

## GEOGRAPHIC PATTERNS IN THE REPRODUCTIVE ECOLOGY OF *AGAVE LECHUGUILLA* (AGAVACEAE) IN THE CHIHUAHUAN DESERT. I. FLORAL CHARACTERISTICS, VISITORS, AND FECUNDITY<sup>1</sup>

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Floral characteristics such as morphology and flower color have been interpreted as adaptive traits that evolved through selective pressures generated by pollinators. Differences among populations in the expression of floral characters could result from natural selection for their adaptive value to local conditions. We describe the patterns of variation of flower morphology, color, and fecundity of *Agave lechuguilla* in 11 populations along a latitudinal gradient encompassing the whole range of the species in the Chihuahuan desert. We found a latitudinal pattern in flower shape and color. Flowers tended to be shorter, more open, and colorful toward the northern part of the gradient. We also recorded flower visitation, discriminating between pollinators and floral robbers. The main pollinators seems to be nocturnal hawk moths (*Hyles lineata*) and diurnal large bees (*Bombus pennsylvanicus* and *Xylocopa californica*). In all populations large bees were the most abundant potential pollinators. However, the abundance of the potential pollinators varied along the gradient. We observed no bat visits along the gradient. The number of visits by all potential pollinators decreased significantly with latitude as did fruit set.

**Key words:** Agavaceae; *Agave lechuguilla*; bees; Chihuahuan desert; hawk moths; hummingbirds; latitudinal gradient; pollination; population differentiation.

Floral traits are usually considered adaptive attributes that have evolved as a result of selective pressures imposed by pollinators (Percival, 1965; Baker and Hurd, 1968; Faegri and Van der Pijl, 1971; Proctor and Yeo, 1973). Although most of the studies have interpreted floral morphology and color as an adaptation to the locally most efficient pollinators (but see Aigner, 2001), relatively few of them have studied these traits within and among populations (Galen, 1989, 1996; Armbruster, 1990; Herrera, 1990a, b, 1993; Johnston, 1991; Andersson and Widen, 1993; Conner, Davis, and Rush, 1995; Inoue, Maki, and Masuda, 1996; Melendez-Ackerman, Campbell, and Waser, 1997). Based on the geographic mosaic model proposed by Thompson (1994, 1997), one may expect plant–pollinator interactions to vary among populations, generating a complex pattern of differential adaptation. In this paper we analyze and compare the variation in floral traits, fecundity, and the associated changes in their floral visitors in 11 populations of *Agave lechuguilla* on a latitudinal gradient in the Chihuahuan desert.

The plants in the *Agave* genus are long-lived succulent rosettes (Gentry, 1982). *Agave* can be abundant and dominant in vast areas of Mexico, in particular in xerophytic environments (Gentry, 1982; Nobel, 1988). Schaffer and Schaffer (1979) suggested that pollinators are the most important factor

in the evolution of their reproductive biology and life history, given their monocarpy. A high dependence of pollinators has been suggested in some species of the genus (Howell and Roth, 1981; Eguiarte, Souza, and Silva-Montellano, 2000). Usually, it is assumed that bats, mainly the genus *Leptonycteris*, pollinate *Agave* (Howell, 1979; Gentry, 1982; Arizaga and Ezcurra, 1995). In particular, Arizaga et al. (2000a, b) demonstrated that bats of genera *Leptonycteris* and *Choeronycteris* pollinate the paniculated *Agave macroacantha* (subgenus *Agave*). Nevertheless, a large number of species of insects and birds also visit *Agave* flowers (Schaffer and Schaffer, 1977; Kuban, Lawley, and Neill, 1983; Martínez del Rio and Eguiarte, 1987; Kuban, 1989; Eguiarte, Souza, and Silva-Montellano, 2000; Slauson, 2000). Schaffer and Schaffer (1977) found that several species in the *Littaea* subgenus (spicate *Agave*; *A. schotii*, *A. parviflora*, and *A. toumeyana*) in Arizona, USA, have flower and nectar traits that suggest co-adaptation to pollination by bees and are mainly pollinated by large bees from the genera *Bombus* and *Xylocopa*.

*Agave lechuguilla* is an excellent system to study plant–pollinator interactions in a geographic mosaic context, as it is a species with an unusually broad distribution for an *Agave*. *Agave lechuguilla* is found throughout the Chihuahuan desert ranging from the Valley of Mexico up to southern Texas and New Mexico, USA (Gentry, 1982; Briones, 1994). Additionally, Gentry (1982) described geographic variation in the size and color of its flowers. Moreover, the distribution of potential pollinators changes along *A. lechuguilla*'s distribution. In its southern range, nectarivorous bats and hummingbirds are more abundant and diverse (Arita, 1991; Johnsgard, 1993; Arita and Santos del Prado, 1999). To the north, the diversity of bees increases (Ayala, Griswold, and Bullock, 1993). Based on that information, we addressed the following questions: How do flower color and morphology of *A. lechuguilla* vary along this latitudinal gradient? Does the pollinator assemblage change

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Fig. 1. Sampled populations of *Agave lechuguilla* along the latitudinal gradient in Mexico. Numbers indicate populations as in Table 1 and "M" refers to Mapimi population (see Materials and Methods).

with latitude? If syndrome adaptation to a specific pollinator occurs in the case of *A. lechuguilla*, we may expect to find clinal variation in floral traits corresponding to the variation in the pollinators.

## MATERIALS AND METHODS

**Study species**—*Agave lechuguilla* Torr. (Agavaceae, subgenus *Littaea*, *Marginatae* Group; Gentry, 1982) is found mainly on limestone soils. The flowering season is in summer, from late May to September (Gentry, 1982). The inflorescence is a spike, as in all species in the subgenus *Littaea*, and the flowers produce pollen and nectar during the night (Gentry, 1982; Freeman and Reid, 1985). Flowers are protandrous, and they open from the bottom to the top of the spike forming a ring of ca. 30 simultaneously open flowers (*A. Silva-Montellano*, personal observation). Pollen is made available on the first night that flowers open. Stigmas are receptive for the 3–4 d that follow. Nocturnal nectar production declines with flower age (Freeman and Reid,

1985). Nectar characteristics are described in Freeman et al. (1983) and in Cadaval (1999). Clonal propagation is important in the species, producing large clonal patches in all the distribution.

**Studied populations**—The study populations were sampled to cover most of the natural distribution of the species in a latitudinal gradient, from 20° N to 32° N, and we attempted to locate a study site at every latitudinal degree (Fig. 1; Table 1). We studied 11 populations, starting from Pachuca, Hidalgo (population 1), in the northern Valley of Mexico, up to Ciudad Juarez, Chihuahua (population 10), near the USA border. For the Mapimi population (M) we have only partial data because we were not able to reach the population during the rainy season.

Field work was done during the 1996 flowering period of *A. lechuguilla* (early July to early September) (Table 1). The flowering season starts earlier in the southern populations, and then proceeds following the latitudinal gradient, starting in September in the northern populations. This flowering pattern

TABLE 1. Dates of visits and Lang's humidity index (Lang's  $I$  = total annual precipitation/mean annual  $T^{\circ}$ ) in 11 populations of a latitudinal gradient of *Agave lechuguilla*, performed during the summer of 1996.

Population	State	Locality	Coordinates	Altitude (m)	Date	Lang's $I$
1	Hidalgo	Pachuca	20°08' N; 98°44' W	1950	3 July	27.1
2	Hidalgo	Zimapán	20°43' N; 99°20' W	1800	11 July	21.2
3	San Luis P.	Zaragoza	22°04' N; 100°40' W	2100	18 July	21.1
4	San Luis P.	Matehuala	23°49' N; 100°32' W	1920	9 August	24.3
5	Coahuila	Saltillo	25°15' N; 101°05' W	1980	11 August	17.2
6	Durango	Bermejillo	26°14' N; 103°50' W	1260	16 August	14.1
7	Chihuahua	Jimenez	27°14' N; 104°46' W	1580	18 August	17.7
8	Chihuahua	Aldama	28°57' N; 105°42' W	1380	22 August	17.0
9	Chihuahua	Ojinaga	29°44' N; 104°36' W	990	26 August	11.2
10	Chihuahua	Cd. Juarez	31°40' N; 106°32' W	1530	1 September	13.5
M	Durango	Ceballos	26°40' N; 103°44' W	1260	4 September	14.1

allowed us to study the 11 populations in a single season. In all sites we found the *A. lechuguilla* populations in full blossom.

We calculated the Lang's humidity index for each locality (= total annual precipitation [in millimeters]/mean annual temperature [in degrees Celsius]; Mohr and Van Baren, 1954) using information from the nearest climate station (García, 1988). Table 1 shows that populations 1–4 were more mesic, whereas populations 6, M, 9, and 10 were more xeric.

Density of rosettes was estimated in 100-m<sup>2</sup> quadrants (four replicates per site). The density of reproductive individuals (inflorescences) was estimated using the nearest neighbor method (Krebs, 1989). We followed the standard sampling procedure: setting 12 random points in the field (about 3 ha), we recorded the distance from those points to the nearest plant and from a random individual to a second one. This gave a first density estimation, which was corrected from possible biases using Diggle's formula (Krebs, 1989). We performed four replicates of this sampling procedure per site in order to compare among populations.

**Color and morphology of flowers**—In each population (except M), we randomly selected 15–20 reproductive individuals. From each individual we analyzed seven flowers at the same stage, i.e., young flowers before anther dehiscence (see Freeman and Reid, 1985). Fresh color of each flower was recorded with a Munsell chart (Wilde and Voigt, 1952). Color data were obtained as the addition of the values of chroma and hue, which permits distinguishing individual differences within populations. Flowers were video-filmed, digitized, and measured using the Morphosys program (Fig. 2; Meacham and Duncan, 1990), following Domínguez et al. (1998).

**Floral visitors**—For eight focal inflorescences per population (except M), we recorded flower visitation. Pollinators were distinguished from pollen or nectar robbers by their behavior (see Dafni, 1992). We noted whether they contacted the stigmas or the anthers and the way that they access the resources in the flowers: frontal or by the side of the corolla, avoiding the stigma. Focal inflorescences were selected because they were easy to observe, in particular during the night. For each focal inflorescence, we measured its total height, estimated the volume of the rosette (in liters) using its diameters and height, and counted the number of open flowers.

In each site, observations were done during the periods of high visitor activity, from 0700 to 1000 and from 1900 to 2200. All observations were done in silence a few meters away from the focal plant to avoid any disturbance to visitors such as vertebrates, but getting closer at times to characterize the behavior of the insect species. Each focal inflorescence was observed in periods of 10 min until 3 h were completed. These observations lasted 2 d for each site, accumulating a total of 12 observation hours (six diurnal and six nocturnal) per site, giving a total of 114 observation hours. Visitors were identified as morphospecies in the field, using collections of insects from the same sites, while vertebrates (birds) were identified using field guides. Insect identifications were corroborated by sending specimens to specialists. Data on nocturnal visitors in population 3 are lacking because of weather conditions.

**Fecundity estimates**—Fecundity data were collected during March of 1997. In each population, we randomly selected 30–50 inflorescences from the previous reproductive season. For each inflorescence we recorded the total number of flowers (as the number of flower scars) and the total number of mature fruits. For each plant we measured the volume of the rosette (using its diameter and height), and the height of the inflorescence to control for any factors related to the size of the plant on the fecundity output. The rosettes at the time of recording the fecundity conserve their former size, since the rigidity of the leaves allows them to maintain their length despite becoming thinner because of resource and water allocation during flowering and maturing of fruits.

**Statistical analyses**—Differences among populations in densities of rosettes and inflorescences were tested using one way ANOVAs. Linear regressions were used to determine the relationship between size of the plants and number of flowers, transforming both variables to natural logarithms to improve linearity. Correlations were used to compare flower morphology characters.

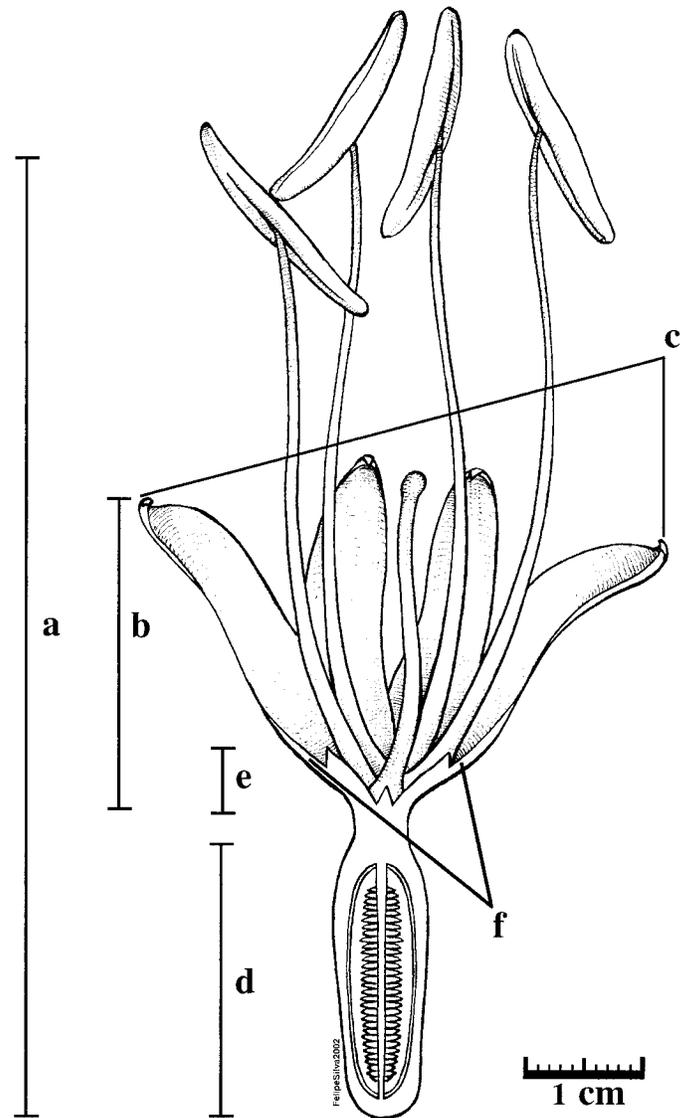


Fig. 2. Morphometric floral characters measured (in millimeters) for *Agave lechuguilla* along latitudinal gradient: (a) floral length; (b) corolla length; (c) corolla diameter; (d) ovary length; (e) tube length; and (f) tube diameter.

Based on these correlations and the fact that we measured few traits, we selected corolla length and the corolla diameter to analyze the latitudinal patterns, because they describe the shape of the flowers and are biologically meaningful in relation to the access of the visitors to the flowers. We compared variation in flower morphometry among populations with nested ANOVAs (Sokal and Rohlf, 1995), using the individual scores of the two selected traits for populations, individuals within populations and flowers within individuals. Individuals within populations was assigned as the random variable in the analysis. Changes in latitude for all characters were tested using regressions for repeated values of *Y*, where every point in each latitude corresponds to an individual plant value (Sokal and Rohlf, 1995). Color data are presented as the proportion of a specific color (red) of the individuals in each population along the latitudinal gradient, and arcsine square-root transformed to fit normality. We used ANCOVA analysis to determine the effect of rosette volume with respect to the reproductive output among populations. The relationship between fecundity and frequency of visits was analyzed with a simple correlation but using the populations means, due to differences in sample size between the variables. Analyses were conducted using JMP program (SAS, 1995).

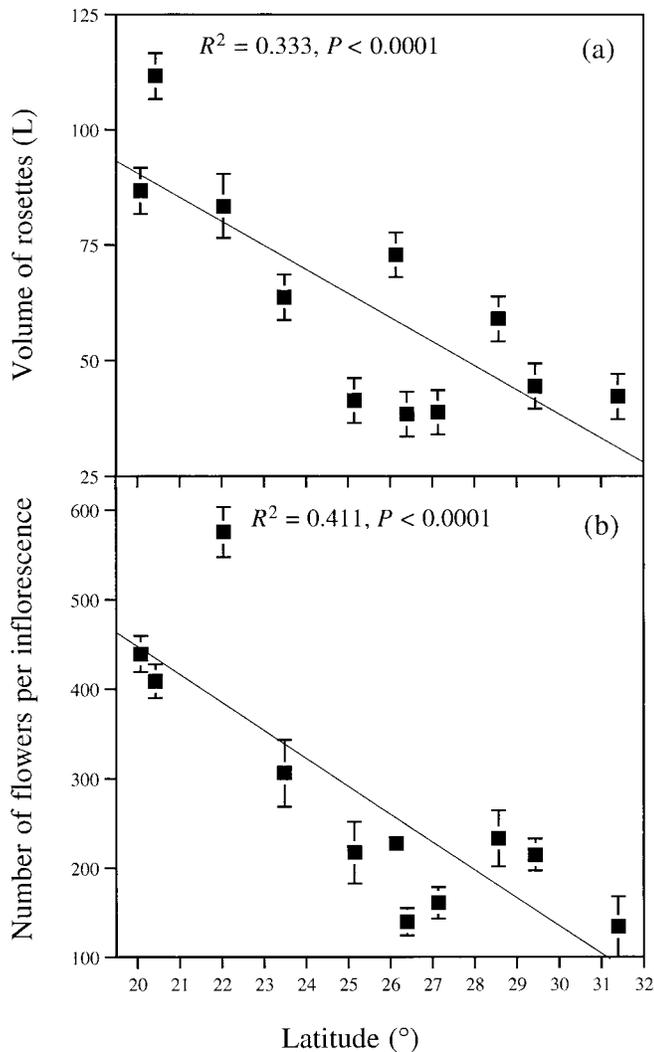


Fig. 3. Decrease in rosette size (in liters) and number of flowers per individual along a latitudinal gradient (mean  $\pm$  SE) for all populations of *Agave lechuguilla*.

## RESULTS

**Densities and morphometry of the individuals**—The density of rosettes (grand mean = 2.04 rosettes/m<sup>2</sup>, SD = 0.77; range = 1.78 in population 1 to 2.96 population 7) and of reproductive individuals (grand mean = 0.0071 inflorescences/m<sup>2</sup>, SD = 0.0113; range = 0.0018 in population 3 to 0.01 in population 6) were not different among the 11 populations (ANOVA, rosettes per square meter;  $N = 44$ ,  $df = 10$ ,  $F = 1.1$ ,  $P = 0.38$ ; ANOVA inflorescences per square meter;  $N = 44$ ,  $df = 10$ ,  $F = 1.92$ ,  $P = 0.076$ ).

There were significant differences in the size of a rosette and the total number of flowers per inflorescence among populations (ANOVA volume rosette:  $N = 350$ ,  $df = 10$ ,  $F = 22.8$ ,  $P < 0.0001$ ; ANOVA number of flowers:  $N = 350$ ,  $df = 10$ ,  $F = 43.47$ ,  $P < 0.0001$ ). Individuals were larger in the southern distribution (Fig. 3a; range of the population means = 111.6–38.3 L in populations 2–M, respectively;  $N = 350$ ,  $F = 172.2$ , slope =  $-5.1$ ,  $t = -13.1$ ,  $P < 0.0001$ ) and populations produced fewer flowers in the north (Fig. 3b; range of the population means = 575.6–133.9 in populations 3–10,

TABLE 2. Descriptive statistics of the floral morphometric variables based in all plants in 10 populations of *Agave lechuguilla* along the latitudinal gradient. Number of flowers per population:  $N$  (range) = 96–140,  $N$  (total) = 1229 flowers; coefficient of variation, CV = SD/mean  $\times$  100.

Variable	Mean (mm)	SD	CV
Floral length	55.08	10.62	19.3
Corolla length	15.34	3.59	23.4
Corolla diameter	19.28	5.43	28.1
Ovary length	16.76	3.31	19.7
Tube length	2.47	1.29	52.2
Tube diameter	6.93	2.42	34.9

respectively;  $N = 350$ ,  $F = 240.4$ , slope =  $-32.9$ ,  $t = -15.5$ ,  $P < 0.0001$ ). There was also a strong correlation between both characters among populations (using all the measured plants:  $N = 350$ ,  $R^2 = 0.546$ ,  $F = 419.9$ , slope =  $0.81$ ,  $t = 20.5$ ,  $P < 0.0001$ ). The correlations was also observed within each of the 11 populations.

**Flower morphometry**—The basic statistics of floral morphometry of all flowers (all populations pooled) are given in Table 2. Estimates of coefficient of variation (CV) indicate that the five measured traits were fairly variable. The length of the flower tube (CV = 52.2%) was the most variable trait, whereas the total length of the flower was less variable (CV = 19.3%). Floral traits were positively correlated among them, with the exception of the corolla diameter, which was negatively or not correlated to the other measures (Table 3).

We found a latitudinal change in corolla length (range =  $20.3 \pm 0.8$  mm in population 1 to  $12.2 \pm 0.7$  mm in population 8), decreasing in the northern populations (Fig. 4a;  $N = 1229$ ,  $F = 1118.7$ ,  $df = 160$ ,  $R^2 = 0.477$ ,  $P < 0.0001$ , slope =  $-0.698$ ,  $t = -33.4$ ,  $P < 0.0001$ ). In contrast, corolla width increased toward the north (Fig. 4b; range =  $13.1 \pm 0.9$  in population 2 to  $28.3 \pm 0.8$  in population 10;  $N = 1229$ ,  $F = 729.6$ ,  $df = 160$ ,  $R^2 = 0.372$ ,  $P < 0.0001$ , slope =  $0.935$ ,  $t = 27.1$ ,  $P < 0.0001$ ). Differences among populations using a nested ANOVA for the same characters (Table 4) shows that population accounted for most of the variation in both cases (57.1% and 53.4%), although there was a substantial proportion related to differences among individual plants within the populations (26.7% and 27.8%). This analysis shows that variation in flower morphology has an important individual component.

**Color of flowers**—Flower color varied from pale light green (glaucous) to deep red. The flower structures that changed in color were the corolla tepals (hereafter tepals) and the stamen filaments (hereafter filaments). The proportion of red color in the tepals increased with latitude (Fig. 5a; data arcsine square-root transformed:  $N = 200$ ,  $F = 421.6$ ,  $R^2 = 0.680$ ,  $P < 0.0001$ ; slope =  $-0.114$ ,  $t = 20.5$ ,  $P < 0.0001$ ); in the south it was very low (less than 20% in populations 1, 2, and 3), and reached more than 70% in the northernmost populations (7–10). The filaments show a parallel change (Fig. 5b;  $N = 200$ ,  $F = 479.7$ ,  $R^2 = 0.708$ ,  $P < 0.0001$ ; slope =  $0.049$ ,  $t = 21.9$ ,  $P < 0.0001$ ), although the southernmost populations (1–3) had an important proportion of red filaments (around 50%), to reach almost 100% in populations 6–10.

**Floral visitors**—The total list of visitors is shown in Table 5, separated as pollinators and robbers. The most abundant

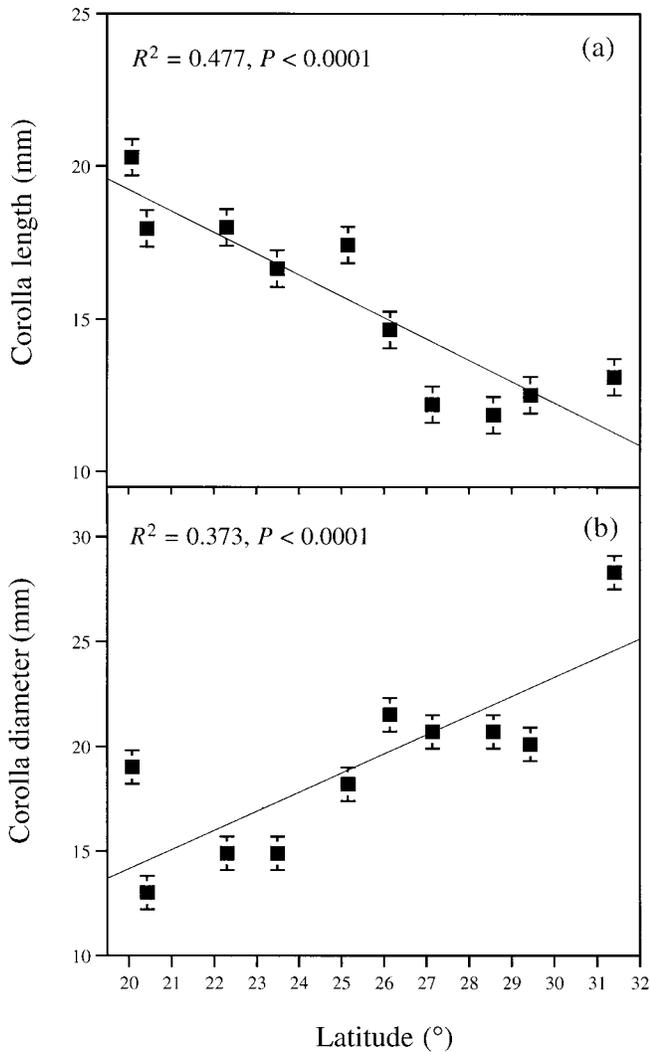


Fig. 4. Latitudinal variation in two selected floral characters in ten populations of *Agave lechuguilla* (mean  $\pm$  SE): (a) corolla length and (b) corolla diameter.

visitor was the introduced European bee *Apis mellifera* (Apidae), accounting for a total of 50.5% of all the visits. We classified *A. mellifera* as a floral robber, because it was too small to touch the stigmas while foraging for pollen and/or nectar in the flowers, always entering them by the side independently of the sexual stage of flowers. The next most important group of visitors were the large native bees—the bumble bee *Bombus pennsylvanicus sonoratus* (Apidae) and the carpenter bee *Xylocopa californica arizonensis* (Anthophori-

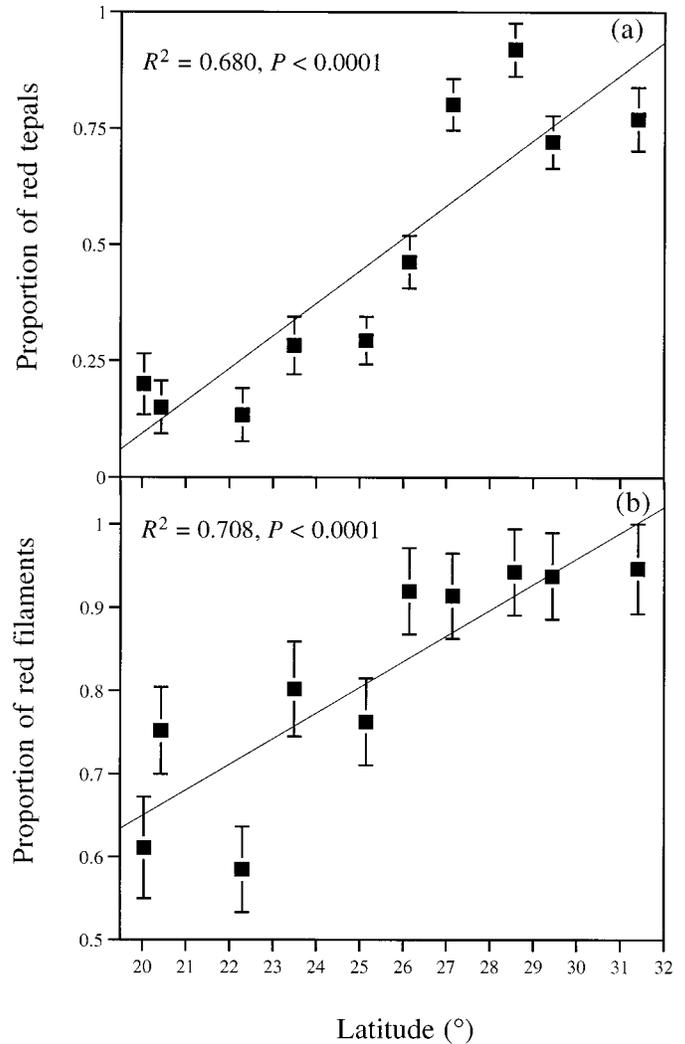


Fig. 5. Increase in proportion of red in flower structures (see Materials and Methods) in populations of *Agave lechuguilla* along the latitudinal gradient (mean  $\pm$  SE): (a) red tepals and (b) red filaments.

dae)—with a total of 23.4% of the total visits. *Bombus pennsylvanicus* was found only in populations 1–5; in the northern populations (6–10) *X. californica* was the main visitor. They behaved as potential pollinators because of the way they reach the flowers and because of their size, which is big enough to touch all the reproductive structures.

The next important visitor was the nocturnal hawk moth *Hyles lineata*, which was the most abundant potential pollinator in populations 2, 7, and 8. Hawk moths reach the flowers

TABLE 3. Pearson's correlation coefficients (*r*) for the floral morphometric variables measured in 10 populations of *Agave lechuguilla*. Number of flowers per population: *N* (range) = 96–140, *N* (total) = 1229 flowers.

Trait	Corolla length	Corolla diameter	Ovary length	Tube length	Tube diameter
Floral length	0.75***	–0.18 ns	0.65***	0.81***	0.35**
Corolla length		–0.64***	0.56**	0.81***	0.25*
Corolla diameter			–0.002 ns	–0.47**	0.14 ns
Ovary length				0.59***	0.20*
Tube length					–0.32**

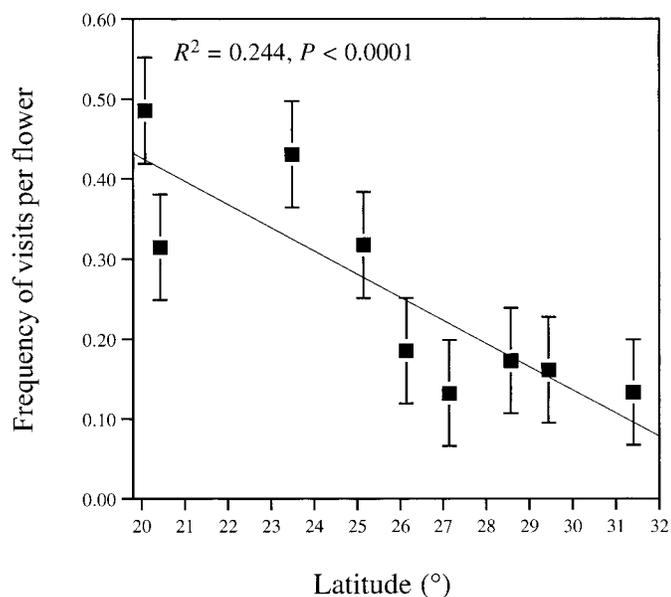
\* *P* < 0.05; \*\* *P* < 0.001; \*\*\* *P* < 0.0001; ns = nonsignificant.

TABLE 4. Values of nested ANOVA (population, individual) for both floral characteristics: corolla length and corolla diameter measured over the flowers ( $N = 1229$ ) in 10 populations of *Agave lechuguilla* (SS = sum of squares; % var. = percentage of variance for each  $F$  value).

Source	Factor	df	SS	$F$ (% var.)	$P$
Corolla length	Population	9	9013.8	42.5 (57.1)	<0.00001
	Individual (Population)	176	4206.5	11.4 (26.7)	<0.00001
	Model	185	13 584.4	34.8 (86.1)	<0.00001
	Total	1228	15 779.1		
Corolla diameter	Population	9	19 342.4	38.1 (53.4)	<0.00001
	Individual (Population)	176	10 074.7	10.2 (27.8)	<0.00001
	Model	185	30 341.1	29.1 (83.8)	<0.00001
	Total	1228	36 210.4		

TABLE 5. Number of observed visitors by species and by percentage for groups of species in 10 populations of *Agave lechuguilla* along a latitudinal gradient. Percentages were calculated over total visitors.

Visitors	Populations										Total species	Group (%)
	1	2	3	4	5	6	7	8	9	10		
<b>Pollinators</b>												
<i>Hyles lineata</i>	6	22	—	4	2	2	4	14	3	3	60	Hawk moths (9.47)
<i>Xylocopa californica</i>	0	0	0	0	0	4	3	2	7	4	20	
<i>Bombus pennsylvanicus</i>	31	9	46	27	15	0	0	0	0	0	128	Large bees (23.4)
<i>Eugenes fulgens</i>	4	3	2	3	3	0	1	0	0	1	17	
<i>Calothorax lucifer</i>	2	0	0	1	1	0	0	0	0	0	4	
<i>Archilochus alexandri</i>	0	0	0	0	0	0	1	1	1	1	4	
<i>Selasphorus</i> sp.	0	0	0	0	0	1	0	0	0	0	1	Hummingbirds (4.11)
Total population	43	34	48	35	21	7	9	17	11	9	234	
<b>Robbers</b>												
<i>Apis mellifera</i>	41	51	17	46	41	20	48	10	29	17	320	Bees (50.55)
<i>Selasphorus</i> sp.	0	0	0	0	0	0	0	0	1	0	1	
Vespidae	4	1	0	2	2	1	0	0	0	0	10	
Other little bees	15	10	6	8	6	5	11	0	2	5	68	Other (12.48)
Total population	60	62	23	56	49	26	59	10	32	22	399	
Total visitors	103	96	71	91	70	33	68	27	43	31	633	

Fig. 6. Decrease in frequency of total potential pollinators visits per flower (no. of visits/no. of flowers), estimated from eight focal inflorescences and 12 h of observation per site along the latitudinal gradient (population mean  $\pm$  SE).

directly, although sometimes they rest on them. Hummingbird visits were recorded in all populations, and accounted for 11.1% of the visits by potential pollinators (4.1% of all the visits). The most common hummingbird species was *Eugenes fulgens*, in particular in southern populations 1–5. Note that in population 9, a *Selasphorus* sp. hummingbird was considered a robber because of its behavior, taking nectar by the side of the flower, thus avoiding the sexual structures.

The remaining visitors were a heterogeneous collection of insects, mainly small bees and wasps, which accounted for 12.3% of the total visits. This last group robbed nectar or pollen and because of their heterogeneity and low proportion per species were not included in the analysis.

In the 54 total hours of nocturnal observation, we were not able to detect a single bat visit, despite our expectations. This lack of visits by bats was confirmed by further and more detailed observations the next year in two selected populations (1 and M; Silva-Montellano, 2001).

We estimated the frequency of visits per flower (number of visits/number flowers, in each inflorescence) in all the populations to avoid the effect on pollinators of the larger density of flowers in the southern populations. For the total set of pollinators, we found differences among populations (ANOVA populations  $df = 8$ ,  $F = 4.1$ ,  $R^2 = 0.339$ ,  $P < 0.0006$ ), and we found also a pattern related to latitude (Fig. 6; slope =  $-0.039$ ,  $t = -4.76$ ,  $P < 0.0001$ ), which explains 24% of the

TABLE 6. ANOVA and linear regression values for each visitor or group of visitors, in *Agave lechuguilla*, as a function of frequency of visits per flower along the latitudinal gradient (SS = sum of squares).

Source of variation	Factor	df	SS	F	R <sup>2</sup>	P
<i>Hyles lineata</i>	Population	8	0.18	3.34	0.298	0.0030
	Total	71	0.61			
	Latitude	1	0.24	7.95	0.102	0.0063
Large bees	Total	71	2.41			
	Population	9	0.85	5.07	0.395	<0.0001
	Total	79	2.15			
Hummingbirds	Latitude	1	0.89	19.04	0.196	<0.0001
	Total	79	4.55			
	Population	9	0.02	2.74	0.261	0.0083
<i>Apis mellifera</i>	Total	79	0.09			
	Latitude	1	0.07	5.14	0.062	0.0261
	Total	79	1.23			
<i>Apis mellifera</i>	Population	9	0.43	3.12	0.286	0.0032
	Total	79	1.49			
	Latitude	1	0.02	0.497	0.006	0.4829
Total	79	3.68				

variance in frequency of visitation, decreasing toward northern populations. For each of the major potential pollinators, we detected the same patterns of decreasing in frequency of visits per flower toward northern populations (Table 6). For *Hyles lineata* (slope = -0.016, *t* = -2.82, *P* = 0.0063), latitude explains 10% of the variance in visitation frequency. For large bees (slope = -0.029, *t* = -4.36, *P* < 0.0001), latitude represents almost 20% of that variance, and the hummingbirds (slope = -0.009, *t* = -2.27, *P* = 0.0261) had a similar pattern in latitude, which explains 6% of the variance, although their visits were nearly an order of magnitude smaller. We found no significant pattern of visitation related to latitude for the main robber, *Apis mellifera*, although there were important differences among populations (Table 6).

**Fecundity patterns**—The total number of fruits per inflorescence decreased toward northern populations (Table 7; slope latitude = -95.26, *t* = -5.2, *P* < 0.0001). However, the plants were smaller in the north and produced fewer flowers (Fig. 3), which have a significant effect on fruit production (Table 7). We also evaluated fecundity in terms of fruit set (total produced fruits/total produced flowers). There was a clinal pattern in the fecundity of populations (Fig. 7; *N* = 347, *F* = 73.2, *R*<sup>2</sup> = 0.156, *P* < 0.0001; slope = -0.068, *t* = -8.55, *P* < 0.0001). The probability that a flower became a fruit was on average more than 0.5 in populations 1–3 (mean

range = 0.55–0.59) and less than 0.4 in populations 7–10 (mean range = 0.33–0.35), reaching only 0.235 in population 9. The differences in fruit set were not due to differences in sizes of the plants (Table 7) but correlate with the visitation frequency per flower (Fig. 8; *y* = 0.672*x* + 0.234, *r* = 0.822, *df* = 7, *P* < 0.007), suggesting that the plants in the clime seem to be not limited in their fecundity by resources, but were somehow limited by pollinators.

DISCUSSION

**Morphology and reproductive traits**—We found geographic differentiation following a clinal pattern on latitude along the Chihuahuan desert in the general plant morphometry, size, shape, and color of the flowers and fecundity of *A. lechuguilla*. The plants in the south were larger; their flowers were longer, tubular, and of a glaucous color; and the fruit set was high; while in the north the plants were smaller; the flowers were

TABLE 7. ANCOVA values for the fecundity variables according to latitude and size of the rosette in ten populations of *Agave lechuguilla* (SS = sum of squares, % var. = percentage of variance).

Source/factor	df	SS	F (% var.)	P
<b>No. fruits</b>				
Latitude	1	51.69	164.1 (20)	<0.0001
Rosette volume	1	15.62	49.6 (6.1)	<0.0001
Model	2	149.75	50.1 (58)	<0.0001
Total	346	258.17		
<b>Fruit set</b>				
Latitude	1	12.92	73.2 (15.6)	<0.0001
Rosette volume	1	0.14	0.8	0.36
Model	2	21.94	62.1 (27)	<0.0001
Total	346	82.69		

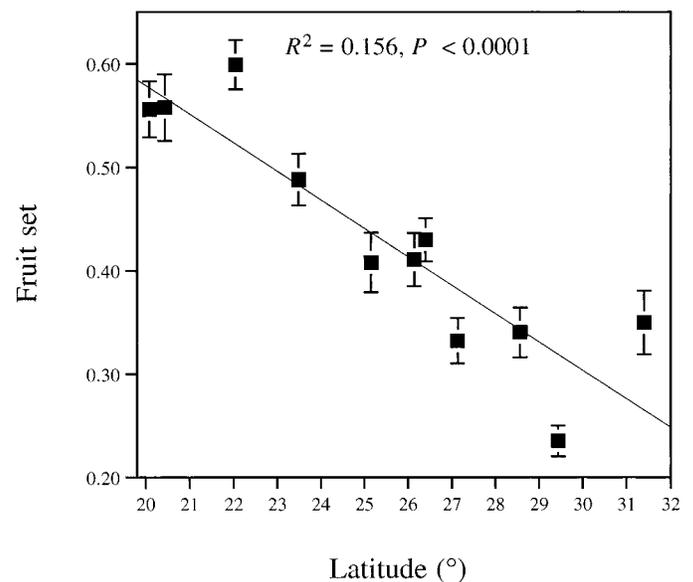


Fig. 7. Latitudinal decrease in fruit set per individual (no. fruits/no. flowers) in 10 populations of *Agave lechuguilla*.

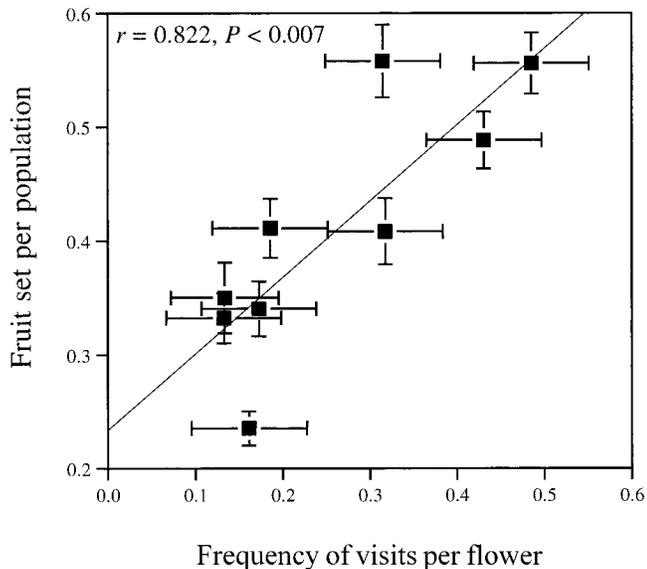


Fig. 8. Correlation (Pearson coefficient) between frequency of visit per flower of the total potential pollinators and fruit set (population mean  $\pm$  SE) for nine populations of *Agave lechuguilla*.

shorter, more open, and red; and the fruit set was lower. A previous study found that nectar characteristics also show a similar clinal pattern: in the south there was more nectar per flower, with lower sugar concentration, and very concentrated nectar in lower volume in the northern populations (Cadaval, 1999). These traits suggest adaptation in the south to nocturnal pollinators, such as bats and/or hawk moths, whereas in the north it seems to change due to diurnal pollinators, mainly bees. In this respect the role of red color in tepals could be difficult to interpret in northern populations, since bees are relatively insensitive to it (Faegri and Van der Pijl, 1971; Proctor and Yeo, 1973). On the other hand, hummingbirds are attracted to red color (Proctor and Yeo, 1973) but their visits decreased to the north. In addition, there is evidence that bees, especially *Xylocopa*, visit some red flowers extensively (Scott, Buchmann, and O'Rourke, 1993).

In all the studied traits we found not only a clinal pattern, but we also estimated significant differences among most of the populations, indicating geographic differentiation and suggesting adaptation at a local scale. Additionally, in most of the traits we found that a substantial component of the variation was due to the differences among individuals within the populations. This may indicate genetic differences among them and will favor the possibility of natural selection acting within each population. Unfortunately, we do not know the genetic basis of this morphological differentiation, and explicit genetic experiments will be needed to advance in this point. Also, environmental or age factors could be contributing to differences among individuals. We also have to consider the effect of vegetative propagation on the expression of the characters, as it maintain genotypes in the populations, retarding the change by pollination pressure.

We found more visits by pollinators towards the south and fewer in the north, which may possibly contribute to the differences in fruit set. We expected to correlate the differences in the reproductive traits among populations with differences in the pollinators on the latitudinal gradient: more bat visits in the south and more bee visits in the north. Nevertheless, the

visitor data indicated not a single bat visit and no clear differences in the proportions of the different groups of visitors in the gradient. In general, bees are the most important visitors to the flowers all along the gradient.

**Floral visitors**—The shape and the pale color of the southern flowers suggest pollinators adapted to a nocturnal habit. The *Agave* genus is traditionally regarded as bat pollinated (Arizaga et al., 2000a, b), but hawk moths and other animals are important visitors to their flowers (Eguiarte, Souza, and Silva-Montellano, 2000; Slauson, 2000). Hawk-moth-pollinated flowers are very similar to bat-pollinated ones, but are smaller and have fewer resources (Baum, 1995; Cadaval, 1999). Nevertheless, we were surprised by the total lack of visits by nectarivorous bats in the range of distribution of *A. lechuguilla*. This may be because our observations were limited, i.e., in other populations or sites or in other years bats may be present or even abundant. At present we only know that observations in other years in selected populations of *Agave* spp. (including *A. lechuguilla*) in the Chihuahuan desert also have not recorded a single bat visit (A. Silva, M. Mandujano, and J. Golubov, UNAM, unpublished data). Declines in the population sizes of nectarivorous bats, in particular *Leptonycteris*, have been reported (Howell, 1979; Howell and Roth, 1981; Wilson et al., 1985; Eguiarte and Búrquez, 1988). This, coupled with the fact that they are a far rarer species in the Chihuahuan desert than in the Sonoran desert and on the Pacific slope of Mexico as well as their migratory habits and foraging behavior, may make them rare and unreliable pollinators in the Chihuahuan desert (Howell, 1979; Cockrum, 1991; Fleming and Nuñez da Silveira, 1993; Wilkinson and Fleming, 1996; but see Kuban, 1989; and Hoyt, Altenbach, and Hafner, 1994).

Hawk moths were the most common potential pollinators in three of the nine evaluated populations. As mentioned above, hawk moths are common visitors to *Agave* flowers, and in some cases may be the most important pollinators. On the other hand, hawk moths are very unreliable pollinators, as they may not be active on cold nights due to physiological restrictions (Martinez del Rio and Búrquez, 1986). Also, their population sizes may fluctuate as a consequence of changes in their larval feeding plant populations, differences in weather, or in parasitoid populations in the previous year (Janzen, 1988; Haber and Frankie, 1989).

Overall, the more common visitors to *A. lechuguilla* flowers were bees. The visitation frequency of large bees was higher in the south than in the north. Nevertheless, given the morphology of the flowers, we suspect that in the north they were more important as pollinators, because the sizes would allow them better pollen transportation and because the fecundity of northern *A. lechuguilla* plants seems to be more limited by pollinators. Considering their foraging behavior and the local sizes and shapes of the flowers, *Xylocopa californica* bees of the north may be more efficient pollinators than the *B. pennsylvanicus* of the south. Data from detailed experiments in other years suggest that this is true (Silva-Montellano, 2001). We have no explanation for the lack of visits of *B. pennsylvanicus* in the north, despite the fact that they visit other *Agave* species in Big Bend National Park in Texas (Kuban, 1989). *Xylocopa californica* bees use dead flowering stalks of *A. lechuguilla* as nest sites (Scott, Buchmann, and O'Rourke, 1993), providing the opportunity to be closer than *B. pennsylvanicus* to the flowers of *A. lechuguilla*. Hummingbirds had a secondary role

as pollinators, because of their lower visitation frequency, and they seemed to use the flowers opportunistically, depending on the other available resources and competition with other organisms.

Our results agree with the interspecific observations of Schaffer and Schaffer (1977) and of Freeman et al. (1983) on the evolution of nectar and morphology adapted to bee pollination in some northern (Arizona) species of *Agave*.

Two critical questions arise from our observations: why do the southern populations maintain a bat pollination syndrome if there are no bats? And why do the flowers in the north maintain nectar and pollen production at night? The easiest answer may be to invoke “phylogenetic constraints,” but the fact that the northern populations changed in floral morphology indicates that some of the traits have changed. This situation may be explained by three different scenarios: (1) Perhaps in the south the selective pressures are less strong. (2) Probably the northern populations have had more time to adapt, because in the south the bat populations have disappeared more recently or because gene flow with other southern bat-pollinated populations or species swamped the efficiency of natural selection. (3) An intriguing possibility was recently raised by Aigner (2001); he suggests that in some cases floral traits may show adaptation to minor or less effective pollinators. We do not have data at the present moment to solve this problem, and we believe the solution will not be easy to determine. The other question is why the nocturnal nectar and pollen production is maintained in all the populations. This could be the result of “phylogenetic constraints,” as all the species in *Agave* and *Manfreda* that have been studied (see review in Eguiarte, Souza, and Silva-Montellano [2000]) had similar nectar production and pollen release patterns. On this point we have to reconsider the role of the main robber *A. mellifera* as an important force in the maintenance of the nocturnal characteristics of the flowers, because they remove most of the pollen in the early morning, preventing the change to diurnal pollination.

**General pattern and evolution**—We consider that in *A. lechuguilla* the differences in floral characteristics along the gradient are mainly adaptive, given the consistency of the clinal patterns and large population sizes and abundance of the populations, coupled with very high levels of genetic variation and gene flow (Silva-Montellano, 2001). Both reproductive traits and animal visitors highlight the problem of understanding the process of adaptation to the pollinators and the reproductive ecology of a species. For each population, the suite of reproductive traits is different. There is not a single “typical” or “average” population. In this particular case, the variation in most traits is more or less congruent and coordinated and follows a clear clinal pattern. The situation for the visitors seems to be more critical, as we showed that they change in space, but given that the data on floral visitors is really an instantaneous “photograph” of a few days in a few plants, it is logical that there is going to be large variation within and among sites and years. These patterns clearly relate to the coevolution mosaic ideas of Thompson (1997). In each population the distribution of floral characters may be different, and the pollinators will be different (in species or abundance). The result could be differential adaptation to each population, which, combined with gene flow, extinction, and colonization, will generate a complicated tapestry of adaptation and coevo-

lution not very different from the shifting balance ideas of Wright (1931, 1932).

**Conclusion**—It is clear from the differences and variability of patterns, not only among populations but also among individuals in each population, that the pollination syndrome characterization, although attractive as a practical and general descriptive tool, may be more of a burden than an asset in detailed evolutionary studies (Waser, 1983; Herrera, 1996; Waser et al., 1996; Aigner, 2001). The requirement of specificity to the most effective pollinator could be one of the major restrictions in using this concept in a practical way, especially if there are several different pollinators with the concomitant difficulties in determining their respective efficiency or in categorizing alternative behaviors and visitation patterns of one pollinator in particular (Thompson and Pellmyr, 1992; Sahley, 1996; Temeles, 1996; Bruneau, 1997; Aigner, 2001). Resource-rich flowers, such as those of *Agave*, attract a broad range of animals that use the flowers, and in some conditions these animals can be efficient pollinators. Many of the floral traits may be better understood as general exaptations (Gould and Vbra, 1982), rather than good adaptations to the pollinators we may see in a given moment. Geographic and temporal variation in floral visitors, reproductive traits, and their interaction, and detailed studies of adaptation should acknowledge the complex geographic mosaic of the interaction (Thompson, 1997) in a model involving differential adaptation, local extinction, and colonization in a metapopulation landscape generating a shifting balance-like evolution. This is a daunting perspective, but if it is not taken into account, we will only have inadequate sketches of the evolution of the reproductive traits of flowering plants.

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## ERRATUM

The publications office of the *American Journal of Botany* regrets that the following names were erroneously omitted from the list of Reviewers of Manuscripts, printed on pp. 160-162 of the January 2003 issue:

Isabelle Dajoz  
Vincent M. Eckhart  
J. Phil Gibson  
Pär Kent Ingvarsson  
John B. Pascarella  
Kathleen L. Shea  
Judy L. Stone  
Dieter Uhl

The work of all reviewers is essential to the success of the publication process.