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SEXUAL REPRODUCTION IN AGAVES: THE BENEFITS OF BATS; THE COST OF SEMELPAROUS ADVERTISING¹

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Abstract. The pollination success of *Agave palmeri* is strongly dependent on nectar-feeding bats. In areas with very low or nonexistent bat populations, *Agave* seed set is <5% of its maximum potential. A 30 yr trend of declining seed set parallels a decline in bat numbers during that period. We speculate that habitat destruction and an increase in human use of *Agave* are causal factors. Over half of the measurable energy in the plant biomass is allocated to advertising and reproduction. We discuss the costs and risks involved in the semelparous strategy when pollinators decline. 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' colonial tendencies.

Key words: *Agave*; bats; chiropterophily; *Glossophaginae*; *Leptonycteris*; pollination; semelparity; reproductive effort; seed set.

INTRODUCTION

Paniculate agaves, or "century plants," such as *Agave palmeri* and other members of the subgenus *Agave*, play a significant role in the ecology of Sonoran desert communities (Gentry 1972). The plants have provided food, moisture, or shelter for a great variety of animals, both recent and extinct (Harrington 1933, Castetter et al. 1938). 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 (Hodge 1963, Felger and Moser 1970). Howell (1974a, 1975) and Howell and Hodgkin (1976) have 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 (1936).

Data from studies by Hayward and Cockrum (1971) and Easterla (1972) show a steady decrease in nectar-feeding bat populations, at least in the northern part of their range. J. Mierhauser, Head Naturalist of Colossal Cave State Park, Arizona, has watched the *Leptonycteris* populations in that cave decline from approximately 5000 to 5 or 6 bats within the last 5 yr (personal communication). In the 1950's, Colossal Cave held 10 000–20 000 nectar bats. D. Howell and Dr. S. Humphrey, University of Florida, visited all known United States localities for *Leptonycteris sanborni* in 1974 and found 135 animals. General habitat destruction coupled with *Agave* exploitation in north-

ern Mexico (for food and "home-brew" alcoholic beverages) may be instrumental in this bat decline. Because of the sharp reduction in the pollinators, it is important to document the critical role of these animals in the reproductive biology of agaves.

MATERIALS AND METHODS

The study subjects

Agave palmeri Engelm (Agavaceae) is a heliophilous xerophyte, patchily distributed in rocky areas between 900 and 1800 m in southern Arizona, USA, and adjacent Sonora, Mexico. Plants are usually clumped in their distributional pattern (Fig. 1), so much so that Gentry (1972) refers to local populations as colonies. Succulent leaves form a basal rosette approximately 100–120 cm broad. *A. palmeri* is a monocarpic perennial, requiring tens of years to mature (Gentry 1972). A single inflorescence is 3–7 m high with 12–20 elliptical panicles averaging 60 flowers each. The 30–50 mm tubular flowers are strongly protandrous. Over the course of a week, a panicle makes the transition from a predominantly male condition to the female or pistillate state. Toward the end of a flower's life, the stamens droop and wither; eventually only the exerted style is obvious; the tripartite stigma is parted and viscid. The buds open in the evening, the anthers are exerted and the stamens unfold exposing ripe pollen. Anther dehiscence occurs at approximately 2000; 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. Nectar production is also nocturnal (Howell 1972, Schaffer and Schaffer 1977). Panicles flower sequentially for about 40 d. In-

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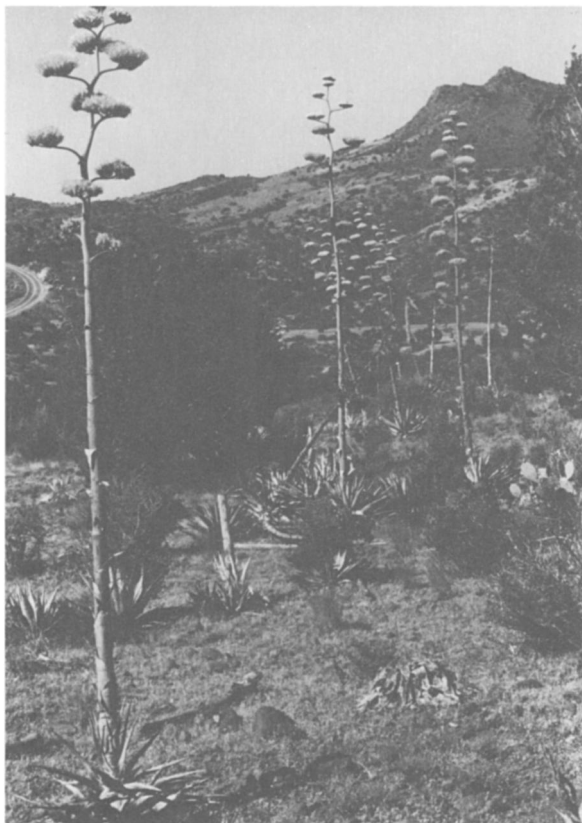


FIG. 1. *Agave palmeri* in flower in the Chiricahua mountains, Cochise County, Arizona. Note highly clumped distribution.

floriscences may be found within the southern Arizona population from late June or early July through early September. After flowering, the plants senesce rapidly and die. If pollinated, the ovary develops into a persistent dry capsule containing hundreds of triangular seeds, approximately 6 mm along the edge. These are shaken out of the fruiting capsule by the action of wind and perhaps by the alighting and departing of birds that commonly use agave peduncles as perches.

Pollination and seed set measurements

To ascertain the degree of allogamy, we used standard techniques of hand pollination (Alcorn et al. 1959, Heithaus et al. 1974, Carpenter 1976). Experiments were executed on *A. palmeri* inflorescences to determine the amounts of seed set under the following conditions:

- A) Autogamous pollination: stigmas on each flower receive pollen from anthers of that flower.
- B) Geitonogamous pollination: each test flower receives pollen from a different flower within the test panicle.
- C) Geitonogamous pollination: each test flower re-

ceives pollen from another flower on the test inflorescence, but not from the test panicle.

- D) Allogamous pollination: test flowers receive pollen from another individual plant within the test population.
- E) Pollination with a sympatric congener of same subgenus (*Euagave*); *A. palmeri* receives *A. parryi* pollen.
- F) Pollination with sympatric congener of different subgenus (*Littaea*); *A. palmeri* receives *A. schottii* pollen.
- G) Control: all manipulations performed on test flowers but no pollen is hand-transferred.

Plants chosen for pollen reception and donation were centrally located within colonies. Test panicles were selected from the middle section of *A. palmeri* inflorescences and loosely covered with fine nylon mesh several days prior to treatment. The mesh excluded animals larger than 1.5 mm, yet allowed microenvironmental temperature and humidity to vary normally. Stigmas of test flowers were covered with sealed lengths of paper drinking straws, taped in place, 3–4 d prior to receptivity. Other flowers within the panicle were removed or emasculated before they reached the dehiscence stage. When pollen from donor flowers was collected, it was kept in glass vials, covered but not airtight. We applied the pollen with cotton swabs until the stigmatic surfaces were coated densely and uniformly yellow. Since receptivity peaks early in the night, hand pollination in these experiments was confined to the hours of 2000–2200. The nylon mesh protected the test panicles through the fruiting period and caught any flowers, fruits or seeds that fell. By September, *Agave* fruiting capsules are dry and are splitting to release seeds, so it was in this month that we gathered the fruits and counted the seeds. The series of treatments was duplicated during two summers.

Details of the treatments are as follows:

- A) Stigmas of 10 numbered flowers within the test panicle were covered with straws 1–2 d prior to dehiscence of pollen, and 3–4 d prior to stigmatic receptivity. On the evening of pollen dehiscence, pollen-laden anthers were clipped from each numbered flower and placed in separate numbered vials. One to two days later, receptive stigmas were treated with pollen from the corresponding vial, and the netting and straws were replaced.
- B) Stigmas of 10 recipient flowers within the test panicle were covered with straws as in A. Anthers were clipped and discarded. Ten donor flowers were designated within the same panicle. One to two evenings later, pollen was collected from the newly dehiscence donors by clipping all donor anthers into a vial. After the vial was shaken to mix the pollen, stigmas were treated in the usual manner. Netting and straws were replaced.
- C) Stigmas of 10 flowers were covered in the usual

manner. Pollen was gathered as in B from 10 donor flowers on an adjacent (usually lower) panicle of test inflorescence and applied to recipient flowers (same inflorescence, different panicle) at time of stigmatic receptivity.

- D) As in C, but 10 donor flowers were selected from a middle panicle of another inflorescence within the population.
- E) As in D, but 10 donor flowers were selected from *A. parryi* approximately 4 km from *A. palmeri* population.
- F) As in E, but 10 donor flowers were selected from *A. schottii* in Guadalupe canyon, their pollen collected at time of dehiscence (1030).
- G) Stigmas of 10 flowers were covered, anthers were clipped, straws were lifted and replaced on the evening of receptivity, but no pollen was transferred.

We also investigated the time of maximum stigmatic receptivity. We used the techniques discussed above to pollinate inflorescences of four plants during a 24-h period beginning on the evening when the stigmas first showed signs of receptivity.

Bat decline and impact on plants

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. In Arizona during 1976 and 1977, the senior author (D. J. Howell) visited every published United States locality for *Leptonycteris sanborni* and all caves and mines in the vicinity of those localities. In the fall of these years, we recorded and photographed fruit set and seed set in paniculate agaves as a function of bat abundance in three Arizona areas: the Chiricahua mountains, Cochise County; the Rincon mountains, Pima County; and foothill areas near Patagonia, Santa Cruz County.

Leptonycteris visit agaves in flocks (Howell 1979); apparently plants that are separated from others receive less attention from the foraging groups. We estimated fecundity (fruit set and seed set) in 32 members of various *Agave* patches and in 32 plants isolated from the nearest patches by 400 m to 18 km. Wherever possible we selected clustered and isolated individuals that were matched for height of inflorescence and number of panicles. Since pods may vary somewhat in size and form, seed set was estimated by counting the number of mature seeds per central 30 mm of locule.

We also examined fruit capsules from herbarium specimens (University of Arizona) of three chiropterophilous *Agave* species from southern Arizona: *A. palmeri* ($N = 70$); *A. parryi* ($N = 140$); and *A. deserti* ($N = 30$). For comparison, we examined 10 specimens each of *A. parviflora* and *A. schottii*, insect-pollinated, spicate agaves also from the southern part of

TABLE 1. Breeding system experiments with *Agave palmeri*. The data show a high degree of allogamy. The few seeds produced in nonoutcrossed treatments may indicate apomixis or contamination by exogamous pollen, an almost inevitable problem in field studies.

	Treatment*	Number of fruits set	Range % fertilized ovules per fruit
A	Individual flower with itself	0 (0, 0)‡	0
B	Different flowers, same panicle	7 (5, 9)	6–12%
C	Different panicles, same plant	5 (5, 5)	4–9%
D	<i>A. palmeri</i> × <i>A. palmeri</i> different plants	9† (10, 9)	84–89%
E	<i>A. palmeri</i> ♀ × <i>A. parryi</i> ♂	0 (0, 0)	0
F	<i>A. palmeri</i> ♀ × <i>A. schottii</i> ♂	0 (0, 0)	0
G	Control (all manipulations, no hand pollination)	1 (2, 0)	7–11%

* $N = 10$ recipient (♀) flowers and 10 donor (♂) flowers for each treatment. Experiments were performed in duplicate (during two summers) so fruit set is the average of two plants.

† Tenth fruit on one plant fallen after partial development, not tabulated.

‡ Numbers in parentheses are numbers of fruits set in experimental years 1 and 2.

the state. Mature seeds are black; unfertilized ovules remain white. The pigment in mature seeds leaves black stripes on the inner surface of the dry fruit capsules; thus the empty pods alone can provide an assessment of reproductive success.

Energy allocated to sexual reproduction

The energy content of *Agave* parts was measured using a Parr bomb calorimeter. Samples from five plants were dried, finely ground using a Wiley mill and run in triplicate.

RESULTS AND DISCUSSION

Pollination and seed set

Although protandry in some plants may be sufficient to insure out-crossing, the unsynchronized blooming of panicles within the *Agave* inflorescence leaves open the possibility of self-fertilization between staminate flowers of one panicle and pistillate flowers on an adjacent panicle. However, the data in Table 1 show that *Agave palmeri* is strongly allogamous with only a slight tendency toward selfing. It can be seen that autogamous seeds constitute only a minor part of the total reproductive output.

Our examination of the time of maximum stigmatic receptivity (Fig. 2) reinforced our field observations that bats were important visitors that might accomplish pollen transfer. Receptivity peaks 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

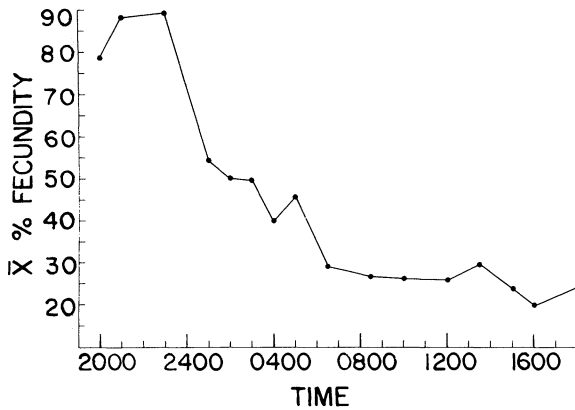


FIG. 2. Seed set of *Agave palmeri* flowers as a function of hour pollinated.

and nectar production (Howell 1979) rule out the reproductive importance of bees and hummingbirds which are frequent diurnal visitors to the nectar left in the flowers. Both bees and hummingbirds tend to enter the flower immediately above the tepals and below the exerted anthers or stigmas; these behaviors minimize their contact with reproductive parts of the flower and further reduce the chances that they effect pollination. Furthermore, bees tend to gather their pollen loads from a single inflorescence (McGregor et al. 1959, Alcorn et al. 1961).

The impact of declining bat populations

In our survey of known *Leptonycteris* roosts and nearby caves and crevices that might serve as potential roosts we found no bats in the Chiricahua or Rincon mountain areas; however, a colony of approximately 200 *L. sanborni* remained in the Patagonia area. Fruit set, and the number of mature seeds within each fruit, reflected the presence or absence of pollinators in these areas (Fig. 3). Apparently one fertile ovule (out of approximately 600 potential) is enough to prevent abortion of the ovary and permit fruit development. At the Patagonia site, 81% (range 63–90%) of the flowers set fruit and fruits showed 70% (range 10–92%) fertilized ovules (2-yr average of 100 plants). In plants from the Chiricahua and Rincon areas approximately 25% of the flowers set fruit. Of their flowers, 69–95% (\bar{x} = 75%) shed without fruits setting. In a random sample of 100 fruits taken each year from the latter two localities, seed set was as low as 5% and never greater than 25% mature seeds; the 2-yr average for both sites was 19.5% mature seeds per fruit. Several agents might account for the small percentage of ovules that were fertilized. The data in Table 1 indicate a minor tendency for autogamy; sphinx moths occasionally visit agaves at night and may contact reproductive parts; and an uncommon, solitary nectar-feeding bat, *Choeronycteris mexicana* inhabits the area

and is known to feed from agaves in some months (Howell 1974b).

The potential impact of declining bat populations on the sexual reproduction of paniculate agaves may be judged by considering the following: Gentry (1972) estimates that under normal circumstances only one 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 per plant might be fertilized. The data from plants in areas without bats indicate that only 4.88% of the maximum potential for seed production is being achieved. Only about 38 000 of 780 000 ovules per plant produce seeds. Combined with the naturally low germination to maturation figures, this may imply a tenuous future for the plant population. Further study is indicated in this regard: if intra-species competition plays an important role in germination and survival to maturity, fewer seeds might change the dynamics of population control without affecting population size. However, a study by Nobel (1977) on *Agave deserti* suggests that survival is highly related to seed predation. Rodents took 84% of seeds on the ground. Further, there was much seedling mortality due to desiccation, suggesting that young plants may survive only during relatively few, rainy years. If these mortality factors pertain as well to the similar *Agave palmeri*, any reduction in the number of mature seeds could indeed depress the population. Further study is needed to determine if density-dependent compensation might occur.

Herbarium specimens of the dry fruiting capsules of paniculate agaves indicate a decline in pollination success over the 30 yr that *Leptonycteris* populations have been diminishing. *Agave palmeri* pods from Rincon 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 1957. *Agave parryi* fruits had 90% seed set in 1935 (N = 20), 70% in 1940 (N = 20), but from my own 1976 counts (N = 100) *A. parryi*, with 4% seed set, was faring as poorly as *A. palmeri* in recent years. For comparison, 10 herbarium specimens each of *A. parviflora* and *A. schottii*, insect-pollinated, spicate agaves (Schaffer and Schaffer 1978) from the same region, showed a predominance of viable seeds for the last 4 yr.

Where *Leptonycteris* 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. Plants that are separate from these aggregations had lower seed set than did plants within patches. Isolated plants averaged 6.6 mature seeds/30 mm of locule (range 0–18, N = 320 fruits). Colonial plants averaged 43 mature seeds/30 mm of locule (range 35–49, N = 320 fruits). Although outlying plants clearly received less pollination, there was no

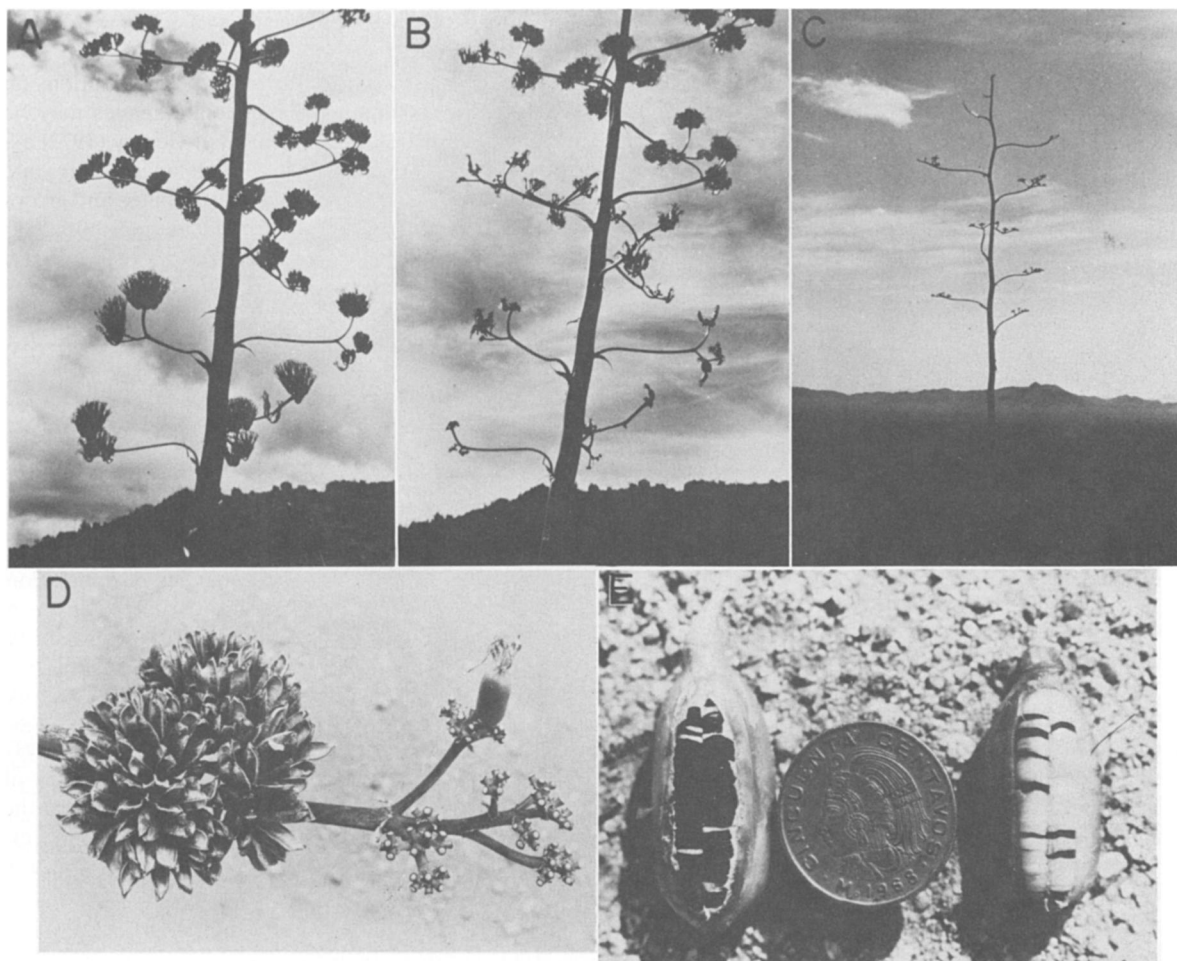


FIG. 3. Fruit and seed set in *Agave palmeri*: (A) 1 August, Chiricahua, in flower; (B) 25 August, no *Leptonycteris* in the area, many ovaries shed; (C) 12 September, no *Leptonycteris* in the area, no fruit set; (D) Panicles gathered in fall: left, panicle with dehiscent capsules, from Patagonia (*Leptonycteris* present); right, panicle from Chiricahua (*Leptonycteris* absent); (E) Seed set (dark seeds are fertilized ovules): left, Patagonia, with *Leptonycteris*; right Chiricahua, without *Leptonycteris*. Diameter of the coin shown is 24 mm.

significant correlation for these plants between the distance from nearest neighbor (400 m–18 km) and number of fertilized ovules (Fig. 4). There was no obvious morphological difference or difference in seed set between central and peripheral plants of a group. The number of fertilized ovules in 150 fruits from 15 plants on the edge of clusters (35–46) was within the range of those in 170 fruits from 17 central plants (35–49). These data and experimental evidence on foraging optimization in *Leptonycteris* (Howell and Hartl 1980) suggest that the flock-foraging bats confine their visits to grouped plants and have probably influenced the evolution of the plants toward clumped distribution.

The cost of semelparous advertising

Although most agaves have some potential for vegetative reproduction via suckers or bulbils, many are classic examples of semelparous organisms. *Agave*

palmeri is not a densely cloning species, especially when compared to examples like *A. huachucensis* or *A. sisalana*. Many populations of *A. palmeri* are characterized by Gentry (1972) as “commonly non-suckering.” Data are unavailable for the exact proportion of mature *Agave palmeri* plants that originated from seed vs. those that arose from nearby plants via underground stems. Such data, in fact, would be most difficult to obtain for the species since stolon connections with the mother plant may be severed once roots and shoots develop on the new plants (Nobel 1977). Even if one were able to follow cohorts of seeds (in spite of high predation) such a study would take many years and an immense sample size. H. Scott Gentry, who had worked on *Agaves* for at least 30 yr, stated (Gentry 1972) that he had never seen a wild seedling *Agave* <1 yr old and encountered 2- and 3-year-olds only sporadically. At the point where young

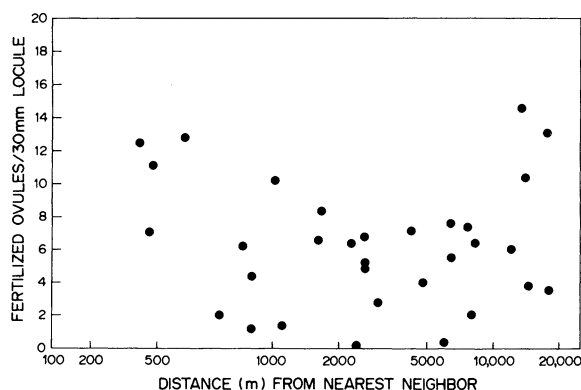


FIG. 4. Seed set in *Agave palmeri* as a function of distance from cluster. Pearson's product-moment correlation coefficient $r = .21$ with 30 degrees of freedom is nonsignificant. Points represent number of mature seeds/30 mm locule, averaged over 10 fruits from each of 32 outlying plants.

Agaves become common enough to be encountered predictably, they may be confused with young vegetative offshoots that have lost stolon connection with the mother plant.

We (the authors) can only take the point of view that most persistent features of an organism are adaptive, and hence sexual reproduction must be important to *Agave palmeri* over the long term. However, the benefits are not achieved without cost. Employing the semelparous strategy when the odds for successful reproduction are so much reduced by pollinator decline clearly has potential risks. When pollinators do not arrive or are scarce, there is little reproductive payoff and advertising effort is wasted. We considered the magnitude of this effort by looking at energy allotment to vegetative and reproductive parts (including "advertising" costs as well as reproductive organs per se). After 8–25 yr of vegetative growth, *A. palmeri* make a single, intense reproductive effort followed by rapid senescence and death. The energy expenditure associated with flowering is 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 energy value of leaves and roots of *Agave palmeri*. The species has a relatively small basal rosette, a standing crop of approximately 4900 dry g of leaf and 2000 dry g of root. A finely milled mixture whole-plant gave bomb calorimetry results of 17.8 kJ/g. We calculate therefore, 122984.5 kJ in the nonreproductive plant parts. The 70805.83 kJ given over to "advertising" and reproduction in the one season then represent over half (59%) of the measurable energy in the biomass of the plant. Nobel (1977) also illustrated the high cost of sexual reproduction in his paper on water relations of *Agave deserti*. Water is mobilized from the leaves to support the inflorescence. Leaves were reduced in

TABLE 2. Bomb calorimetric determination of reproductive effort of a typical *Agave palmeri* in an area where *Lepidopteryx* 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 per ovary) is sufficient to insure fruit set. Energy data represent averages of samples run in triplicate. No samples showed more than 5% variation. The total energy expended is sufficient to support the author (D. J. Howell) for 10 d.

Part	Quantity	Energy (kJ)
Corollas	1265	6702.77
Ovaries and ovules	1265	16 643.95
Stamens, styles, stigmas	8855	2397.43
Nectar	948.75 cc	3175.66
Pollen	38 g	845.17
Fruit capsules	67	4117.06
Unfertilized ovules	18 462	3150.55
Stalk	1	33 773.25
Total		70 805.83

thickness by 75%; almost 18 kg of water was lost from the rosette to the inflorescence. Due to the increased surface area of plants with flowering and fruiting stalks, water loss continued to be much higher for sexual plants than for plants with only vegetative growth. Maccallum (1908) commented on such a crucial diversion of water in *A. americana* as well. Nobel's 1977 study also showed that the photosynthetic capacity of the plants could not keep up with the demands of the growing inflorescence, so massive movement of carbohydrates and other materials from the leaves had to occur. Hence the rosette dies, and the plant can have but a single sexual period.

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. If *Agave* populations are diminishing, the decline of glossophagine bats may be hastened. The saguaro cactus (*Carnegiea gigantea*), and Organ Pipe cactus (*Stenocereus = Lemaireocereus thurberi*), for which the bats (in other months) are also important pollinators (Alcorn et al. 1959, Alcorn et al. 1962, McGregor et al. 1962), may be affected. The decline of such major plants as columnar cacti and agaves in desert areas could result in a decrease in animal diversity. Baker et al. (1971) conclude that large bat-adapted plants with their copious nectar may provide an unwitting service to the community by feeding smaller organisms. Likewise, *Agaves* and columnar cacti provide unique shelter for many types of organisms. Baker reminds us that "the utilization of resources in natural ecosystems is a subject in need of much more intensive study, with implications that go far beyond the 'who eats whom' level of complexity."

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