

Host Specificity of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), an Exotic *Opuntia*-feeding Moth, in Florida

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ABSTRACT The recent arrival of the cactus moth, *Cactoblastis cactorum* (Berg) in Florida in 1989 has raised concern for the native *Opuntia* cacti. At particular risk is *Opuntia spinosissima*, whose entire U.S. population consists of 12 plants in the Florida Keys. We examined host choice of both *C. cactorum* larvae and ovipositing females to determine if any species of native *Opuntia* are preferred by *C. cactorum*. In addition, larval performance among *Opuntia* hosts was examined. Ovipositing moths showed no host preference in interspecific host choice experiments. Although larvae significantly preferred *O. spinosissima* over the other *Opuntia* species, larval survivorship on *O. spinosissima* was less than on *O. stricta* and *O. humifusa*. We also examined intraspecific host choice between pads of *O. spinosissima* to see if any of the 12 remaining plants is more resistant to attack than others. Such information is valuable for future restoration efforts to protect *O. spinosissima*. No adult or larval host choice was demonstrated in the intraspecific experiments.

KEY WORDS *Cactoblastis cactorum*, *Opuntia*, host choice

THE CONTROL OF *Opuntia* cacti by the cactus moth, *Cactoblastis cactorum* (Berg) is one of the classic success stories in biological control. In the 1920s, *C. cactorum* was introduced into Australia to control exotic cacti, including *Opuntia stricta* Haworth, that rendered >12 million hectares of cattle grazing land unusable (Dodd 1940). It was later introduced into South Africa for the same purpose. *Cactoblastis cactorum* was very successful in Australia, allowing reclamation of 6 million hectares of land (Dodd 1940) and was moderately successful in South Africa (Zimmermann and Moran 1982).

Cactoblastis cactorum is a Phycitine moth native to Northern Argentina, Uruguay, Paraguay, and Southern Brazil (Mann 1969). *C. cactorum* larvae are phytophagous, feeding on *Opuntia* spp. of cactus, primarily of the subgenus *Platyopuntia* (Mann 1969). The female moth lays eggs in a chain, usually extending from the tip of a cactus spine or node but occasionally from the cactus surface (Annecke 1978). Known as egg sticks, the chains average 50–80 eggs (Myers et al. 1981, Robertson 1987). Each female lays an average of 3–4 egg sticks in its adult lifetime of ≈ 9 d (Dodd 1940, Robertson 1987). The larvae are gregarious feeders, feeding on the internal cactus tissue and moving to new pads upon destruction of those in which they were feeding (Dodd 1940). Previous studies

indicate that ≈ 4 pads of *O. stricta* are needed to support complete development of larvae from an average egg stick (Monro 1967, Myers et al. 1981). *C. cactorum* has 2 generations per year with a possible 3rd generation in Australia (Dodd 1940) and South Africa (Robertson 1989).

In 1957, *C. cactorum* was introduced onto the Caribbean island of Nevis as a biological control agent for pest *Opuntia* spp. and in 1960 was introduced onto Montserrat and Antigua (Simmonds and Bennett 1966). The moth later dispersed, either naturally or by unrecorded introductions, to other islands such as Cuba, Puerto Rico, Hispaniola, and the Bahamas. The 1st record of *C. cactorum* in the continental United States was in the Florida Keys in October 1989. Although the mechanism of *C. cactorum* arrival into the continental United States was assumed to be by natural dispersal from Cuba (Habeck and Bennett 1990), an alternative hypothesis is that the moths arrived by commercial shipment of cacti to Miami from the Caribbean (Pemberton 1995).

Florida has 6 species of native *Opuntia* [*O. stricta*, *O. humifusa* (Rafinesque) Rafinesque, *O. spinosissima* (Martyn) Miller, *O. triacantha* (Willdenow) Sweet, *O. cubensis* Britton & Rose, and *O. pusilla* (Haworth) Haworth] (Benson 1982). *C. cactorum* has been found on all native *Opuntia* except *O. pusilla* (unpublished data). The United States ranges of 3 of these cacti, *O. spinosissima*, *O. triacantha*, and *O. cubensis*, are limited to local populations in the Florida Keys. Our studies con-

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centrated on 4 species: *O. stricta*, *O. humifusa*, *O. triacantha*, and *O. spinosissima*. *Opuntia stricta* variety *dillenii* is a common cactus found in sandy soils and shell mounds throughout coastal Florida (Benson 1982). *O. humifusa* variety *humifusa* is a wide ranging cactus, growing in sandy soil and rock outcrops from 1.5 to 600 m (Benson 1982). In Florida, *O. humifusa* variety *humifusa* is common in sandhill, scrub, and sometimes in coastal habitats. *O. triacantha* grows in sandy areas back from the beach on limestone reefs near sea level (Benson 1982). In the Florida Keys, *O. triacantha* grows in disturbed areas and openings in coastal hammocks. *O. spinosissima* grows on bare rocks with a humus covering in coastal hammocks near sea level (Benson 1982). The southern coast of Jamaica is the only other known location of *O. spinosissima*. The morning opening flowers of *O. spinosissima* are red and narrowly tubular, indicative of flowers pollinated by hummingbirds. Sexual reproduction, however, has not been documented in the Florida Keys population.

Opuntia conspecifics usually exist in patchy distributions where distances between plants are easily within the range of dispersing *C. cactorum* larvae as well as adults. Furthermore, *O. stricta* often shares habitat with *O. humifusa* throughout coastal Florida and with *O. spinosissima* and *O. triacantha* in the Florida Keys (unpublished data). Because neighboring plants are within the ambit of adult and larval dispersers, host choice should be examined in both forms.

Dan Austin (Florida Atlantic University, personal communication) suggests that the Florida Keys population of *O. spinosissima* is a distinct species, *O. corallicola*, first described by Small (1930). Only 12 individual plants currently remain at a single site on Nature Conservancy land in the Florida Keys, therefore if this population is a separate species, it would be among the rarest organisms in the world.

Although many *Opuntia* cacti are attacked by *C. cactorum*, the most immediate concern is for *O. spinosissima*. Soon after the discovery of *C. cactorum* in Florida, it was discovered damaging 1 of the remaining *O. spinosissima* plants (unpublished data). Most of these plants were caged in 1991 and all are regularly monitored. Although the cages may help protect individual *O. spinosissima* plants, they can not ensure survival of the population because they may eliminate pollinators and seed dispersers, thus lowering the fecundity of the cacti. Reduction of light, increased moisture, and outbreaks of other insects are other possible cage effects that could damage the cacti. One of the cages was removed in 1993 because the cactus showed ill effects.

Although much work has been done on *C. cactorum* elsewhere in the world, and although this information is valuable, it does not necessarily reflect the life history of *C. cactorum* in the United States. In Florida, management goals are aimed at

the control of *C. cactorum* to protect native *Opuntia* population, whereas the goals in Australia, South Africa, and the Caribbean are to control pest species of *Opuntia*. Furthermore, no information is available on possible host preferences of *C. cactorum* among *Opuntia* species native to the United States, which would assist in any conservation or restoration program. Therefore, any management plan aimed at the control of *C. cactorum* in the United States should first include a study of *C. cactorum* in Florida.

Materials and Methods

Larval No Choice Experiment. Individual 1st instar *C. cactorum* larvae were placed in the center of a ceramic tile (15 by 15 cm). The larvae were from 2nd-generation cultivated stock, raised on *O. stricta*. Both the larvae and feed-cactus were collected from several locations in south and central Florida. Thirty trials were run where 1 individual *O. stricta* propagule was placed against 1 side of the tile so that the choice for a *C. cactorum* larva was the test cactus or nothing. The test *O. stricta* propagules were mature single pads (200–300 cm²) collected at Walton Rocks Beach in St. Lucie County. The larva was allowed to crawl along the tile until it reached 1 of the sides, at which point the choice of side and the elapsed time were recorded. If after 60 min the larva had not reached a side of the tile, then the trial was terminated and the side of the tile nearest to the larva was recorded as the choice. Each larva was used only once. After each trial the tile was cleaned using methanol and any silk trails laid down by the larva were removed. The pad was then moved to the opposite end of the tile and a trial with a new larva was performed. Thirty replicates were performed (60 trials total).

Single/Multiple Larval Host Choice and Feeding. Host choice of a single larva between 2 pads from different *O. stricta* plants, collected at Walton Rocks Beach in St. Lucie County, was compared with host choice of a group of ≈ 20 first-instar larval siblings from the cultivated stock. The pads were the same propagules used in the no choice experiment. The 2 pads, of similar size and shape, were placed at opposite ends of the tile and the larva(e) were placed in the center of the tile. From 12 to 16 single and multiple larva(e) trials were run between each of the 6 pairs of pads. The positions of the pads were reversed after every trial and every larva was used only once. The percentage of single larvae that moved to the pads was compared with the percentage of groups of larvae that moved to the same pads using the product-moment correlation coefficient (Sokal and Rohlf 1981). This comparison tested whether the choice of 1 larva was representative of the group (entire egg stick) of larvae as a whole.

The ≈ 20 larval siblings were given a choice between the 2 *O. stricta* pads and were allowed to

feed. The plants were placed at opposite ends of the tile and 15 trials were run. The larvae were allowed to climb onto and bore into the plants. The 1st plant that the larvae climbed onto was recorded as the host choice. The plant not chosen was recorded as the rejected plant. The larvae were given time to leave the chosen plant and move to the rejected plant. The numbers of larvae choosing each pad and the numbers boring into the same pad were recorded.

Interspecific Larval Host Choice Experiment.

A single 1st instar *C. cactorum* larva was offered a choice among 4 propagules of 4 species of native cacti (*O. stricta*, *O. humifusa*, *O. triacantha*, and *O. spinosissima*), of similar size and shape, placed on each side of the tile. Six groups of propagules (replicates) were used. Twenty-four trials were run per group, with the propagules rearranged in every trial so that all possible combinations of propagule position were used. Each larva was allowed to crawl along the tile until it reached 1 of the sides, at which point the choice of *Opuntia* species and elapsed time were recorded. If after 60 min the larva had not reached a side of the tile, then the trial was terminated and the side of the tile nearest to the larva was recorded as the choice. The number of larvae choosing each cactus species was recorded as a proportion and a single classification analysis of variance (ANOVA) (Wilkinson 1988) was performed on the data. The proportions fit a normal distribution and variance was homoscedastic; thus, the data were not transformed. The times taken by larvae in moving to their chosen cacti were analyzed using the Kruskal-Wallis test (Sokal and Rohlf 1981).

The *O. stricta* propagules were collected in Manatee County, Florida. The *O. humifusa* propagules were collected in both Collier and Hillsborough counties in Florida. The *O. spinosissima* and *O. triacantha* propagules were provided by Fairchild Tropical Garden.

Interspecific Larval Performance Experiment. Ten newly hatched *C. cactorum* larvae, collected from egg sticks laid in the laboratory, were placed in cages with each of 4 *Opuntia* species (*O. stricta*, *O. humifusa*, *O. triacantha*, and *O. spinosissima*). The larvae were allowed to feed on the cactus and were given additional cactus pads as needed. Surviving larvae pupated and emerged as moths, at which point the moths were placed in a deep freeze. Later, the number of emerging moths within each replicate, the weights of emergent moths, and the number of eggs per female were recorded and tested using a single classification ANOVA. Five replicates were run using all *Opuntia* species except *O. triacantha*, in which case 3 replicates were run because of a lack of available cactus pads.

The *O. stricta* pads were collected at several sites throughout south and central Florida. The *O. humifusa* pads were collected in both Collier and Hillsborough counties in Florida. The *O. spinos-*

issima and *O. triacantha* propagules were provided by Fairchild Tropical Garden.

Intraspecific Larval Host Choice Experiment with *O. spinosissima*. An intraspecific larval host choice experiment was run on clones from all 12 of the *O. spinosissima* plants in the Florida Keys population. The clones were provided by Fairchild Tropical Garden, were cultivated in similar environmental conditions, and were of similar size and shape. Three replicates were run on 10 of the 12 clones and 2 replicates were run on the remaining 2 clones. Two clones of *O. spinosissima* were placed beside the tile at opposite ends. With the clones switched in position, a 2nd trial was run with a new larva. Each larva was used only once. The 2 trials were run for every combination of clones 3 times; thus, 6 trials were run for every combination of clones within each replicate. Sub-sample means were analyzed using the single classification ANOVA. Each sample point represented the proportion of times that a clone was chosen when it had been run in 1 trial with a clone from every other plant. The data satisfied the assumptions of normality and homoscedasticity; thus, they were not transformed. This test allowed the detection of differences in susceptibility to attack among the 12 plants. The times taken by larvae in moving to their chosen cacti were analyzed using the Kruskal-Wallis test.

Interspecific Oviposition Host Choice Experiment. Interspecific oviposition site selection was tested on 4 species of native Florida cactus; *O. stricta*, *O. humifusa*, *O. triacantha*, and *O. spinosissima* (collected from the same sources as in the interspecific larval host choice experiment). Four newly emerged adult *C. cactorum* moths, 2 males and 2 females, were placed in a cage with a group of 4 propagules, 1 from each of the 4 *Opuntia* species. The females were allowed to oviposit until all of the moths died or until at least 4 d had passed without an oviposition. Egg sticks were removed daily, identity of each plant with egg sticks was recorded, and number of eggs per egg stick was counted. The experiment was replicated 5 times. The total numbers of egg sticks laid on the propagules from each plant species were compared using the chi square 1-sample test for goodness-of-fit. Egg sticks from the replicates were pooled because of low sample sizes. The number of eggs per egg stick among *Opuntia* species was analyzed using the Kruskal-Wallis test. The ranked preferences of larvae and ovipositing females were compared using Spearman's coefficient of rank correlation (Sokal and Rohlf 1981).

Intraspecific Oviposition Host Choice Experiment With *O. spinosissima*. Oviposition site selection by adult *C. cactorum* females was tested among clones from 10 of the 12 remaining *O. spinosissima* plants in the Florida Keys (propagules from the other 2 plants were not available). The clones were provided by Fairchild Tropical Garden. The experimental method and analysis was

Table 1. ANOVA for interspecific larval *C. cactorum* host choice and performance among 4 host *Opuntia* species and intraspecific larval host choice among *O. spinosissima* clones

Experiment	Source	df	Mean squares	F	P
Interspecific host choice ^a	Among species	3	62.111	9.885	<0.001
	Within species	20	6.283		
Interspecific survivorship ^a	Among species	3	0.470	10.609	0.001
	Within species	14	0.044		
Interspecific performance ^{a,b}	Among species	2	0.138	0.811	0.45
	Within species	38	0.171		
	—Males	1	0.045	1.759	0.21
	—Females	24	0.025		
Intraspecific host choice ^c	Among clones	11	1.595	0.586	0.82
	Within clones	22	2.724		

^a Among *O. stricta*, *O. humifusa*, *O. triacantha*, and *O. spinosissima*.

^b Performance is measured as dry weights of emergent moths (weights were log transformed for normality) among *O. stricta*, *O. humifusa*, and *O. spinosissima* for males and *O. stricta* and *O. humifusa* for females.

^c Among 12 *O. spinosissima* clones.

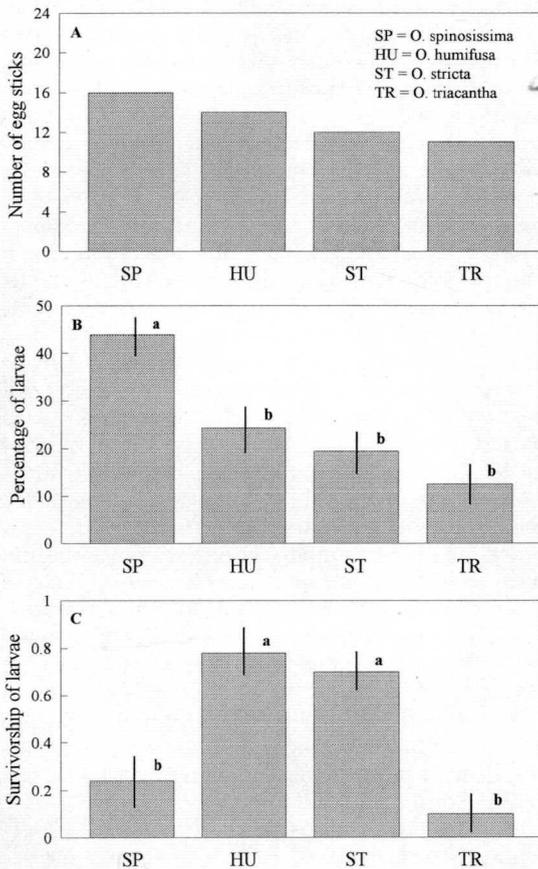


Fig. 1. *C. cactorum* interspecific experiments among 4 *Opuntia* species. (A) Oviposition site selection. (B) Larval host choice expressed as mean \pm SEM. (C) Larval survivorship expressed as mean \pm SEM. Different letters imply significant differences among species based on the Tukey post hoc comparison (Wilkinson 1988).

similar to that in the interspecific trials with the following exceptions. Five female and 5 male moths were used in 1 trial, the 10 propagules were rearranged randomly following every day with an oviposition, and 2 replicates of the experiment were run, each with 10 different propagules.

Results

Larval Host Choice-Single Plant. When a single *C. cactorum* larva was given a choice between an *O. stricta* plant on 1 side of the tile and nothing on the opposite side, the larva crawled to the side with the plant 58 out of 60 trials. The larva reached the edge of the plant in 43 of the 58 trials in which the plant was chosen.

Single/Multiple Larval Host Choice and Feeding. There was a strong correlation ($R^2 = 0.817$, $P = 0.01$) between the percentage of single larva and the percentage of a group of 20 larvae choosing 1 *O. stricta* plant over another. Groups of larvae did not disperse between the 2 different plants, typically they all either went to 1 plant or the other.

Fifteen groups of 17–33 *C. cactorum* larvae were given a choice between 2 *O. stricta* plants and were allowed to feed. No groups of larvae in a trial split in their feeding choice. In 11 of the 15 trials, > 95% of the larvae bored into the chosen plant. The larvae in the other 4 trials did not bore into either plant. None of the larvae subsequently rejected the chosen plant and chose the other plant.

Interspecific Larval Host Choice Experiment. *C. cactorum* larvae chose *O. spinosissima* propagules significantly more than *O. stricta*, *O. humifusa*, or *O. triacantha* propagules (Table 1; Fig. 1). In addition, *C. cactorum* larvae walked to *O. spinosissima* propagules in less time than they did to *O. stricta*, *O. humifusa*, and *O. triacantha* ($\chi^2 = 9.53$, $df = 3$, $P < 0.05$). Host choice and time of

Table 2. Mean \pm SEM survivorship, moth weights, and eggs per female of newly emerged *C. cactorum* moths raised on 4 species of *Opuntia*

Species	Survivorship	Weights		Eggs/Female
		Males	Females	
<i>O. humifusa</i>	0.78 \pm 0.10a (50)	17.49 \pm 2.04a (18)	39.07 \pm 2.81a (15)	98.62 \pm 10.16a (13)
<i>O. stricta</i>	0.70 \pm 0.08a (50)	16.21 \pm 1.29a (16)	49.39 \pm 6.42a (10)	123.33 \pm 16.39a (9)
<i>O. spinosissima</i>	0.24 \pm 0.11b (50)	13.64 \pm 2.21a (7)	27.73 (1)	101.00 (1)
<i>O. triacantha</i>	0.10 \pm 0.08b (30)	11.91 (1)	— (0)	— (0)

Means followed by the same letter are not significantly different from other means in the same column using 95% CI. Numbers in parentheses indicate sample sizes.

choice among *O. stricta*, *O. humifusa*, and *O. triacantha* was not significantly different ($P > 0.50$).

Interspecific Larval Performance Experiment. The survivorship of *C. cactorum* larvae was significantly higher on *O. stricta* and *O. humifusa* than on *O. spinosissima* and *O. triacantha* (Table 1; Fig. 1). Because of the large dichotomy between weights of males and females, the 2 groups could not be pooled. Moth weights, however, were pooled between replicates because of low sample sizes. When the number of samples was < 2 for a treatment, that treatment was excluded from the comparison. The weights were log transformed to satisfy the assumption of normality. There were no significant differences among the weights of males or females from *O. stricta*, *O. humifusa*, and *O. spinosissima* (Table 2).

The number of eggs per female was compared among *O. stricta* and *O. humifusa*. *O. triacantha* and *O. spinosissima* were excluded from the comparison because of a lack of samples. Although females raised on *O. stricta* had more eggs than *O. humifusa*, the difference was not significant (Table 2).

Intraspecific Larval Host Clone Experiment with *O. spinosissima*. There were no significant differences in host choice among clones (Table 1; Fig. 2). *C. cactorum* larvae, thus, did not consistently choose all propagules from 1 plant over the propagules of another. Larval times in choosing a host were also not significantly different among clones ($\chi^2 = 7.75$, $df = 9$, $P > 0.50$).

Interspecific Oviposition Host Choice. The data were pooled because of the low number of ovipositions. Sixteen egg sticks were laid on *O. spinosissima*, 14 on *O. humifusa*, 13 on *O. stricta*, and 11 on *O. triacantha* (Fig. 1). The numbers of egg sticks laid among the 4 *Opuntia* species were not significantly different ($\chi^2 = 1.11$, $P > 0.50$). There was no significant difference in the number of eggs per egg stick among the 4 species of *Opuntia* ($\chi^2 = 7.23$, $df = 3$, $P > 0.05$).

Intraspecific Oviposition Host Choice with *O. spinosissima*. Oviposition site selection data from the 2 replicates of 10 *O. spinosissima* clones was pooled because of the low numbers of ovipositions. Propagules were not available from plant numbers 8 and 10, thus they were excluded from this experiment. No oviposition preference was detected among propagules from the 10 *O. spinosissima* plants ($\chi^2 = 9.33$, $df = 9$, $P > 0.05$) (Fig. 2). In addition, there was no significant difference in the number of eggs per egg stick laid on propagules from the 10 *O. spinosissima* plants.

Discussion

Cactoblastis cactorum larvae can detect the presence of a cactus and move toward it, as evidenced by the single plant experiment. In addition, the choice made by a single larva is an accurate indication of the choice made by a group of larval siblings. Therefore, we are confident that single-

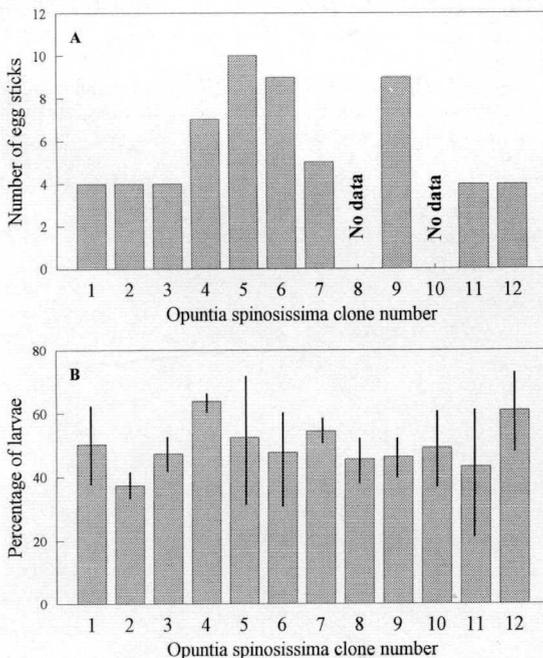


Fig. 2. *C. cactorum* intraspecific host choice among *O. spinosissima* clones. (A) Oviposition site selection. (B) Larval host choice expressed as mean \pm SEM.

larva trials are a valid tool for determining host choice by these gregarious larvae.

Cactoblastis cactorum larval host choice and adult oviposition choice were similar. When given a choice of 4 species of *Opuntia* cacti, the larvae and adults displayed the same trend in ranked preference ($r_s = 1.00$, $n = 4$, $P = 0.042$), both tending to choose *O. spinosissima* over the other species of *Opuntia*. In addition, *C. cactorum* crawled to *O. spinosissima* faster than to the other 3 *Opuntia* species. The survivorship of *C. cactorum*, however, was significantly higher on *O. humifusa* and *O. stricta* than on *O. spinosissima* and *O. triacantha*. For *C. cactorum* to prefer a host species on which it has a relatively low survivorship seems paradoxical until the nature of this interaction is examined. Because *C. cactorum* is an exotic moth, there is no historical interaction to serve as a vehicle for natural selective devices to shape host preference or survivorship of *C. cactorum* on native Florida *Opuntia*.

Future studies are necessary to determine what characteristics of the cacti are being chosen or rejected by *C. cactorum*. Pads were selected for the experiments according to a standard size and shape, and although the ages of the pads were not known, none were new growth nor were they visibly thick old growth. Chemical characteristics may, thus, be the most likely influence on choice or rejection of pads by *C. cactorum*.

Because *O. spinosissima* is preferred over other *Opuntia* species by *C. cactorum* larvae and ovipositing females, the lone population of *O. spinosissima* could be in great danger of extirpation. The cages should probably remain on the plants as long as they do not promote outbreaks of other insects or reduce available light. Manual pollination should be easily manageable with only 12 plants.

In intraspecific experiments involving *O. spinosissima*, where differences between clones are perhaps more subtle than differences between species, there were no significant preferences of larvae or ovipositing moths between different *O. spinosissima* clones. Therefore, all of the remaining *O. spinosissima* plants are probably in danger of *C. cactorum* attack.

How do we best restore *O. spinosissima* in the field? Because our results suggest that larvae do not prefer some clones over others, any restoration program should use propagules from all of the remaining individual plants in equal proportions.

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