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Floral biology of the saguaro (*Cereus giganteus*)

I. Pollen harvest by *Apis mellifera*

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Abstract. A saguaro cactus (*Cereus giganteus*) produces an average of 295 flowers per season, each of which produces 286 mg fresh weight of pollen and 543 mg of nectar containing 24% sugar. At 7600 pollen grains/mg pollen, the yearly output per saguaro plant is 6.4×10^8 grains. Based on the measured saguaro density of 6.56 plants/ha, 553 g/ha of pollen is produced yearly. The enormous variation among individual plants in terms of flower numbers and floral bloom patterns is documented.

Honey bees (*Apis mellifera* L.), the main collectors of saguaro pollen, collect an average of 12.2 mg pollen per foraging trip and can thus harvest 23.5 pollen loads from one flower. An average honey bee colony collects 290 g of saguaro pollen over the season, which is 24.4% of their total intake. Individual colonies exhibit wide variation in pollen collecting activities with some closely tracking the pollen resource and others almost totally ignoring it. The average for seven colonies indicates that even though variation is great the overall trend is toward closely tracking and exploiting the saguaro pollen resource. Based on the pollen productivity of saguaro and a hypothetical 90% pollen harvesting efficiency of bees, the pollen harvest potential of the saguaro environment is 1.72 colony equivalents of pollen/ha and 0.5/ha for saguaro alone. This is the first quantitative reporting of the total pollen productivity and pollen resource utilization for any plant and an opportunistic pollinator.

The saguaro (*Cereus giganteus* Engelm.) is a large columnar cactus indigenous to the Sonoran Desert region of Sonora, Mexico and Arizona and California, USA. The plant often grows to a height of more than 9 m with a trunk diameter greater than 40 cm and lives from 150 to 175 years (Hastings and Alcorn 1961; Steenbergh and Lowe 1983; Shreve 1931). The plant grows slowly at first reaching a height of approximately 2.2 m in 30–35 years at which time reproduction commences (Steenbergh and Lowe 1977). The flowers, produced mainly in May and June, are located almost entirely on the growing tips of the main trunk and the side arms. Arms, whose main function appears to be to increase the number of points for flower and fruit production, begin to appear on the sides of the main trunk when the plant reaches a height of 4.5–5.0 m (Steenbergh and Lowe 1977).

Saguaro flowers are white with yellow anthers and stigma and open shortly after dark (2100–2300 h). They remain open until early to late afternoon the next day (1300–1700 h) at which time they close permanently (Peebles and Parker 1941). Saguaro fruits mature in 31–45 days, weigh about 50 g and contain approximately 2,250 seeds (McGregor et al. 1962; Steenbergh and Lowe 1977). Until this study, precise estimates for total numbers of flowers produced per plant were not available. The energetic cost to the plant to produce flowers and fruit is high: plants allowed to reproduce normally grew only $^2/_3$ as much as those whose floral buds were repetitively removed (Steenbergh and Lowe 1977).

The saguaro is an ideal species for studies of energetics and plant–pollinator interactions. The reproductive individuals are large and easily located and counted as are their large, conspicuous flowers. Moreover, saguaro flowers bloom only one day, and the bloom is very predictable (i.e., rainfall levels have little influence). The saguaro also produces large quantities of both pollen and nectar and is attractive to a variety of floral visitors including the polylectic honey bee (*Apis mellifera* L.) which is an imported and easily managed species. Because of the special attributes of both the saguaro and the honey bee, we selected this system as a model for the study of ecological and energetic aspects of a plant and a pollen forager.

We report here for the first time the total available resource (pollen) from one species in its environment, its temporal availability, and the behaviors and efficiencies of a social polylectic bee in tracking and exploiting that resource.

Material and methods

Pollen monitoring site

The investigations were conducted from May 10 through July 15, 1983 in the Saguaro National Monument located on the west facing slope of the Rincon Mountains near Tucson, AZ. The center of the site was located at an elevation of 915 m in an area 1.6 km from the nearest human habitation. The area has been free of grazing by cattle since 1958 and has been allowed to remain undisturbed by economic activities since that time. The surrounding area contains numerous reproductive to senescent saguaros and relatively few young saguaros. Other dominant plants in the area are palo verde (*Cercidium microphyllum* (Torr.)), mes-

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quite (*Prosopis velutina* (Woot.)), catclaw acacia (*Acacia greggii* Gray), creosote bush (*Larrea tridentata* (DC)), triangle leaf bursage (*Ambrosia deltoidea* (Torr.)) plus numerous small annuals and perennials.

Survey of suguaro bloom

Twenty saguaro plants were selected randomly in about equal numbers from the two major subhabitats – rocky slopes and the flat areas surrounding the slopes – and given numbered tags. Twice weekly, beginning May 10 and ending July 15, (one week after the last flower was observed) all the flowers on every arm of each plant were counted. This was accomplished by using a 10 × 14 cm convex mirror mounted on a 13 × 20 cm flat mirror which was attached at a right angle with a 30 cm section of pipe to the top of a 2.7 cm diameter aluminum pole. The pole was adjusted to any length by adding or removing 2.44 m sections. One investigator held the mirror slightly above each plant top or arm and, with the aid of 8 power binoculars, the other investigator counted the number of open flowers (Fig. 1). Counts were made between 0600–0930 h MST. At this time blooming flowers could easily be distinguished from the previous day's flowers and from ones that would open the next day.

Bees and their management

Seven average strength colonies (ca. 1.5 kg adult bees, plus a queen and immature stages) of honey bees were present at the center of the study site. Each colony had been surveyed weekly during the previous year for pollen foraging activities by means of OAC (Ontario Agricultural College) pollen traps placed on the bottoms of the hives. When the experiment began, traps were emptied on each survey day, and the pollen was weighed and frozen for later analysis of species composition.

Pollen production per flower

The amount of pollen produced by individual saguaro flowers was determined by collecting six random flowers shortly after they opened (2230 h) on June 21, 1983. The flowers, which were located with the aid of moonlight, were obtained from four different plants by placing a ladder against the trunk and climbing 3–4 m to the flowers. The flowers were carefully transported to the lab, the basal most part containing the nectaries removed with a razor blade, and they were inverted over aluminum foil and allowed to remain undisturbed until they started to close the next afternoon. At this time a vibrating tuning fork (256 Hz) was touched to the anthers to remove any remaining traces of pollen. The pollen from each flower was weighed and stored at −20°.

The number of pollen grains per mg of pollen collected in this fashion was determined by suspending the pollen in methanol, degassing the samples and counting with a HIAC model PC-320 particle counter.

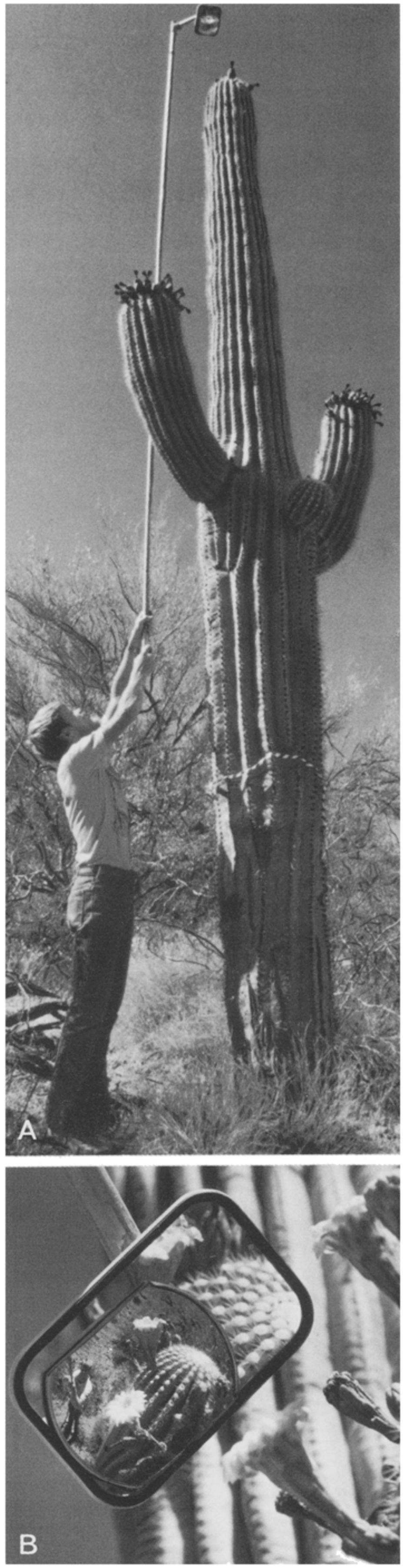

Fig. 1 A. Method used to determine and record the number of flowers on each arm of a saguaro cactus; **B** close-up view of flowers as seen through binoculars (photos by Martha Cooper © 1984 National Geographic Society)

Nectar production per flower

Nectar production of 91 saguaro flowers was measured during early, peak, and late bloom periods by covering flowers with paper bags just as the flowers were opening (one to two h after sunset). The bags were left on during the night and removed after 0800 MST the next morning, at which time the nectar was measured by removal with 100 µl micro capillary tubes. From phenological studies we knew that nectar secretion had ceased by this time (Schmidt and Buchmann, unpublished). The concentration of sugars in the nectar was determined as total dissolved solids using a Bellingham and Stanley hand refractometer.

Other measurements

The number of saguaros in the study area was counted from a 1:1,200 scale aerial photograph of an area of 1.53 km^2 surrounding the study site. The accuracy of this count was checked by ground survey of the actual number of plants in a portion of the area.

Species identities of corbicular pollen from each survey day and from each honey bee colony were determined by microscopic examination. To obtain percentage composition of the different pollen types in the sample, 100 pellets were sampled.

The weight of pollen collected by a honey bee forager was determined by weighing 54 corbicular pellets of saguaro pollen randomly drawn from a survey pollen trap. The amount of nectar (or honey) added to the pellets by the bees was estimated by determining the percentage of sugars (fructose, glucose, and sucrose) in both bee collected corbicular pollen derived from several locations and hand collected pollen. The amount of bee-added sugar was calculated according to the formula:

$$\% \text{ bee-added sugar} = \frac{a-b}{1-b}$$

$a = \%$ (wt/wt) sugar in corbicular pollen.
$b = \%$ (wt/wt) sugar in hand collected pollen.

The quantities of sugars in the two forms of pollen were determined by extracting the pollen in a 100 fold excess of water to which inositol (Aldrich) had been added as an internal standard, removing lipids (and precipitating proteins) from the extract with chloroform, evaporating the extract to dryness at 60° with a stream of nitrogen, and derivatizing the sugars with N-trimethylsilyl imidazole (Pierce Chem. Co.) for one h at 60°. The derivatized sugars were injected onto a 10 m DB-1 (J&W Scientific) fused silica capillary column in a Varian Model 4600 gas chromatograph with peak area integration performed with a Varian CDS-401 integrator. A standard consisting of derivatized fructose, glucose, inositol and sucrose was also analyzed to calibrate the detector responses to each sugar and thereby allow the recorded values to be corrected for differences in derivatization efficiency and detector response.

Caloric energy content of pollen was determined by bomb calorimetry using a Phillipson Microbomb Calorimeter (Gentry Instruments) according to the manufacturer's directions.

Results

The number of saguaro flowers produced during the 1983 saguaro bloom season based on the 20 survey plants is illustrated in Fig. 2. The peak blooming period occurred between May 28 and June 17. Bloom data for each of the 20 individual plants are shown in Table 1. The individual plants exhibited marked variability in their blooming patterns. For example, the length of bloom varied between 27 and 61 days with an average of 37 days. The plants with the shortest blooming periods did not have the fewest flowers, nor did the longest blooming plants produce the most. Similar variability among plants in the total estimated number of flowers produced, the mean number of flowers

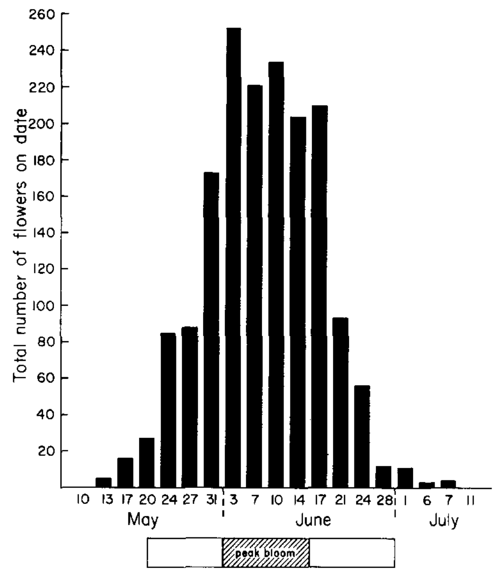

Fig. 2. Phenology of the saguaro bloom during the 1983 year based on the number of flowers present on 20 plants on the given date

Table 1. Days in bloom, total flowers produced per season and estimated total pollen production for 20 study plants

Saguaro number	Bloom length (days)	Estimated number of flowers	Mean number flowers/night	Estimated total pollen produced (g) (286 mg/flower)
1	31	266	8.58	76.1
2	34	166	4.88	47.5
3	38	192	5.07	54.9
4	34	220	6.48	62.9
5	41	304	7.43	86.9
6	38	186	4.88	53.2
7	27	108	4.02	30.9
8	27	84	3.11	24.0
9	38	84	3.22	24.0
10	31	172	5.53	49.2
11	40	407	10.18	116.4
12	31	980	31.61	280.3
13	44	336	7.64	96.1
14	61	577	9.46	165.0
15	39	82	2.09	23.5
16	30	272	9.05	77.8
17	38	102	2.67	29.2
18	42	655	15.60	187.3
19	31	259	8.35	74.1
20	46	449	9.76	128.4
$\bar{x} \pm$ SD	37.0 ± 7.9	295 ± 228	8.0 ± 6.4	84.3 ± 65.1
Ranges	(27–61)	(82–980)	(2.09–31.61)	(23.5–280.3)

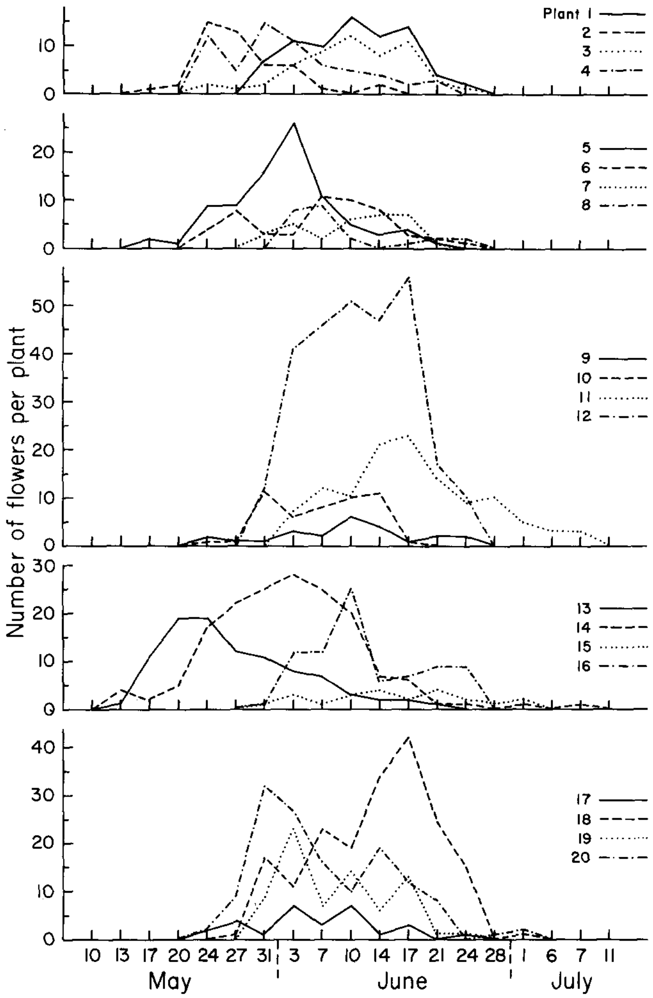

Fig. 3. Individual floral phenologies for the 20 plants surveyed during the 1983 floral season

Table 2. Floral phenology and pollen production of saguaros based on a sample of 20 plants

Floral data:	
Date of first flower	May 11
Mean date of first flower/plant ($\pm$SD)	May 23.4$\pm$6.2
Date of peak bloom	June 3
Number of flowers/plant on June 3 (range)	12.6$\pm$10.6 (3–41)
Maximum one day number $\pm$SD of flowers/plant (range)	19.4$\pm$13.1 (4–56)
Mean date of last flower/plant ($\pm$SD)	June 26.9$\pm$6.2 days
Date of last flower	July 10
Plant data:	
Mean $\pm$SD of plant height (range)	6.24$\pm$1.69 m (3.96–9.45)
Mean $\pm$SD of numbers of arms/plant (range)	4.55$\pm$2.37 (1–9)
Mean $\pm$SD total numbers of flowers/arm (range)	67.5$\pm$32.3 (21–129.5)
Plant density (plants/ha)	6.563
Pollen production:	
Pollen grains/mg pollen ($n=4$) (range)	7,600$\pm$1,330 (6,190–9,310)
Pollen wt$\pm$SD/flower ($n=6$) (range)	286$\pm$94 mg (189–457)
Mean pollen grains/flower	2.17×10^6
Mean pollen $\pm$SD/plant (range)	84.3$\pm$65.1 g (23.5–280.3)
Mean pollen grains produced/plant	6.41×10^8
Pollen produced/plant at peak date [June 3] (range)	3.60$\pm$3.03 g (0.86–11.73)
Total pollen grains produced/ha	4.2×10^9
Pollen produced/ha	553$\pm$427 g
Maximal 1 day pollen production/ha (June 3)	23.6$\pm$7.8 g

per night, and the total estimated pollen produced per plant can be seen in Table 1.

Figure 3 is a graphical representation of the floral phenology for the 20 individual plants. No two plants exhibited near identical patterns; rather, the overall pattern appears to be one of great individual variation. Features that vary include the bloom initiation, termination, the total bloom length, and the shape of the flowering phenological curve. Example plants with different bloom profiles are: plants 2 and 13 which started blooming early, peaked early and decreased early; plants 1 and 18 which exhibited reverse patterns; plant 12 which exhibited a very short intense bloom during the middle of the period; plant 14 which started very early, peaked at the mean peak date (June 3), and ended late; and plant 11 which started late (May 31), peaked late (June 17), and then its flowering gradually decreased.

Table 2 provides a summary of features relating to the saguaro bloom phenology, the saguaro plants themselves, and the production of saguaro pollen. The 1983 bloom was somewhat later than average with the peak of blooming occurring June 3. On this date the average plant had 12.6 flowers with a range among the 20 plants of 3 to 41 flowers. The greatest number of flowers simultaneously observed was 56 which occurred June 17 on plant 12, an individual with 9 arms including the top (the maximum number for any of the survey plants).

Based on four independent counts of the saguaros present in the 1.53 km^2 area on the aerial photograph of the study area, 1,040 sexually mature plants were present. In a smaller area bordered by two washes and a road 58 plants were counted on the map. Ground survey revealed 56 actual plants in this area. By assuming the ground survey was correct and adjusting the values from the aerial survey accordingly, a final count of 656.3 reproductive plants/km^2 was obtained.

In the survey area, eleven plants were located on the rocky slopes, eight in the less rocky lower areas, and one at the interface between the two. When the eleven and eight plants were compared no statistical differences between the two groups in the total numbers of flowers per plant, the plant heights, the numbers of arms per plant, the number of flowers per arm, the number of flowers per day, or the length of the floral phenology were observed. This indicates that for the purpose of this survey, saguaro plants from the two areas could be jointly analyzed. When all 20 plants were analyzed, plant height ($P<0.05$; $r^2=0.29$) and number of arms ($P<0.001$; $r^2=0.58$) were directly related to the total number of flowers per plant.

The length of the floral blooming period was not related to the total number of flowers produced per plant, the plant height, the number of arms per plant, or the number of flowers per arm. Also, the number of flowers per arm was not related to the number of arms on the plant.

Saguaro pollen productivity can be readily calculated from the known number of flowers per plant, plants per km^2, and weight of pollen per plant. The latter value (Table 2) based on a sample number of six flowers was 286 ± 94 mg pollen/flower. When the number of pollen grains per mg was analyzed, a value of $7{,}600 \pm 1{,}330$ grains/mg was obtained. Thus, an average saguaro pollen grain weighs 0.13 μg and an average flower produces 2.17×10^6 pollen grains. An average plant produces 84.3 g pollen during the season or 6.41×10^8 pollen grains. In the environment a total yield of saguaro pollen is 553 g/ha or 4.2×10^9 pollen grains/ha.

Saguaro floral nectaries begin nectar production about 1–2 h after sunset with secretion continuing all night. In bagged flowers, the total nectar production observed on the morning following anthesis was 543 ± 154 (SD, $n = 91$) μl/flower (range = 300–840 μl/flower) (Buchmann and Schmidt, unpublished). Based on an average of 8.0 flowers $\times$ plant^{-1} $\times$ night^{-1} and 295 flowers $\times$ plant^{-1} $\times$ season^{-1} (Table 1) each plant produces 4.3 ml of nectar per night and 160 ml per season. Thus, in the study area, *Cereus* contributes 1.05 l $\times$ ha^{-1} $\times$ year^{-1}. As determined by refractometer readings, the total dissolved sugars in saguaro nectar is 24 g/100 ml. The dry weight of sugar in the 1.05 l of nectar produced is therefore 252 g $\times$ ha^{-1} $\times$ season^{-1}.

Based on an energetic value of 16.5 j/mg sucrose, the energetic value of the saguaro nectar is 2,150 j per flower. At 8 flowers per night, each plant produces 17,200 j available nectar energy. The saguaros in the study area produced 113 kj $\times$ ha^{-1} $\times$ night^{-1} and 4,161 kj $\times$ ha^{-1} $\times$ season^{-1}.

Bomb calorimetry of *Cereus gigantea* pollen yielded a value of $23{,}870 \pm 138$ (SD, $n = 3$) j/g. Based on 0.286 g pollen per flower (Table 2) each flower produces 6,830 j of energy in the form of pollen. This value is over three times that of the energy in the nectar suggesting that pollen is the primary floral reward offered to pollinators.

Honey bees were the main floral visitors in the study area. Pollinating bats were absent or scarce and other bee visitors were infrequent. By 0900 to 1000 MST virtually all the pollen in saguaro flowers was gone indicating a 100% harvesting efficiency by *Apis*. Doves (*Zenaida asiatica mearnsi* (Ridgway)) were observed on saguaro flowers, but any of their activity after 0900 MST would be of doubtful pollinating value.

The combined pollen influx for saguaro and other species into seven colonies of honey bees is shown in Fig. 4. The saguaro pollen collected during that time is shown in the Figure as the white area beneath each of the bars in the histogram. The shape of this saguaro pollen influx is similar to that of the saguaro floral bloom (Fig. 2) except that it is delayed approximately one week. The overall result for these seven colonies indicates that the honey bee colonies closely tracked the phenology of the saguaro bloom.

Although the overall foraging behavior of the honey bees indicated a close tracking of the saguaro pollen resource, the behavior of individual colonies varied greatly. The rate of pollen influx of each of the colonies is shown in Fig. 5. At near peak saguaro bloom five of the seven colonies (1, 2, 4, 5, 7) responded by greatly increasing pollen collecting. Colony 6 was somewhat slower in responding

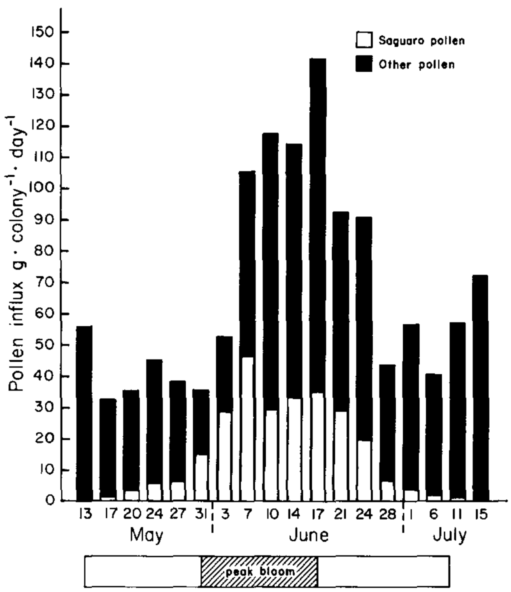

Fig. 4. Combined pollen influx from seven colonies of honey bees during the 1983 saguaro bloom. White portions of the bars represent the amount of saguaro pollen collected and the black is the combined total for all other types of pollen

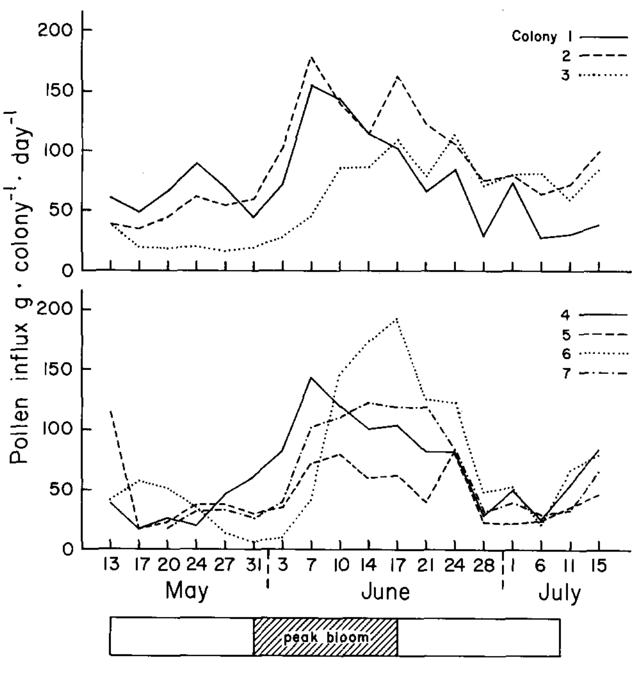

Fig. 5. Influx of pollen for individual colonies of honey bees

and colony 3 only responded near the end of the peak saguaro bloom. All colonies decreased pollen collecting as the saguaro bloom approached its end.

The exact pollen collecting behavior of the seven individual colonies vis-à-vis pollen species collected is illustrated in Fig. 6. In this Figure the species composition of the collected pollen is recorded for each colony and sample date. Here major differences in colony behavior are evident suggesting that colonies "majored" and "minored" on different species seasonally, but also that colonies could adjust their foragers to a new pollen source rapidly. Colony 7

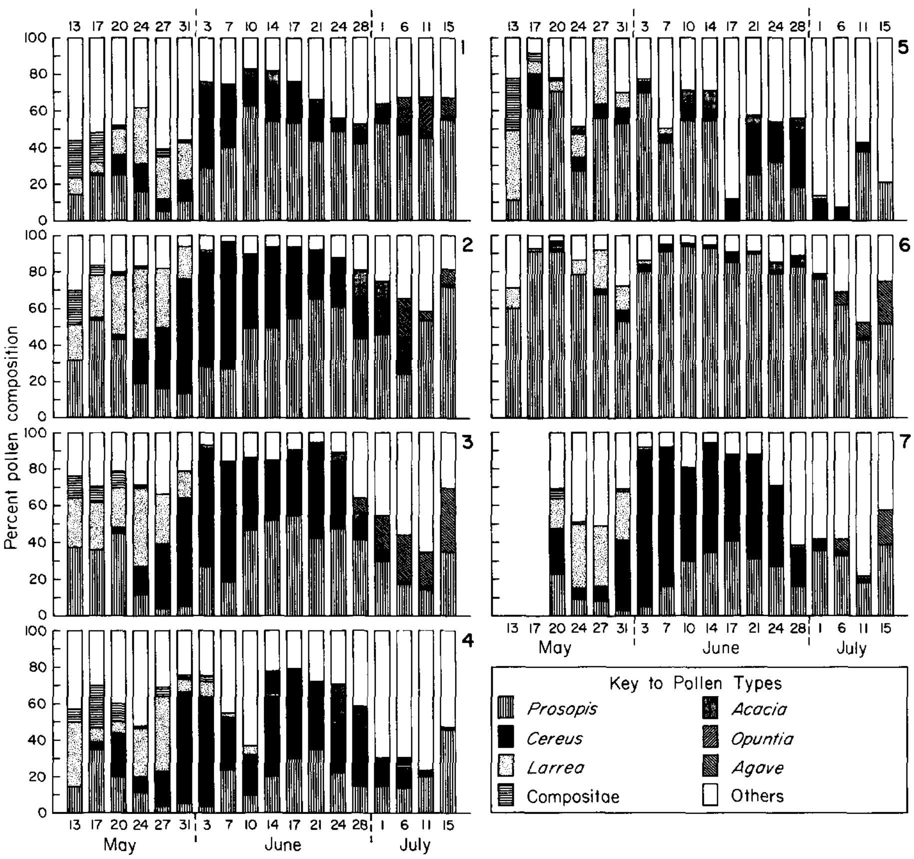

Fig. 6. Composition of pollen types collected by each of the seven colonies for each survey date

tracked the saguaro bloom closely and during the peak bloom saguaro was its major source of pollen. Colonies 2, 3, and 4 somewhat tracked the resource of saguaro pollen, though they did not collect as high a percentage as colony 7. Colonies 1, 5, and 6 provide a striking contrast to the previous four. Colony 1 appeared to track the saguaro bloom but only collected small quantities of it. Colony 5 did not track the saguaro bloom at all. Rather it appeared to collect some saguaro pollen from the first bloom to the last with its major collection occurring well after peak bloom. Colony 6 was a mesquite specialist which collected very little of any other pollen including saguaro during peak bloom. It essentially ignored the saguaro resource over the entire bloom and saguaro constituted only 4% of its total collected pollen on the peak date (June 3) of the saguaro bloom. Figure 6 therefore indicates that although the major trend (Fig. 4) of tracking the saguaro resource continued during the bloom, individual colonies displayed variation in their tracking of the resource.

The efficiency of *Apis* in harvesting the saguaro pollen resource and the carrying capacity of saguaro in terms of pollinator density per unit area are calculated in Table 3. When honey bees collect saguaro pollen they add sugars that account for 30% of the pellet weight. The values of sugars added to saguaro pollen collected in drier but similar locations west of Tucson were similar, being 33 and 35%. Because a bee has two metathoracic legs it can carry two corbicular pellets, or 17.4 mg of pollen plus added sugar. When the weight of the sugar is subtracted, a net bee load is 12.2 mg saguaro pollen. Thus an average flower contains 23.5 "bee trips" worth of pollen. A hectare area produces enough pollen for 4.5×10^4 bee trips.

The total harvest of saguaro pollen for the entire season and for the period of peak bloom by *Apis* is shown in Table 3. Colonies averaged about 261 g of corbicular saguaro pollen, which comprised about 25% of the total pollen collected. During peak bloom, colonies averaged 186 g of saguaro pollen which was about 34% of the total pollen collected. To convert weight of collected corbicular pollen into pure pollen, two factors must be considered: the 30% wt of corbicular pollen that is bee-added sugar and the 63% trapping efficiency (Buchmann and Shipmann, unpublished) of the OAC pollen traps (i.e., the percentage of corbicular pollen removed from the bees as they enter the hive). Combining these two estimates, each gram of corbicular pollen represents 1.11 g of saguaro pollen actually collected. Thus an average colony collected 290 g of saguaro pollen over the season and 207 g during the peak three weeks of bloom.

The seasonal pollen harvest potential of the saguaro study site for colonies of *Apis mellifera* is readily calculated. One factor which we did not calculate is the efficiency with which honey bees actually harvest the available pollen resource. Thus, the pollen harvest potential of the environment as shown in Table 3 for both the entire season and the peak bloom is calculated for three different estimates of efficiency (100, 90, and 75%) of pollen harvesting. We know from our own observations that virtually 100% of pollen in saguaro flowers is harvested (inverted flowers when touched with a tuning fork yield no pollen). We also know that *Apis* accounts for at least 90% of the pollen removed. These factors yield a probable pollen harvest potential, based on a harvest efficiency of 90%, of 1.72 colonies/ha over the the entire season, 1.76 for the peak bloom.

Table 3. Honey bee activity as saguaro pollen collectors and the harvest potential of the environment

Pollen harvesting capacity of honey bees:				
Percent sugars added to pollen during collecting	30%			
Mean wt corbicular pollen pellet ($n=52$)	8.71 ± 1.93 mg			
Mean wt corbicular pollen/bee trip	17.4 ± 3.9 mg			
Mean wt actual pollen harvested/bee trip	12.2 ± 2.7 mg			
Minimum pollinator trips/average flower	23.5			
Seasonal pollen productivity in bee trips/ha	4.54×10^4			
Maximal one day pollen productivity in bee trips/ha	0.19×10^3			
Pollen harvested by honey bees: (7 colonies)	Season Total		Peak Bloom (28 May–17 June)	
Grams ± SD total corbicular pollen trapped/colony (range)	1,069 ± 267 (642–1,498)		548 ± 154 (339–784)	
Grams ± SD saguaro corbicular pollen trapped/colony (range)	261 ± 184 (20–528)		186 ± 143 (17–407)	
Percent saguaro of total trapped pollen (range)	24.4% (1.7–45.5)		34.0% (3.0–58.3)	
Grams ± SD saguaro pollen harvested/colony (range)[a]	290 ± 204 (22–587)		207 ± 159 (19–452)	
Environmental harvest potentials:	Season Total		Peak Bloom (28 May–17 June)	
Saguaro pollen produced/ha	553 g		405 g	
Harvest potential (colony equivalents/ha) pollen harvest efficiency of:	If 24.4% of pollen is saguaro	If 100% of pollen is saguaro	If 34.4% of pollen is saguaro	If 100% of pollen is saguaro
100%	1.91	0.47	1.96	0.67
90%	1.72	0.42	1.76	0.61
75%	1.43	0.35	1.47	0.50

[a] This figure takes into account the 30% weight of corbicular pollen that is bee-added and the 63% efficiency of the pollen traps

If the bees relied entirely on saguaro pollen for their food resource then 0.42 and 0.61 colonies/ha could be supported over the entire season and peak bloom periods respectively.

Discussion

Although the overall saguaro bloom followed a normal distribution of flower numbers with time, this average obscures the real floral dynamics observed when individual plants are investigated. Few plants exhibited a normal distribution of flowering over time or had a floral phenology similar to the mean for the 20 plants. Such polymorphism in floral bloom is probably highly adaptive. Until about 100 years ago (when honey bees were introduced) populations of the saguaro's pollinators, bats, native bees and possibly doves (Alcorn et al. 1961), varied from year to year depending on such factors as temperature and rainfall. Thus contrary to previous assertions (Alcorn et al. 1961; McGregor et al. 1962) pollination may well have been an important limitation for the saguaro's reproductive potential. Data by the same authors (Alcorn et al. 1961; McGregor et al. 1962) suggest pollination might be a limitation on reproduction. In their experiments even when the densities of pollinators were extreme, doves, bats, and honey bees pollinated only 45, 62 and 52% of the flowers and natural open pollination was 54%. In contrast hand cross-pollination effected 71% seed set in one test and 99.5% in another. We unfortunately cannot determine the pollinating efficiency of the various natural saguaro pollinators before the advent of competition from *A. mellifera*. Hence, the degree to which pollination may now be limiting in the reproductive biology of the species cannot be determined.

Previous reports relating to saguaro flowering and fruit set were based on estimates such as 200 fruits per plant (Shreve 1951; McGregor et al. 1962; Steenbergh and Lowe 1977). These were best guesses apparently based on large plants. We have made a count of the number of flowers over the entire season produced by a cross section of all sizes of reproductive plants. Our results indicate that an average plant produces 295 flowers/season and, based on fruit set rates in the Tucson area of 47 to 54% (Alcorn et al. 1961; McGregor et al. 1962), sets close to 150 fruits.

In an independent analysis of saguaro nectar, Scogin (1985) reported a value of 25% total dissolved solids (as sugars) in the nectar and stated that on average, the energetic value of the nectar is 1,973 j/flower. This value is close to our values of 24% and 2,150 j/flower.

Very little data is available in the community pollination ecology literature for the amount of nectar or dry weight of sugar produced on a seasonal basis/ha either for individual plants or for entire natural plant communities. In two tundra sites, Hocking (1968) reported that these communities produced from 1,020 to 1,540 g sugar $\times$ season^{-1} $\times$ ha^{-1}. In comparison, the one species we investigated contributed 16–25% as much carbohydrate per hectare as these entire tundra communities.

One of the goals of this study was to determine the pollen production by saguaro per unit area of habitat. Productivity depends on the quantity of pollen produced per flower, the number of flowers per plant and the density of plants in the environment. These three quantities are seldom known for any species, and plants for which data exist are usually domestic crop plants growing in unnatural densities and conditions. Corn (*Zea mays* L.), for example, produces 3.5 g pollen per plant and 2×10^4 plants are raised per hectare. Under these conditions, 175 kg of pollen/ha are produced (Nowakowski and Morse 1982), a figure many times that produced by saguaro in our study (553 g/ha). But unlike saguaro, corn is an anemophilous species and its large production of pollen is necessary for effective wind transport from anther to stigma.

The potential production of saguaro pollen would be expected to vary with the environment. Our value was obtained in an area with 6.56 reproductive plants/ha, but densities as high as 15.5 plants/ha are evident in one study area of Niering et al. (1963). Under such conditions 1307 g/ha of saguaro pollen would be produced.

The main saguaro pollen collector is now the common honey bee, a polylectic species which was imported into the region about a hundred years ago. The findings of this study indicate that overall our seven colonies tracked the resource well. This apparent uniformity of pollinator response is not, however, a simple resource availability-pollinator response phenomenon. Instead each pollination unit (colony) exhibits its own idiosyncratic behavior in response to the new resource. Some colonies virtually ignored the resource (colony 6) while others tracked the resource well (colonies 1–4) and one even became a saguaro specialist (colony 7). These differences illustrate that this biological situation is not simple and that total reliance upon lumped data for conclusions can cause erroneous conclusions.

Lack of uniformity in response of a polylectic pollen feeder is likely adaptive. Among other features, the variation in pollen preference would reduce intraspecific competition for a single resource. In the environment investigated several alternative resources were available: especially mesquite pollen, but also creosotebush, acacia, composites, agaves and others. These alternative pollen sources allowed different specializations by individual colonies. One colony (number 6), for example, specialized on mesquite and most colonies utilized mesquite, the major floral source during the study interval, to a greater or lesser extent.

Our calculations indicate an average saguaro flower produces enough pollen for a theoretical 23.5 honey bee pollen gathering trips. McGregor et al. (1959) actually counted the number of pollen loads obtained per flower by honey bees and found that an average flower yields 25 loads. This agrees well with our theoretical calculation and indicates that *Apis* is an extremely efficient collector of saguaro pollen. Our own observations that by 1000 MST no pollen is available in a saguaro flower support this conclusion.

The plants in the studied environment produced 553 g/ha of saguaro pollen, equivalent to 1.91 colony harvest equivalents in this test and assuming alternate sources were available as occurred during 1983. If a very dry year occurs (1983 was wet) most other sources of pollen will disappear, leaving only the dependable saguaro (which blooms consistently every year [Peebles and Parker 1941]). Under these conditions our study area would provide pollen for up to 0.47 colonies assuming they collect the same amount of pollen as in this test and that it is all saguaro. These colony pollen harvest equivalents might represent only approximations. For example in an excellent stand such as that discovered by Niering et al. (1963) the 15.5 plants/ha could alone yield a theoretical 5.24 colony pollen harvest equivalents during the saguaro floral season.

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