:  $F = 0.03$ ;  $df = 1,111$ ;  $P = 0.87$ ) or in males (TDF:  $F = 0.65$ ;  $df = 1,92$ ;  $P = 0.42$ ; LSF:  $F = 0.92$ ;  $df = 1,92$ ;  $P = 0.33$ ; NOF:  $F = 0.36$ ;  $df = 1,92$ ;  $P = 0.54$ ; Table 3). Because no differences were detected between laboratory 1 and laboratory 2 moths that consumed field-grown cactus but were reared under constant indoor conditions, the seasonal change of host food quality likely does not affect *C. cactorum* flight. Thus, the direct comparison of wild moths collected in the field at different times of the year would demonstrate the effect of the change in environmental conditions between seasons and not host plant quality. The results from the comparison of the two laboratory-reared moth categories allow for direct comparison of overwintered and nonoverwintered field-collected moths without any confounding effect of seasonal food quality change.

**Comparison of Overwintered Versus Nonoverwintered Moths.** In females, there was no significant difference between field-collected overwintered and nonoverwintered moths in any flight parameter (TDF:  $F = 0.94$ ;  $df = 1,187$ ;  $P = 0.36$ ; LSF:  $F = 0.01$ ;  $df = 1,187$ ;  $P = 0.93$ ; NOF:  $F = 2.08$ ;  $df = 1,187$ ;  $P = 0.15$ ). Male overwintered and nonoverwintered moths had similar values for TDF ( $F = 0.56$ ;  $df = 1,116$ ;  $P = 0.45$ ) and NOF ( $F = 0.14$ ;  $df = 1,116$ ;  $P = 0.71$ ); however, the LSF was significantly higher in overwintered than in non-overwintered males ( $F = 6.43$ ;  $df = 1,116$ ;  $P = 0.012$ ; Table 3). This difference was further analyzed by comparing the frequency distribution of the LSF flown by field-collected males (Fig. 1). Up to 70.8% of the nonoverwintered males flew 20 m and less during the analyzed time period, whereas in overwintered males, this frequency was only 50.0%, a significant difference ( $\chi^2 = 5.08$ ;  $df = 1$ ;  $P = 0.024$ ). Moreover, only 2.0% of the nonoverwintered moths flew 100 m or

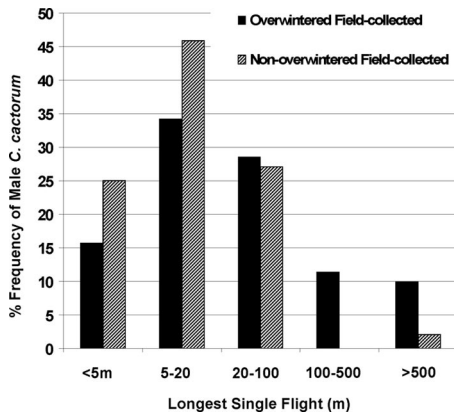


Fig. 1. Frequency distribution of the longest single flight of overwintered ( $n = 70$ ) and nonoverwintered ( $n = 48$ ) field-collected male *C. cactorum*.

longer in their LSF, whereas a significantly larger percentage of the overwintered moths (21.4%) flew this distance ( $\chi^2 = 9.09$ ;  $df = 1$ ;  $P = 0.002$ ; Fig. 1).

### Discussion

Environmental changes experienced during development affect flight performance in some lepidopteran species (Shirai 1991, Fric and Konvicka 2002, Hughes et al. 2004); however, such potential effects were yet unknown for *C. cactorum*, an invasive pyralid herbivore in the southeastern United States. Variations in environmental conditions are known to influence fitness parameters of *C. cactorum* (Petty 1948, Legaspi and Legaspi 2007). We tested the hypothesis that body size and flight performance of overwintered and nonoverwintered *C. cactorum* moths differ, and our findings should help to fine tune the application of SIT strategies that have been developed to manage the geographical expansion of this pest (Bloem et al. 2007).

**Adult Body Size.** All laboratory-reared moths used in this study developed at controlled, constant conditions at 26°C and were fed excised cladodes from naturally grown *Opuntia*. The body size of the laboratory 1 moths (tested in parallel to overwintered moths) and laboratory 2 moths (tested in parallel to nonoverwintered moths) did not differ significantly within gender. Seasonal changes may occur in *Opuntia* cactus nutritional value (Retamal et al. 1986, Orona-Castillo et al. 2004), but this variation did not seem to affect the body size of moths that developed under constant laboratory temperature and humidity.

Field-collected overwintered *C. cactorum* had experienced average monthly temperatures of 10–15°C in their egg and larval stage, whereas nonoverwintered ones experienced an average temperature of 18–26°C. Field-collected *C. cactorum* that had developed at lower temperatures (overwintered) reached larger body size in their adult stage than those that had developed at higher temperatures (nonoverwintered). These results parallel and verify recent labo-

ratory findings showing that adults of both genders were smaller after development at 26°C than at 22°C (Legaspi and Legaspi 2007). Consistently, all data from the current and previous investigations (Legaspi and Legaspi 2007) strongly support the postulate that *C. cactorum* adult body size is dependent on temperature during development. Because seasonal changes in the *Opuntia* quality did not seem to affect body weight, it is likely that the longer developmental period at lower temperatures, hence a prolonged feeding larval stage, led to the larger body size of overwintered moths. Higher pupal weight may result in increased fecundity in Lepidoptera (Carriere 1992), whereas the length of development is positively correlated to the exposure time of vulnerable larval stages to natural enemies (Feeny 1976, Benrey and Denno 1997). Field-collected moths always reached larger body size than laboratory-reared moths, regardless of the season. This difference is most likely caused by feeding conditions encountered by larvae. Although field-collected *C. cactorum* had been exposed to unlimited food on a cactus plant, laboratory-reared larvae were supplied excised cladodes in a growth chamber. Sexual dimorphism for size was shown in both field-collected and laboratory-reared moths, because females always reached larger body size than males. Recently published data showing this difference in laboratory-reared moths are in support of these findings (Legaspi and Legaspi 2007, Sarvary et al. 2008).

**Flight Capacity.** Analysis of the data collected by the electronic data logger showed no evidence that either overwintered or nonoverwintered *C. cactorum* pupae were exposed to extreme temperature or humidity during transportation from the United States to Switzerland. On the flight mill, the larger field-collected moths did not outperform the smaller laboratory-reared moths. This finding provides important information for SIT programs where mass-reared *C. cactorum* moths are being released to mate with wild moths (Carpenter et al. 2005, Klassen 2005). The efficiency of SIT programs relies on comparable flight abilities between the released and targeted populations (Lance and McInnis 2005, Vreysen 2005, Bloem et al. 2006a). This study indicated a consistent body size and level of flight performance in the laboratory-reared population of moths, irrespective of the time of the year they were reared. Therefore, provided that the dose of irradiation used to treat the moths does not negatively affect their flight capacity (Bloem et al. 2006b), laboratory-reared *C. cactorum* of the present quality are expected to successfully compete in dispersal with wild populations during the implementation of SIT programs (Carpenter et al. 2001, Bloem et al. 2007). Variability in the food quality (Retamal et al. 1986, Orona-Castillo et al. 2004) or other uncontrolled seasonal changes did not affect flight performance of the laboratory-reared moths; thus, the comparison of overwintered and nonoverwintered field-collected moths directly reflects the effect of the abiotic conditions that eggs and larvae were exposed.

Adult *C. cactorum* are not capable of feeding; hence, the larger body size that overwintered females

reached after their longer feeding period might allow increased mobility, similarly to what has been postulated based on body mass quantification in several Lepidoptera species (Shirai 1991, Fric and Konvicka 2002, Fric et al. 2006). However, adult females flew similar distances regardless of the season, suggesting that overwintering does not increase dispersal ability for this species.

In contrast, adult overwintered males were able to perform longer single flights than smaller, nonoverwintered males, indicating an effect of the altered abiotic conditions the overwintered males had experienced as eggs and larvae in the field. In the oriental fruit moth a decrease in photoperiod and temperature during larval development was correlated with an increase of the longest single flight (Hughes et al. 2004). In this study, differences between the overwintered and nonoverwintered *C. cactorum* male flight were caused by a seasonal shift in the proportion of long flyers and short flyers. Although almost a quarter of the overwintered field-collected males performed longest single flights of 100 m or greater, in nonoverwintered males only 2% of the population flew this distance without interruption. In earlier studies, both the codling moth (Schumacher et al. 1997) and laboratory-reared cactus moth populations (Sarvary et al. 2008) showed strong heterogeneity for flight, consisting of both short and long flying individuals. The ability to continuously fly long distances can be advantageous to overwintered males. Adult cactus moths eclose 1–2 h after sunset with males, emerging  $\geq 1$  d before females (Petty 1948) to maximize their mating success by being present when the females emerge. Petty (1948) observed that longevity of overwintered moths was substantially higher and the period of their emergence was 10–17 d longer than in nonoverwintered moths. Consequently, provided that brood sizes of overwintered and nonoverwintered *C. cactorum* in the field are similar, the density of female moths on any given day is lower for the winter brood than for the summer brood. Hence, overwintered males are required to perform longer flights to successfully locate the more sparsely distributed overwintered females. For nonoverwintered males, long single flights are less necessary because of higher female densities.

*Cactoblastis cactorum* males had similar or weaker flight capacity than females, providing further evidence of the previous postulate that male captures in pheromone traps likely indicate the simultaneous presence of females (Sarvary et al. 2008). Mating did not limit the flight performance of young female and male cactus moths, similarly to several other Lepidoptera, such as the oriental tea tortrix, *Homona magnanima* Diakonoff (Shirai 1998), smaller tea tortrix, *Adoxophyes honmai* (Yasuda) (Shirai and Kosugi 2000), and the peach fruit moth, *Carposina sasakii* Matsumura (Ishiguri and Shirai 2004). Hence, wild *C. cactorum*, including in particular young mated females, hold the potential to colonize new habitats, similar to what has been suggested for oriental fruit moth based on comparative laboratory studies (Hughes and Dorn 2002).

**Overall Conclusions.** The main objective of this study was to test whether seasonal changes in environmental conditions during egg and larval development affect flight performance of *C. cactorum* adults. Seasonal changes in *Opuntia* quality did not adversely affect flight, and this consistency in the flight performance of the mass-reared laboratory population throughout the year is beneficial for SIT programs. In field-collected *C. cactorum*, the larger overwintered females performed similar flights to smaller, nonoverwintered females, suggesting that environmental conditions during development and body size do not affect female flight performance. In field-collected males, change detected in the longest single flight from overwintered to nonoverwintered specimen was caused by the seasonal shift in the proportions of long-flyers and short-flyers. Although overwintered males consisted of a larger proportion of long-flyers, nonoverwintered males were short flyers. This may be advantageous for overwintered *C. cactorum* males to locate females, which are more patchily dispersed in the winter brood than during other times of the year. Mating did not decrease female flight performance, suggesting that mated females may play an important role in invading new habitats.

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