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The Importance of Bats to Agaves

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Abstract:

The success of sexual reproduction in paniculate agaves is strongly dependent on nectar-feeding bats. Since bat populations have declined, Agave seed set has been reduced to less than 5% of its maximum potential. Where bats remain, agaves in dense patches show higher seed set than do outlying plants, suggesting that the pollinators favor grouped plants. This behavior may reinforce the plants' tendency toward a clumped dispersal pattern.

Paniculate agaves, or century plants, play a significant role in the ecology of Sonoran desert communities (1). The plants have provided food, moisture or shelter for a great variety of animals, both recent and extinct (2). They have been exploited by people for food, fiber and alcoholic beverages since pre-Columbian times and still serve as food plants to many country peoples (3). Howell (4) has shown a mutualism between nectar-feeding bats, primarily the genus Leptonycteris, and several species of Agave. Morphological, biochemical and temporal characters of the plants are consistent with the syndrome of chiropterophily (bat - pollination) as elucidated by Van der Pijl (5). With the steady decline of nectar-feeding bat populations, at least in the northern part of their range (6), it is important to show the role of these animals in the reproductive biology of agaves.

In this article, we report that Agave palmeri Engelm. is strongly allogamous; that there is a strong decline in fecundity when bats do not visit the plants, and that a trend of declining sexual reproduction in the last 30 years parallels a decline in bat numbers during that same period. In addition, we show that seed set of "outlying" plants is low, even when bats are in the area, suggesting that the animals concentrate their visits on grouped plants, providing a strong stimulus for, or reinforcing, the tendency of the plants to cluster (Fig. 1).

To ascertain the degree of allogamy, we used standard techniques of hand pollination (7). Results shown in Table 1 indicate only a minor tendency toward self-fertilization. Such results are not unexpected in a plant with strong protandry. The maturing of A. palmeri stigmas usually occurs 3-4 days after the shedding of pollen. In the unlikely event of autogamy, self-fertilized seeds cannot constitute more than a very minor part of the total reproductive output.

Since the plants rely strongly on pollen from other individuals for sexual reproduction, we examined the time of maximum stigmatic receptivity to reinforce field observations that bats were frequent and important visitors which might accomplish pollen transfer. We used the techniques referenced above to pollinate inflorescences of 4 plants during a 24 hr. period beginning on the evening when the stigmas first showed signs of receptivity. Anther dehiscence occurs at approximately 8 P.M.; prior to that time anther sutures are closed and no pollen is available. During the night, animals or desert breezes remove pollen from the anthers; by morning there is virtually no pollen present. Figure 2 shows receptivity peaking early in the night, decreasing somewhat toward dawn and further diminishing during the daytime hours. These results, and the visibly nocturnal nature of the anthers, stigma and nectar production (8) rule out the reproductive importance of bees and hummingbirds which are frequent diurnal visitors to the nectar-rich plants.

In Arizona during 1976 and 1977, the senior author (DJH) visited every published U.S. locality for L. sanborni and all caves and mines in the vicinity of those localities. No nectar-feeding bats could be found in the Chiricahua or Rincón mountain areas; however, a colony of approximately 200 Leptonycteris remained in the Patagonia area. In the fall of these years, we recorded fruit set from paniculate agaves in the 3 areas (Fig. 3) and calculated the ratio of viable/inviable seeds in those fruits that were set (9). At the Patagonia site, 81% of the flowers set fruit and fruits showed 70% seed viability (2 year average of 100 plants). In plants from the Chiricahua and Rincón areas approximately 25% of the flowers set fruit. 69-95% ($\bar{x}$ = 75%) of their flowers shed without fruits setting. In a random sample of 100 fruits taken each year from the latter

two localities, no fruit showed greater than 25% mature seeds; the overall average was 19.5% viable seeds/fruit. The potential impact of declining bat populations on the sexual reproduction of paniculate agaves may be judged by considering the following: Gentry (1) estimates that under normal circumstances only 1 seed in a half million to a million germinates and grows to maturity. A typical A. palmeri has approximately 1300 flowers; each fruit contains on the order of 600 ovules so that under the best conditions 780,000 ovules/plant might be fertilized. The data from plants in areas without bats indicate that only 4.88% of the maximum potential for sexual reproduction is being achieved. Only about 38,000 of 780,000 ovules per plant produce seeds. Combined with the naturally low germination/maturation figures, this implies a tenuous future for the plant population (10).

Where bats are still in residence, there is a difference in seed set between plants which are part of a cluster and those which are outliers to the usual aggregations. Leptonycteris visit agaves in flocks (8); apparently plants that are separated from others receive less attention from the foraging groups. We estimated fecundity in 32 members of various Agave patches and in 32 plants isolated from the nearest patches by 400 m to 18 km. Within patches, plants averaged 43 viable seeds/30mm locule (range 35-- 49, N=320) (11). There was no difference between central and peripheral plants. Isolated plants averaged 6.6 viable seeds/30mm locule (range 0 - 18, N = 320). Although outlying plants clearly produce fewer mature seeds, there is no correlation between the distance from nearest neighbor (400 m - 18 km) and number of viable seeds. These data and experimental evidence on foraging optimization in Leptonycteris (12) suggest that the flock-foraging bats confine their visits to grouped plants and have likely influenced the evolution of the plants toward clumped distribution.

Since there was considerable evidence for the critical role of bats, we became interested in the reproductive success of the plants before and during the years of bat decline. We examined fruit capsules (13) from herbarium specimens (University of Arizona) of 3 chiropterophilous Agave species from the bats historic range in Arizona. Agave palmeri pods from the Rincón mountain area showed 80% fecundity ($N = 10$ fruits) in 1938, 90-100% fecundity ($N = 30$) in 1940 and 1941, but 0-10% fecundity ($N = 30$) in 1976. The seed set of Agave deserti fruits dropped from 80% ($N = 20$) in 1930 to 50% ($N = 10$) in 1975. Agave parryi fruits had 90% viable seeds in 1935 ($N = 20$), 70% in 1940 ($N = 20$), but from my own 1976 counts ($N = 100$), A. parryi was faring as poorly as A. palmeri in recent years. For comparison, ten each herbarium specimens of A. parviflora and A. schottii, insect pollinated, spicate agaves (14) from the same region, showed predominantly viable seeds for the last 4 years.

The paniculate agaves are classic examples of semelparous organisms. After 8-25 years of vegetative growth, they make a single, intense reproductive effort followed by rapid senescence and death. The magnitude of energy expenditure associated with flowering as shown in Table 2. These figures are conservative since they cannot reflect the energy involved in the work of growth and maintenance of the flowering stalk. In an unrelated study ongoing in our laboratory we measured the caloric value of leaves and roots of Agave palmeri. The species has a relatively small basal rosette, approximately 4900 dry grams of leaf and 2000 dry grams of root. A finely milled mixture gave bomb calorimetry results of 4.26 kcal/gm. We calculate therefore, 29394 kcal in the non-reproductive plant parts; this energy amassed over approximately 2 decades. The 16923 kcal given over to "advertising" and reproduction in the one season then represent over half (59%) of the measurable productivity of the plant. Schaffer and

Gadil (15) discuss the natural environmental conditions under which this reproductive strategy is advantageous. A supply of pollinators is taken for granted. When a highly allogamous, zoophilous species is faced with sporadic pollinator availability, due to decline of numbers and eventual disappearance of the animals from the area, the risk of such a "big-bang" reproductive mode becomes obvious. The decline of any major organism within a community has widespread ramifications. In cases of mutualism, there is reciprocal negative feedback. Diminishing Agave populations may hasten the decline of glossophagine bats. The saguaro cactus (Carnegiea gigantea), and Organ Pipe cactus (Lemaireocereus thurberi), for which the bats are also important pollinators (16), may be effected. The decline of such major plants as columnar cactus and agaves in desert areas could result in a decrease in animal diversity.

Treatment *	# fruits set	Range % viable seeds/fruit
Individual flower with itself	0	0
Different flowers, same panicle	7	6-12%
Different panicles, same plant	5	4- 9%
<u>A. palmeri</u> x <u>A. palmeri</u> different plants	9**	84-89%
<u>A. palmeri</u> ♀ x <u>A. parryi</u> ♂	0	0
<u>A. palmeri</u> ♀ x <u>A. schottii</u> ♂	0	0
Control (all manipulations, no hand pollination)	2	7-11%

Table 1: Breeding system experiments with A. palmeri ♀♀. The data show a high degree of allogamy. The few fertile seeds produced in non-outcrossed treatments may indicate apomixis or contamination by exogamous pollen, an almost inevitable problem in field studies. * N = 10 for each treatment ** 10th fruit fallen after partial development, not tabulated.

Quantity	part	kcal
1265	corollas	1602
1265	ovaries & ovules	3978
8855	stamens, styles, stigmas	573
948.75 cc	nectar	759
38 g	pollen	202
67	fruit capsules	984
18462	non-viable seeds	753
1	stalk	8072
Total		16923

Table 2: Bomb Calorimetric determination of reproductive effort of a typical Agave palmeri in an area where Leptonycteris are no longer found. Pollen carried by incidental animal visitors or wind may account for the 67 fruits (of 1265 potential). One fertile ovule (in ± 600) is sufficient to insure fruit set. Figures are averages of samples run in triplicate. No samples showed more than 5% variation. The caloric total represents energy sufficient to support the author (D.J.H.) for 10 days.

Figure 1: Agave palmeri in flower in the Chiricahua mountains,
Cochise Co., Arizona. Note highly clumped distribution.

Figure 2: Fecundity of Agave palmeri flowers as a function of
hour pollinated.

Figure 3. Fruit and seed set in Agave palmeri. A) Aug 1, Chiricahua, in flower, B) Aug 25, no bats in area, many flowers shed, C) Sept 12, no bats in area, no fruit set, D) Panicles gathered in fall: left Patagonia, with bats; right Chiricahua, without bats, E) Seed set (dark seeds are viable): left Patagonia, with bats; right Chiricahua, without bats.

References and Notes

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