

SONORAN DESERT COLUMNAR CACTI AND THE EVOLUTION OF GENERALIZED POLLINATION SYSTEMS

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Abstract. We studied variation in flowering phenology, fruit and seed set, and the abundance of the pollinators of four species of night-blooming Sonoran Desert columnar cacti for up to eight years at one site in Mexico and one year at one site in Arizona. We determined how spatiotemporal variation in plant–pollinator interactions affects the evolution of generalized pollination systems. We conducted pollinator exclusion and hand pollination experiments to document annual variability in pollinator reliability and to determine whether pollination systems were redundant (different species are partially or totally substitutable) or complementary (different species have an additive effect on fruit set). The cacti we studied included three species with generalized pollination systems involving bats, birds, and bees (cardon, *Pachycereus pringlei*; saguaro, *Carnegiea gigantea*; and organ pipe, *Stenocereus thurberi*) and one specialized moth-pollinated species (senita, *Lophocereus schottii*). We predicted that the migratory lesser long-nosed bat, *Leptonycteris curasoae*, is a less reliable pollinator than birds and bees, and that cacti with generalized pollination systems have more variable flowering phenologies than the specialized species.

Annual time of peak flowering and mean size of flower crops were relatively invariant in saguaro and organ pipe. Time of peak flowering in cardon varied by as much as six weeks, and mean flower crop size varied three-fold over six years. In senita, peak flowering varied by as much as 5–8 wk among years. Peak numbers of the nectar bat *L. curasoae* varied among years, and bat density (0.9/ha) was an order of magnitude lower than that of cactus-visiting birds at both study sites. The abundance of migratory hummingbirds was also highly variable among years.

Pollinator exclusion experiments indicated that bats were major pollinators of cardon, whereas diurnal visitors accounted for most fruit set in saguaro (except in 1995 when bats were most important) and organ pipe at our Mexican site; honeybees accounted for 64–87% of diurnal fruit set in these species. Annual variation in the contribution to fruit set by bats was substantially higher than that of diurnal pollinators in saguaro and organ pipe, but not in cardon. There was little geographic variation in the relative importance of nocturnal vs. diurnal pollinators in saguaro and senita, but bats were much more important for fruit set in organ pipe in Arizona than in Mexico. We generally detected no effect of different pollinators on number of seeds per fruit in any species.

Annual variation in fruit set was lowest in saguaro, the species with the most diurnal pollination system, and highest in organ pipe, the species with the most generalized pollination system. Fruit set was strongly pollen limited only in females of cardon (a trioecious species) and in organ pipe (at both sites). The “missing” pollinators in both species are likely *Leptonycteris* bats. The pollination systems of saguaro and cardon were partially redundant, whereas that of organ pipe was complementary.

The four species of cactus that we studied occur at the northern geographic limits of Mexican columnar cacti where many vertebrate pollinators are seasonal migrants. In the Sonoran Desert, variation in rainfall and spring temperatures affects timing of flowering and the extent of competition between cacti for pollinator visits and causes the relative importance of particular pollinators, especially *Leptonycteris* bats, for fruit set to vary annually. Under such conditions, selection has favored generalized pollination systems (as seen in organ pipe) or shifts from reliance primarily on nocturnal pollinators (as seen in cardon) to reliance primarily on diurnal pollinators (as seen in saguaro). Nonetheless, as exemplified by the senita–senita moth system, highly specialized pollination mutualisms can also evolve in this habitat in plants that rely on sedentary insects rather than migratory bats and birds for pollination.

Key words: bat pollination; bird pollination; columnar cacti; flowering phenology; fruit set; functional redundancy and complementarity; generalized pollination systems; geographic variation; Sonoran Desert; specialized pollination systems.

INTRODUCTION

A major question in pollination biology is when should plants evolve specialized vs. generalized pollination systems (Waser et al. 1996, Johnson and Stein-

er 2000). Specialized pollination systems are those attracting a limited subset of potential pollinators, often of a particular taxonomic group (e.g., long-tongued bees, butterflies, hummingbirds, bats), with flowers reflecting the size, morphology, physiology, and behavior of those animals (Baker 1961, Baker and Hurd 1968, Faegri and van der Pilj 1979). In contrast, generalized

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pollination systems are those attracting a wide range of potential pollinators, often representing a diverse array of taxonomic groups. According to Stebbin's (1970) "most effective pollinator principle," plants should specialize on the most abundant and/or most effective pollinator(s) whenever its spatiotemporal reliability is high (also see, Schemske 1983, Howe 1984, Herrera 1996, Travis 1996). Whenever the reliability of the most effective pollinator(s) is low, then plants should not specialize on that pollinator. In addition to the spatiotemporal reliability and relative effectiveness of pollinators, plant size, reproductive longevity, successional status, and density are thought to influence the evolution of pollination systems (Feinsinger 1983, Waser et al. 1996). Large, long-lived, late successional plants are more likely to have specialized pollination systems than plants having the opposite characteristics. Feinsinger (1983) further predicted that selection should favor specialization in chronically rare plants to promote effective pollination. Specialization should also be more common in self-incompatible than in self-compatible plants to maximize effective pollination.

In addition to its intrinsic ecological and evolutionary importance (Ollerton 1996, Waser 1998), the issue of specialization vs. generalization in pollination systems has important conservation implications, through the concepts of pollinator redundancy and complementarity (Walker 1992, Bond 1994, Kearns and Inouye 1997, Kearns et al. 1998). Redundant pollination systems are those in which different groups of pollinators (e.g., nocturnal vs. diurnal species) are substitutable for each other without a loss in overall fruit set. Redundancy can be total (i.e., when different groups are completely substitutable) or partial (i.e., when different groups are not completely substitutable). Redundancy is most likely to occur in plants whose fruit set is limited by resources rather than by pollinators. In contrast, complementary pollination systems are those in which fruit set is limited by the sum of the contributions of individual pollinators. In such systems, loss of any pollinators will result in reduced fruit set. By definition, plants with specialized pollination systems are not likely to experience redundant or complementary relationships with their pollinators. Their extinction probability is high whenever their specialized pollinators disappear (unless they also reproduce vegetatively; see Bond 1994). Plants with a generalized pollination system, in contrast, will likely experience either redundant or complementary relationships with their pollinators, depending on whether fruit set is resource or pollen limited, respectively. Which of these two relationships exists for a plant is important because compensation for missing pollinators is more likely to occur whenever pollinators are redundant rather than complementary.

Columnar cacti of the tribe Pachycereeae (Cactaceae) appear to be an excellent system for examining the conditions that favor the evolution of specialized

vs. generalized pollination systems. Based on flower morphology and nocturnal anthesis, Valiente-Banuet et al. (1996) estimated that a majority (42 of 70 species) of Mexican members of this tribe are pollinated by bats. Pollinator exclusion experiments conducted in south central Mexico, Curaçao, and northern Venezuela indicate that nectar-feeding bats (mainly the lesser long-nosed bat *Leptonycteris curasoae* [Phyllostomidae, Glossophaginae] in Mexico and *L. curasoae* and *Glossophaga longirostris* in Curaçao and Venezuela) are the exclusive pollinators of several species of columnar cacti (Petit 1995, Valiente-Banuet et al. 1996, 1997a, b, Nassar et al. 1997). Although flowers of these species sometimes remain open after sunrise and are visited by birds and bees, diurnal visitors are not effective pollinators because floral stigmas are not receptive after dawn. These cacti thus appear to have specialized pollination systems involving bats. In contrast, similar experiments with three species of Sonoran Desert columnar cacti indicate that both nocturnal (*L. curasoae*) and diurnal animals (birds and bees) are effective pollinators (Alcorn et al. 1959, McGregor et al. 1962, Fleming et al. 1996). Sahley (1996) also demonstrated experimentally that both nocturnal (the phyllostomid bat *Platalina genovensium*) and diurnal (the hummingbird *Patagona gigas*) visitors are effective pollinators of the columnar cactus *Weberbauerocereus weberbaueri* in the Peruvian Andes. These studies thus indicate that the importance of bats as pollinators varies geographically and that both nocturnal and diurnal species are effective pollinators at the northern and southern limits of the distributions of vertebrate-pollinated columnar cacti. Generalized pollination systems (i.e., with effective nocturnal and diurnal pollinators) replace specialized (i.e., bat pollination) systems at the geographic distributional limits of some groups of columnar cacti.

The general question we address in this study is this. Why do three species of "bat-pollinated" Sonoran Desert columnar cacti have more generalized pollination systems than their southern relatives? Using a relatively long-term data set, our specific aim was to test the hypothesis, proposed by Valiente-Banuet et al. (1996), that these cacti have generalized pollination systems because their most effective pollinator, the migratory nectar-feeding bat *L. curasoae*, is unreliable in the Sonoran Desert. We suggest that effective pollinators (i.e., species delivering substantial amounts of conspecific pollen to stigmas per visit) can be unreliable for at least three reasons: (1) they are dietary generalists and do not restrict their foraging to one or a few flower species; their faithfulness to a particular species depends on the availability of alternate food sources; (2) they are dietary specialists, but their abundance varies widely among sites and years so that their contribution to fruit set relative to other pollinators is variable (a common situation in many pollination systems; e.g., Schemske and Horvitz 1984, Herrera 1988, 1995, Thompson and Pellymyr 1992, Fishbein and Ven-

able 1996, Gomez and Zamora 1999); and (3) they are dietary specialists, but their abundance is chronically low relative to the availability of flowers and/or other potential pollinators. Based on prior carbon stable isotope analyses, we already knew that *L. curasoe* was a dietary specialist on CAM plants (Cactaceae and/or Agavaceae) in the Sonoran Desert (Fleming et al. 1993), so we focused on testing predictions (2) and (3) in this study.

Because pollinator reliability is also influenced by spatiotemporal variability in the timing and abundance of their flower resources (see reviews in Lee 1988, Zimmerman 1988, and Bronstein 1995), we documented year-to-year variation in cactus flower production at two sites in the Sonoran Desert to see whether flower production is more variable in the three species of generalized, vertebrate-pollinated, columnar cacti than in a specialized, moth-pollinated, columnar cactus. Finally, we documented the relative importance of resource vs. pollen limitation for fruit set in these four cacti and used pollinator exclusion experiments to determine whether they have redundant or complementary pollination systems. We predicted that complementary pollination systems would occur in plants whose fruit set is limited by pollen, and that redundant pollination systems would occur in plants whose fruit set is limited by resources.

METHODS

The plant species

Our study species included cardon (*Pachycereus pringlei*), saguaro (*Carnegiea gigantea*), organ pipe (*Stenocereus thurberi*), and senita (*Lophocereus schottii*). Each species is large and multi-branched (cardon, saguaro) or multi-stemmed (organ pipe, senita). Flowers of the first three species are large and light colored and conform to a classic bat-pollination syndrome (Heithaus 1982). They open at night, last for less than one day, and produce substantial amounts of nectar and pollen. They are visited at night by the bat *Leptonycteris curasoe* and by migrant and resident birds and bees, beginning just before sunrise (Fleming et al. 1996). The fourth species, senita, is also a night-blooming species, but is pollinated by a highly specialized pyralid moth, *Upiga virescens*, in an obligate pollination relationship similar to that of the yucca–yucca moth mutualism (Fleming and Holland 1998, Holland and Fleming 1999a, b).

The four species we studied are the most northern of Mexico's columnar cacti (Fig. 1). Three of the four species (saguaro, organ pipe, senita) have hermaphroditic, self-incompatible breeding systems (McGregor et al. 1962, Fleming et al. 1996, Fleming and Holland 1998), whereas cardon has a trioecious breeding system in which self-compatible hermaphrodites co-occur with males and females (Fleming et al. 1994, Murawski et al. 1994). Basic features of the pollination biology of

these species are described by Fleming et al. (1996), Fleming and Holland (1998), and Holland and Fleming (1999a). Flowers of saguaro open later at night (1.5–2 h after sunset rather than at sunset) and close much later the next day (by mid to late afternoon rather than 2–6 h after sunrise) than the other three species.

Study sites

This study was conducted between 1989 and 1999 at two sites in the Sonoran Desert (Fig. 1). Fieldwork occurred in April–June in 1989–1990 and 1995–1999 and in May–July in 1992–1993. Brief visits to count bats and cactus flowers were also made to our Mexican study site in mid-April in 1991, 1992, 1994, 1997, and 2000 and to our Arizona site in May 1998 and June 2000. In 1989–1996 and 1998–1999 we worked near Bahia de Kino (hereafter designated as BK), Sonora, Mexico, in the central coastal region of the Sonoran Desert (Shreve and Wiggins 1964, Fleming et al. 1994, 1996; Fig. 1). Adults of the four cactus species are patchily distributed at this site. We worked in one relatively dense patch of the three vertebrate-pollinated species (Tortilla Flats) each year, but studied saguaro and senita in another patch (Seri Flats) located 2.2 km from the first site in 1995–1996. Adult densities of cardon, saguaro, and organ pipe at Tortilla Flats were 7.7, 7.3, and 19.3 per ha, respectively; adult densities of senita and saguaro at Seri Flats were 7.7 and 8.3 per ha, respectively (Fleming et al. 1996, Holland and Fleming 1999b). In 1997 we worked at Organ Pipe Cactus National Monument (hereafter designated as ORPI), Pima County, Arizona, where we studied saguaro, organ pipe, and senita at Senita Basin (Fig. 1). Parker (1988) has described this site. Adult densities of saguaro, organ pipe, and senita on our mapped plot were 45.3, 16.5, and 4.2 per ha, respectively. ORPI is located ~355 km north-northwest of BK and is ~150 km northwest of the northern geographic limit of *Pachycereus pringlei* (Fig. 1).

Maximum, minimum, and mean air temperatures in spring (March–June) and annual rainfall data at our two study sites are summarized in Table 1. Compared with ORPI, minimum and mean air temperatures at BK in the spring tend to be lower and more variable, and maximum air temperatures tend to be higher and more variable. Annual precipitation is also lower and more variable at BK. Both sites have two principal rainy periods, a winter period (December–March) and a summer period (July–September).

Flowering phenology

We quantified the reproductive phenology of each species by weekly counts of the number of flower buds, open flowers, and fruits on 20 plants scattered across several hectares in our study sites. The same series of plants was monitored at BK in 1989–1990; a different series was monitored in 1995–1996 and 1998–1999. Because several of our 1995–1996 saguaro census

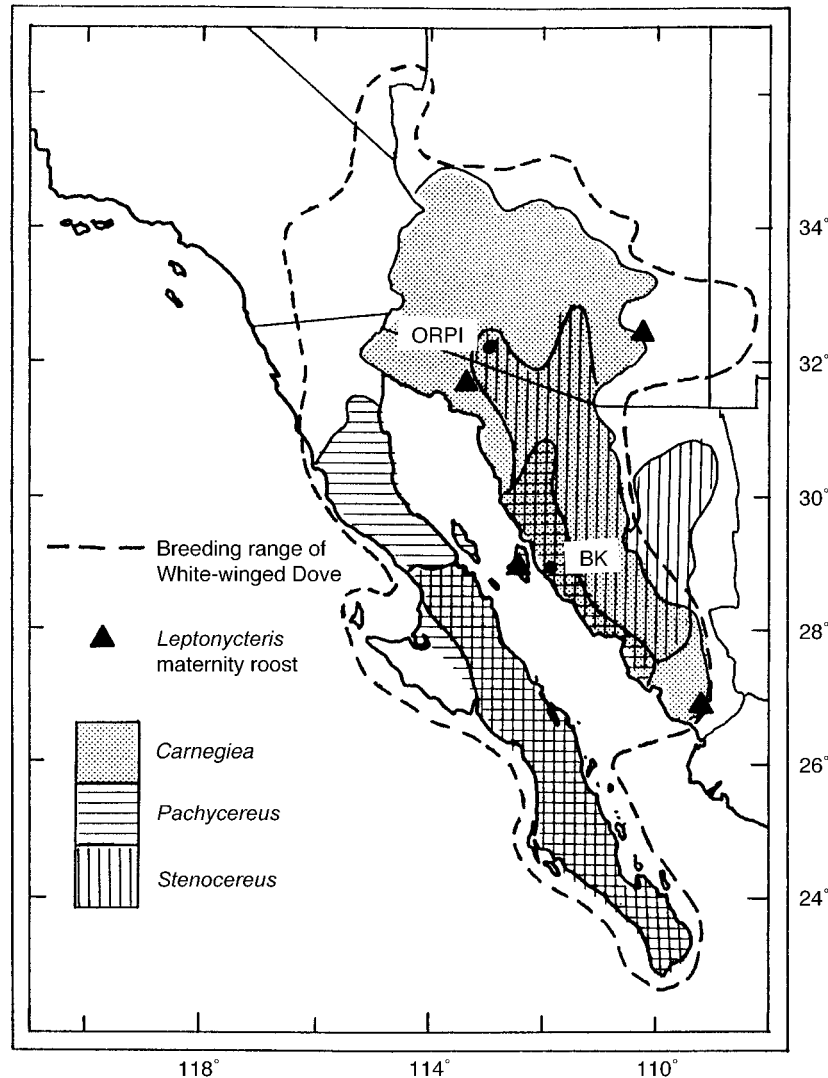


FIG. 1. Map showing the locations of the two study sites and the geographic ranges of three species of vertebrate-pollinated columnar cacti. Work was done at Bahia de Kino, Sonora, Mexico (BK) in 1989–1996 and 1998–1999 and at Organ Pipe Cactus National Monument, Arizona (ORPI) in 1997. The cacti include cardon (*Pachycereus pringlei*), saguaro (*Carnegiea gigantea*), and organ pipe (*Stenocereus thurberi*). The distribution of a fourth species of cactus, senita (*Lophocereus schottii*), is similar to that of organ pipe except that it does not occur in south-central Arizona. Major historical roosts of the lesser long-nosed bat (*Leptonycteris curasoae*) are indicated by triangles. A dashed line indicates limits of the breeding range of the White-winged Dove (*Zenaida asiatica*). Range or roost data come from Arita (1991), Cockrum and Petryszyn (1991), Haughey (1986), and Turner et al. (1995).

plants died in 1997–1998, we monitored a third series of saguaro plants in 1999. In 1992–1993, only organ pipe was studied, and the same 40 plants were censused in both years. Our flowering data allowed us to estimate the week of peak flowering in each species each year as well as the intensity of flowering, defined as the average number of flowers produced per census plant per season. We estimated seasonal flower production within species each year by integrating the area under the flower curve for each census plant and calculating a mean for the species. We extrapolated to the tails of these curves by assuming that flowering seasons lasted

10 wk in cardon and saguaro, 15 wk in organ pipe, and 20 wk in senita. We tested for between-year differences in total flower production within each species in 1989–1990, 1995–1996, and 1998–1999 (only cardon and organ pipe) using paired *t* tests or one-way ANOVAs.

To further examine flowering variability, we quantified the extent of flowering overlap within species between years and between species within years using a percentage similarity index $PS = \sum \text{minimum}(p_{ij}, p_{ik})$ where p_{ij} = proportion of total census flowers produced by species *j* in week *i* and p_{ik} = proportion of total census flowers produced by species *k* in week *i*.

TABLE 1. Temperature and rainfall data at Bahia de Kino (BK) (1975–1993) and Organ Pipe Cactus National Monument (ORPI) (1974–1994).

Month	Site	N years	Maximum	Minimum	Mean
Air temperature (°C)					
March	BK	16	29.3 ± 2.0 (0.067)	4.0 ± 1.5 (0.375)	15.7 ± 1.2 (0.074)
	ORPI	21	24.8 ± 1.2 (0.050)	7.1 ± 0.4 (0.055)	15.9 ± 0.8 (0.048)
April	BK	17	32.0 ± 3.3 (0.104)	5.6 ± 1.6 (0.287)	18.0 ± 1.3 (0.072)
	ORPI	21	29.5 ± 2.2 (0.076)	9.9 ± 1.8 (0.183)	19.7 ± 2.0 (0.100)
May	BK	17	34.6 ± 3.0 (0.088)	8.4 ± 1.4 (0.172)	20.7 ± 1.3 (0.061)
	ORPI	21	33.3 ± 1.2 (0.035)	13.7 ± 0.6 (0.047)	23.5 ± 0.9 (0.038)
June	BK	14	37.0 ± 3.7 (0.099)	12.2 ± 2.0 (0.161)	25.3 ± 2.6 (0.103)
	ORPI	21	38.8 ± 0.9 (0.024)	18.6 ± 0.9 (0.050)	28.7 ± 0.9 (0.033)
Annual precipitation (mm)					
	BK	14	138.2 ± 74.6 (0.540)		
	ORPI	20	269.0 ± 107.7 (0.401)		

Notes: Temperature data are for March, April, May, and June. Rainfall data are for the entire year. Sources of data: U.S. Western Regional Climate Center and Comision Nacional del Agua, Gerencia Estatal en Sonora. Data include mean ± 1 SE (coefficient of variation).

This index ranges from zero (no overlap) to 1.0 (complete overlap). We did not use the 1989 data for these analyses because data collection began two weeks later than in subsequent years.

Pollinator abundance

In 1995–1997 and 1999 we used the method of Hutto et al. (1986) to determine the relative abundances of cactus-flower-visiting birds and *Leptonycteris* bats (1995–1997 only) in our study areas. This method involved counting the number of vertebrate cactus pollinators (documented at BK by Fleming et al. [1996] and at ORPI by T. H. Fleming, *unpublished data*) in or passing through a series of five circles with a radius of ~30 m for 10 min each between 0600 and 0800 (birds) and 2100 and 2230 (bats) once a week while we were conducting pollinator exclusion experiments. The centers of each circle were ~100 m apart along a transect through the experimental areas. At night we centered our observations on flowering cactus plants nearest each point and scanned for bats with dim headlamps. Except in 1993, we also counted the number of *Leptonycteris* bats leaving the Sierra Kino cave located 7 km west of Tortilla Flats at sunset every two weeks during each field season. On 21 May 1997 at ORPI, we estimated the number of *Leptonycteris* bats departing from a maternity roost located 21 km from our study site by counting the number of bats exiting during four 1-min periods between 1950 and 2130.

Resource supply:demand ratios

To determine whether pollinator abundances were high or low relative to flower and nectar production, we used our data on flower phenology and pollinator abundance to provisionally estimate seasonal and site differences in nectar energy supply and demand in cardon, saguaro, and organ pipe. We converted weekly flower data into number of cactus flowers produced per hectare at the Tortilla Flats plot in 1995–1996 and at

ORPI in 1997, and converted the weekly pollinator census data into number of individuals per species per ha. The total area censused in our pollinator surveys was ~1.4 ha. We then converted flower densities into kJ of sugar per hectare by calculating the energetic value of nectar in an “average” cactus flower (7.35 kJ) using data on nectar production and sugar concentration in Fleming et al. (1996) and methods described in Kearns and Inouye (1993). Daily energy requirements of the major cactus visitors were either taken from the literature (Horner et al. [1998] for *L. curasoe*) or were estimated for White-winged Doves, Costa’s Hummingbirds, Gila Woodpeckers, House Finches, and Verdins using data on mass and allometric equations in Nagy et al. (1999). In early spring, most or all of the daily energy used by *L. curasoe* and Costa’s Hummingbirds and ~40% of the daily energy of White-winged Doves comes from cactus nectar (Horner et al. 1998, Wolf and del Rio 2000; T. H. Fleming, *personal observations*). The other birds are more generalized feeders, and we arbitrarily used a value of 10% for the portion of their daily energy coming from cactus nectar.

Pollinator exclusion experiments and seed set

To determine the relative importance of nocturnal and diurnal pollinators for fruit and seed set and to quantify pollinator redundancy and complementarity, we conducted pollinator exclusion experiments each year through 1997. Additional experiments with senita at BK were conducted in 1998–2000 (J. N. Holland and T. H. Fleming, *unpublished data*). Whenever possible, the experiments were conducted when at least 80% of the phenology census plants of a species were flowering. Experiments typically included four treatments: open-pollinated controls, nocturnal pollination, diurnal pollination, and diurnal pollination with birds excluded (Fleming et al. 1996). We used bridal veil netting (mesh size = 1 mm) to exclude pollinators, placing or removing the netting at sunset and just be-

fore sunrise depending on treatment. We used chicken wire tubes (mesh size = 2.5×3.0 cm) placed over flowers to exclude birds but not bees during the day. Experimental flowers were tagged, and their status (aborted, fruit developing) was determined two weeks after they closed. When they ripened, we collected the experimental fruits and removed their seeds, which were counted gravimetrically as described by Fleming et al. (1996).

Exclusion experiments at BK were conducted using one set of plants in 1989–1990 (cardon, saguaro, and organ pipe), another set in 1992–1993 (organ pipe only), and a third set in 1995–1996 (all four species). Sample sizes in 1989–1990 included 61 individuals of cardon (the 1989 cardon experiments “failed” because many of our treatment plants were males), 30–34 individuals of saguaro, and 37–54 individuals of organ pipe; 20 individuals of organ pipe in 1992–1993; and 10 individuals of cardon, 12 of saguaro, 12 of organ pipe, and 10 of senita in 1995–1996. Sample sizes at ORPI in 1997 included 13 individuals of saguaro, 10 of organ pipe, and 10 of senita. Whenever possible, one replicate of each treatment was applied to each plant each day for 10–14 d per species. To make our data comparable with our earlier studies and with many studies in the literature, we will report fruit set as the percentage of treated flowers that set fruit, except as noted. By doing this, we are explicitly ignoring the effects of different plants and nights on fruit set within species. We used 500 bootstraps to estimate the mean and 95 percent confidence limits of the contributions of nocturnal and diurnal pollinators to open-pollinated fruit set for each species. Contributions of nocturnal and diurnal to fruit set were calculated as %NFS/%OPFS and %DFS/%OPFS, where %NFS, %DFS, and %OPFS refer to percentage nocturnal, diurnal, and open-pollinated fruit set, respectively. Data from both study sites were combined for this analysis.

Hand pollinations

We conducted hand pollination experiments to determine whether fruit set was likely to be pollen or resource limited in each species. Experiments involved rubbing the anthers of a flower bearing fresh pollen on the stigma of a conspecific individual within 2.5 h after flowers had opened. These experiments were conducted at BK in 1990 (cardon, saguaro, and organ pipe), 1991 (cardon), 1995 (senita), 1996 (cardon, organ pipe), and 1999 (organ pipe). Sample sizes were 2–4 flowers per plant on 8–20 plants each year. In 1997 at ORPI we hand pollinated two flowers on each of 20 individuals of saguaro and organ pipe and 10 flowers on each of 10 individuals of senita. We compared fruit set in hand-pollinated flowers with that of open-pollinated controls from pollinator exclusion experiments conducted the same year. Because we could not hand pollinate all or even a substantial fraction of flowers on cactus plants, our hand pollination experiments do not provide de-

finite evidence for pollen-limited fruit set (Zimmerman and Pyke 1988). Nonetheless, our methods are similar to those of many studies in the literature (Burd 1994) and provide considerable insight into differences in response to hand pollination in the cacti we studied.

Pollinator redundancy vs. complementarity

We used results of the pollinator exclusion experiments to determine whether or not each species had a redundant or a complementary pollination system. Pollinator redundancy occurs when the sum of percentage fruit set from nocturnal and diurnal pollination exceeds percentage fruit set from open pollination; pollinator complementarity occurs when the sum of nocturnal and diurnal pollination equals open-pollinated fruit set. We calculated a redundancy index R for each species as $R = (\%NFS + \%DFS - \%OPFS) / \%OPFS$. This index ranges from zero to 1.0. Partial redundancy occurs when $0 < R < 1.0$; total redundancy occurs when $R = 1.0$. Pollinator complementarity occurs when $R = 0$. While this index can distinguish redundancy from complementarity, it does not distinguish between complementarity and specialization. A plant species with a value close to zero could be specialized, rather than complementary, as occurred for senita. We used 500 bootstraps to calculate mean R and its 95% confidence limits for each species, combining data from both study sites.

RESULTS

Annual variation in flower production

The timing and intensity of flowering in the four species at BK differed both within and between years. Based on onset of flowering and order of flower peaks, the “normal” blooming sequence in the three vertebrate-pollinated species at BK was cardon–saguaro–organ pipe (Fig. 2A), but the sequence in 1995 was saguaro–cardon–organ pipe (Fig. 2B). Spring 1995 was unusually cool, and flowering in cardon was delayed nearly one month and few plants flowered heavily. In 1996 (and in 1997 and 2000; T. H. Fleming, *personal observation*), flowering in cardon and organ pipe began early (in mid to late March) compared with other years, and many individuals flowered heavily. Length of the flowering season was ~10 wk in cardon and saguaro and ~15 wk in organ pipe. Except for organ pipe in 1990, each of these species had a unimodal flowering curve (Fig. 2). The flowering season of senita lasted ~20 wk and was multimodal (Fig. 3).

Timing and intensity of flowering at BK was most variable in cardon (Table 2). In this species, dates of peak flowering differed by ~6 wk in 1995 and 1996. Annual variation in the date of peak flowering in saguaro, organ pipe, and senita was only 1–3 wk. Annual variation in intensity of flowering in cardon differed among pairs of years when the same plants were monitored by an average factor of 2.7. Flowering intensity

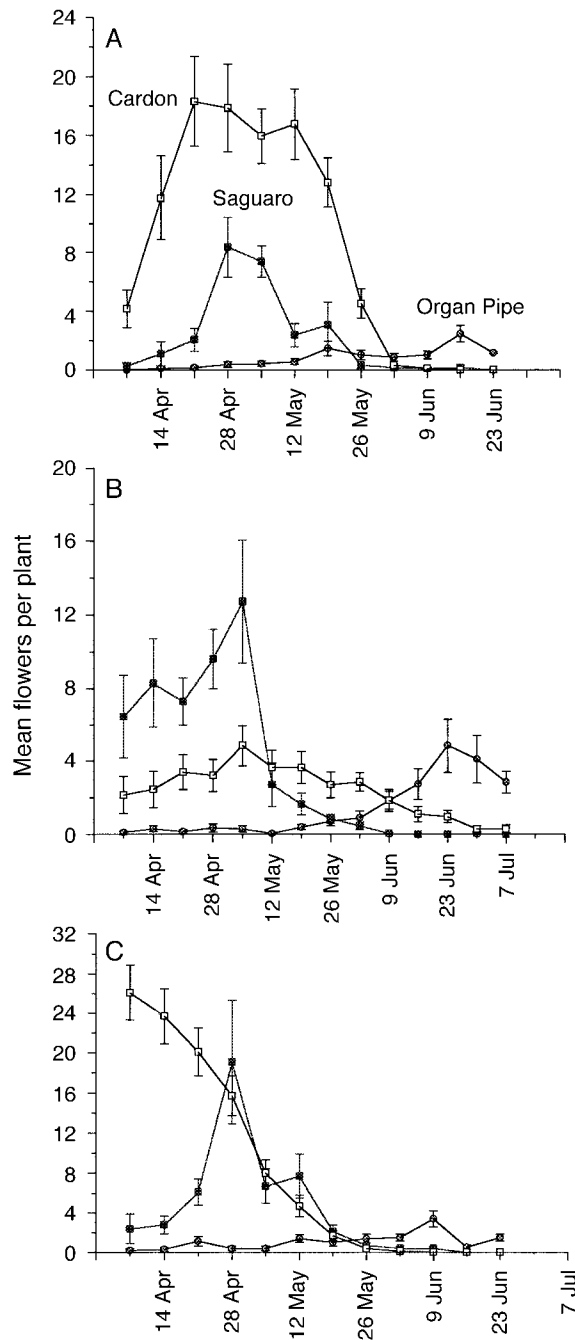


FIG. 2. Flowering curves of cardon, saguaro, and organ pipe in three years at Bahia de Kino: (A) 1990, (B) 1995, and (C) 1996. Data are means ± 1 SE. Sample sizes are 20 plants per species. The 1990 curves are redrawn with permission from Fleming et al. (1996).

was especially low in 1995 (Table 2). Annual variation in flowering intensity was lower in saguaro, organ pipe, and senita and differed between pairs of years by an average factor of 1.2, 1.6, and 1.1, respectively (Table 2). Flowering intensity in organ pipe in 1992–1993 was similar to that in late May and June of other years

(Sahley 2001). The three vertebrate-pollinated cacti differed significantly in total flower production per season (e.g., 1995: one way ANOVA, $F_{2,57} = 9.11$, $P < 0.005$; 1996: $F_{2,57} = 32.28$, $P < 0.0001$; Table 2). Annual flower production was highest in cardon and lowest in organ pipe. Senita produced about an order of magnitude more flowers per season than the other three species (Table 2).

Interspecific (within-year) flowering overlap at BK was about twice as high between cardon and saguaro (mean = 0.58 ± 0.04 SE, $N = 4$ yr) than between cardon and organ pipe (mean = 0.24 ± 0.02 , $N = 5$) and saguaro and organ pipe (mean = 0.33 ± 0.07 , $N = 4$). Intraspecific (between-year) overlap was high in organ pipe (mean = 0.84 ± 0.03 , $N = 10$ pairs of years), intermediate in cardon (mean = 0.66 ± 0.05 , $N = 10$) and saguaro (mean = 0.60 ± 0.05 , $N = 6$), and low in senita (0.36 , $N = 1$).

Flowering in saguaro, organ pipe, and senita began ~1–2 wk later at ORPI in 1997 than at BK in 1996 (cf. Figs. 2C and 3B), but peak flowering in saguaro and senita occurred at about the same dates at both sites (Table 2). In contrast, the flowering peak in organ pipe was 1.5 mo earlier at ORPI than at BK. Intensity of flowering in saguaro was similar at the two sites; in organ pipe it was over twice as high at ORPI compared with BK; and in senita it was twice as high at BK compared with ORPI (Table 2).

Unlike the situation at BK, where their flowering peaks differed by nearly two months, the flowering peaks of saguaro and organ pipe were nearly coincident at ORPI in 1997 (Fig. 3B). Flowering overlap between these species was nearly twice as high at ORPI than at BK (0.59 vs. 0.33). Overlap was also high there in 1998 and 2000 (T. H. Fleming, *unpublished data*).

In summary, timing and intensity of flowering in columnar cacti varied among species, sites, and years. At BK, timing and intensity was most variable in cardon; it was less variable in saguaro, organ pipe, and senita. There were geographic differences in flowering dates and flowering intensity in organ pipe and senita, but not in saguaro. Contrary to our prediction, spatio-temporal variation in the timing and intensity of flower production was similar in two of the three vertebrate-pollinated cacti to that in the specialized moth-pollinated cactus.

Variation in the abundance of nocturnal and diurnal pollinators

The pool of potential pollinators of flowers of columnar cacti was similar at both study sites and included nocturnal and diurnal vertebrates and insects. The most common nocturnal visitor to flowers of cardon, saguaro, and organ pipe was the nectar-feeding bat *L. curasoae*. Moths rarely visited these flowers at night at both sites. Major diurnal vertebrate flower visitors included migratory species such as White-winged Doves, hummingbirds (Costa's, Black-chinned, and

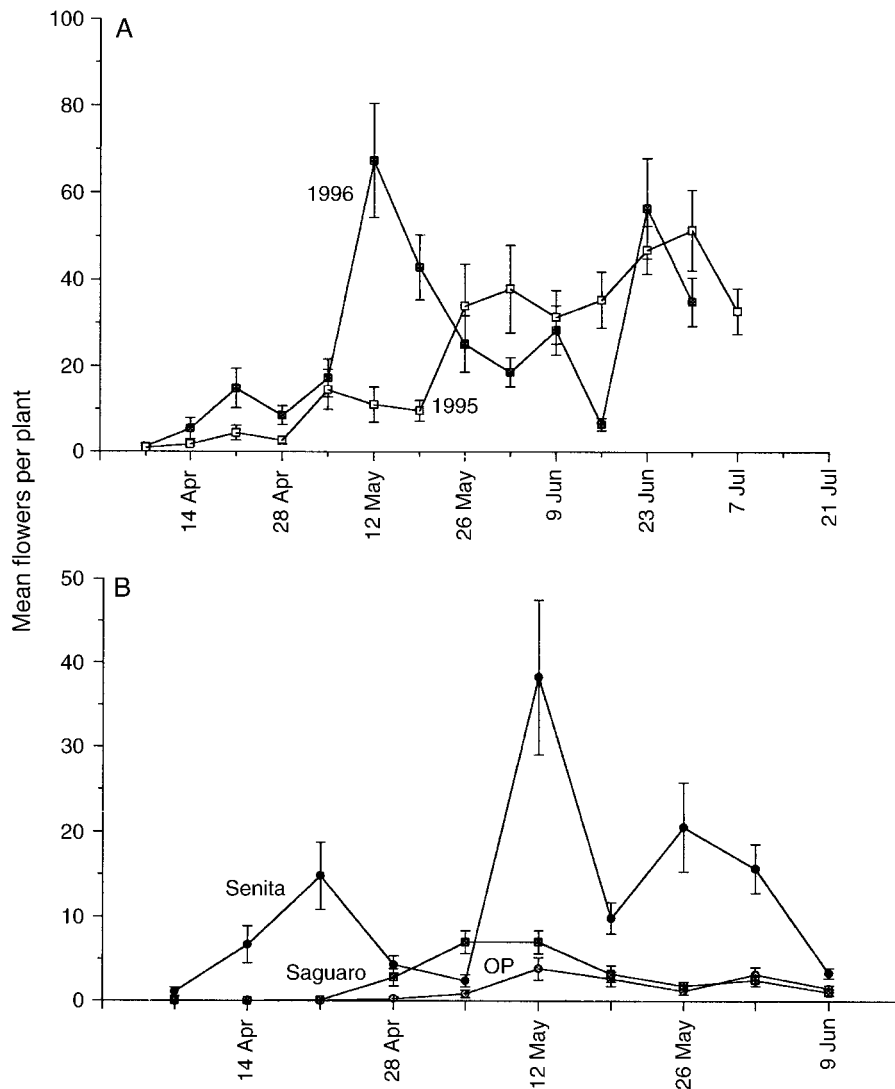


FIG. 3. Flowering curves of (A) senita at Bahia de Kino in 1995 and 1996 and (B) senita, saguaro, and organ pipe at Organ Pipe Cactus National Monument in 1997. Data are means $\pm$ 1 SE. Sample sizes are 20 plants per species. The curves in (A) are redrawn with permission from Holland and Fleming (1999a).

Broad-billed), and orioles (Hooded and Scott's), as well as resident species such as woodpeckers (Gila and Gilded Flicker), Verdins, and House Finches. Honeybees were the dominant diurnal invertebrate flower visitors at both sites. Flowers of senita were heavily visited at night by the senita moth, *Upiga virescens*, and by halictid bees (*Dialictis*, *Augochlorella*, and *Agapostemon* species) whenever flowers remained open after sunrise (Fleming and Holland 1998).

Numbers of *Leptonycteris* bats recorded in our nocturnal censuses at BK in 1995–1996 and at ORPI in 1997 averaged 1.3 per census ($\sim 0.93/\text{ha}$) and were an order of magnitude lower than numbers of birds in the diurnal censuses (Table 3). Mean number of bats per nocturnal census did not differ among years or sites (Kruskal-Wallis ANOVA, $H = 4.13$, $df = 4$, $P = 0.39$).

Observations at BK in 1999 also indicated that bat densities were low at Tortilla Flats in April (T. H. Fleming, *unpublished data*).

The number of *Leptonycteris* bats residing in the Sierra Kino cave 7 km from our study plots at BK varied seasonally and annually. As discussed by Horner et al. (1998), bat numbers in this cave usually are highest (up to 7600 individuals) in early April. They decline to very low numbers in May when many individuals either move 29 km to maternity roosts on Isla Tiburon in the Gulf of California or migrate elsewhere. Bat numbers increase again in mid-June when females and their recently weaned young return to the mainland to roost. Exit counts in mid-April over 10 yr indicated that bat numbers ranged from 69 to 7600 (Fig. 4A). Part of this variation appears to be correlated with the

TABLE 2. Annual variation in the time of peak flowering and the estimated number of flowers produced per season in four species of columnar cacti at two sites in the Sonoran Desert.

Species	Year	Approximate flowering peak	Total flowers per plant per season	Paired <i>t</i> tests or one-way ANOVA
Bahia de Kino				
Cardon	1989	28 April	276.5 ± 43.5	$t = 6.38, P < \mathbf{0.001}$
	1990	28 April	883.8 ± 108.5	
	1995	5 May	225.5 ± 40.3	$F_{3,76} = 17.95, P < \mathbf{0.001}$
	1996	~25 March	872.3 ± 84.9	
	1998	14 April	508.0 ± 62.1	
Saguaro	1999	21 April	444.3 ± 58.3	
	1989	5 May	127.0 ± 55.9	$t = 1.00, P = 0.33$
	1990	28 April	176.3 ± 24.6	
	1995	5 May	404.1 ± 57.3	$t = 0.12, P = 0.91$
	1996	28 April	394.3 ± 78.8	
Organ pipe	1999	19 May	101.8 ± 18.0	$t = 2.29, P = \mathbf{0.03}$
	1989	30 June	62.3 ± 10.9	
	1990	23 June	103.3 ± 19.4	$F_{3,76} = 3.65, P = \mathbf{0.02}$
	1995	30 June	137.4 ± 34.2	
	1996	16 June	106.2 ± 22.1	
Senita	1998	23 June	74.1 ± 11.5	
	1999	≥30 June	38.8 ± 13.4	$t = 1.44, P = 0.17$
	1995	2 June, 30 June	3076.4 ± 561.0	
	1996	12 May, 23 June	3398.6 ± 517.5	
Organ Pipe Cactus National Monument				
Saguaro	1997	5 May	195.0 ± 18.1	
Organ pipe	1997	12 May	284.9 ± 52.5	
Senita	1997	12 May, 26 May	1472.9 ± 249.0	

Notes: Data are means $\pm$ 1 SE. Sample sizes are 20 plants. Brackets indicate the same sets of plants that were monitored in different years. Statistically significant *P* values are in bold type.

cardon flowering peak. Peak bat numbers occurred early in the season (before 1 April) in three out of three years of very early cardon flowering (1996–1998), in early April in five out of five years in which the cardon peak occurred then, and in May in 1995 when the cardon peak was very late (Fisher's Exact Test with the latter two groups combined, $P = 0.018$).

Leptonycteris bats arrive at ORPI in the latter half of April. The maternity roost at ORPI contained over 10 000 adults in late May 1997, and numbers in this roost remain high throughout the cactus flowering and fruiting seasons (T. Tibbitts, *personal communication*).

Results of the bird censuses in 1995–1999 indicated that the number of potential pollinators in our study areas fluctuated on a weekly basis. The presence of some species (e.g., woodpeckers, Verdins, and House Finches) was constant within seasons because of their status as breeding residents. Other species, particularly hummingbirds, were variable in presence and abundance (Fig. 4B). Costa's Hummingbirds, for example,

were much more common at BK in late May and June 1996 than in 1995. They were present from early April to at least mid-June in 1999. Mean number of birds per census ranged from 11.6 (at Tortilla Flats in 1995) to 17.6 (at ORPI in 1997) and averaged 14.8 (~10.6/ha); means did not differ significantly between sites and years (Kruskal-Wallis ANOVA, $H = 4.06$, $df = 5$, $P = 0.54$; Table 3).

Despite the absence of site and year differences in the absolute densities of flower-visiting birds, the relative abundance of different species varied by year and site. Based on focal flower observations (Fleming et al. 1996), the most common avian visitors to flowers of cardon and saguaro in 1989 were hummingbirds (59% of cardon visits, $N = 39$; 75% of saguaro visits, $N = 504$), whereas White-winged Doves were the most common visitors to cardon and saguaro in 1990 (73% of cardon visits, $N = 11$; 78% of saguaro visits, $N = 115$). Only at organ pipe flowers were hummingbirds the most common visitors in both 1989 and 1990 (92%

TABLE 3. Summary of the number of birds and bats recorded in weekly censuses in 1995–1997.

Taxon	Site and year					
	Seri 1995	Seri 1996	Tortilla 1995	Tortilla 1996	Tortilla 1999	ORPI 1997
Birds	14.3 ± 2.0 (6)	15.1 ± 1.6 (7)	11.6 ± 1.8 (7)	14.6 ± 2.6 (8)	15.7 ± 1.0 (11)	17.6 ± 1.1 (5)
Bats	1.2 ± 0.7 (5)	0.7 ± 0.6 (7)	1.4 ± 0.5 (7)	1.8 ± 1.6 (8)	...	1.0 ± 0.5 (5)

Notes: Data are means $\pm$ 1 SE. Numbers of censuses are indicated in parentheses.

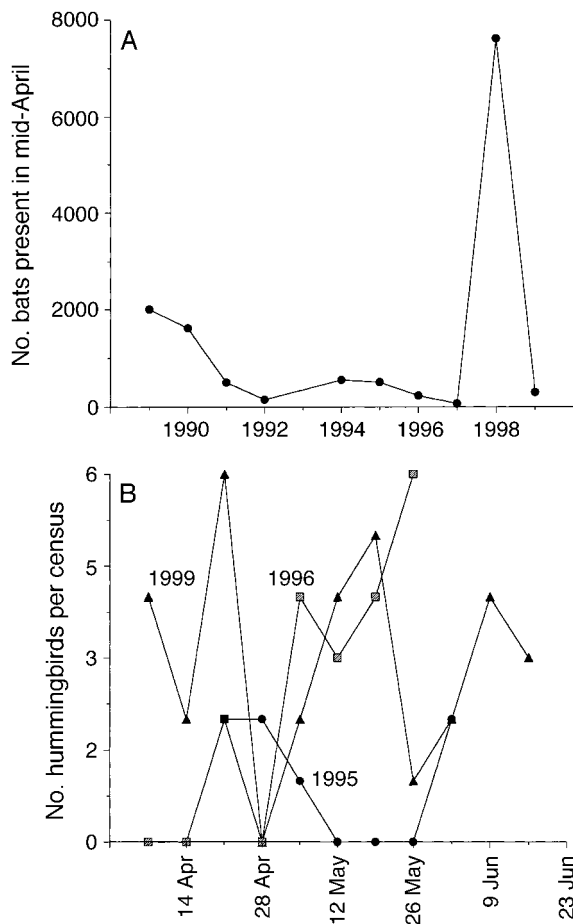


FIG. 4. Censuses of (A) the bat *Leptonycteris curasoae* at the Sierra Kino cave between 1989 and 1999 and (B) hummingbirds at the Tortilla Flats site at Bahia de Kino in 1995–1996 and 1999.

of visits in 1989, $N = 78$; 98% of visits in 1990, $N = 154$). Similarly, at BK in 1995–1996, the relative abundance of White-winged Doves decreased, whereas that of Verdins increased between years on the Seri plot ($\chi^2 = 19.71$, $df = 4$, $P < 0.001$; Fig. 5). On the Tortilla Flats plot, the relative abundance of White-winged Doves and woodpeckers decreased, whereas that of hummingbirds, Verdins, and House Finches increased from 1995 to 1996 ($\chi^2 = 11.56$, $df = 4$, $P = 0.021$); the relative abundances of birds there were similar in 1995 and 1999 (Fig. 5). Woodpeckers were relatively much more common, and hummingbirds and Verdins much less common at ORPI than at BK (Fig. 5).

In summary, density of the bat *L. curasoae* was much lower than that of diurnal avian flower visitors, and its numbers in mid-April varied considerably among years at BK. Observations at focal flowers also indicate that visitation rates to cactus flowers by both bats and birds were low and variable among sites and years (Fleming et al. 1996; T. H. Fleming, unpublished data).

Variation in the ratio of energy supply to demand

Our data on flower production and pollinator abundance can be used to estimate the ratio of nectar production to pollinator energy demand during the spring at our study sites. These calculations indicate that the size of the nectar energy supply varied substantially between April and June at both study sites (Fig. 6). At BK it was highest in April during peak cardon flowering; at ORPI it was highest in the first half of May during peak saguaro flowering. In most weeks at both sites, energy supply was substantially greater than energy demand (Fig. 6). Because of its low foraging density, energy demand by *Leptonycteris* bats was especially low (Horner et al. 1998). Weekly estimates of energy supply exceeded demand by bats by a factor of at least 4.1, 3.1, and 9.2 at BK in 1995 and 1996 and at ORPI in 1997, respectively. Adding the energy demands of birds to that of bats increased total energy demand, but supply still exceeded demand, especially at ORPI where the density of saguaro cacti is very high (Fig. 6).

The contributions of nocturnal and diurnal pollinators to fruit set and seed production

Fruit set differed strongly among cactus species due to different contributions of nocturnal and diurnal pollinators (Table 4). Open-pollinated fruit set in cardon averaged 32% in three years. We also determined open-pollinated fruit set in 15 phenology plants at BK in 1998 and 1999; mean values were 30.9% and 36.7%, respectively. In five years, open-pollinated fruit set av-

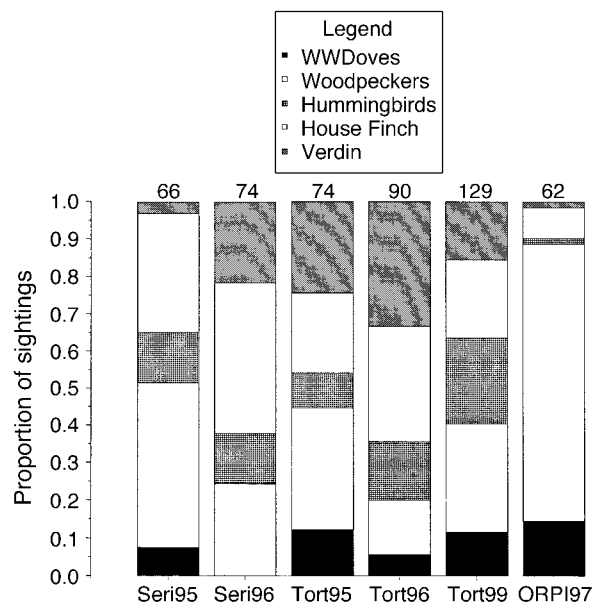


FIG. 5. Relative abundance of potential avian pollinators of cactus flowers at two sites (Seri and Tortilla Flats) at Bahia de Kino in 1995–1996 and 1999, and at one site in Organ Pipe Cactus National Monument in 1997. Sample sizes are above the bars. WWDoves = White-winged Doves.

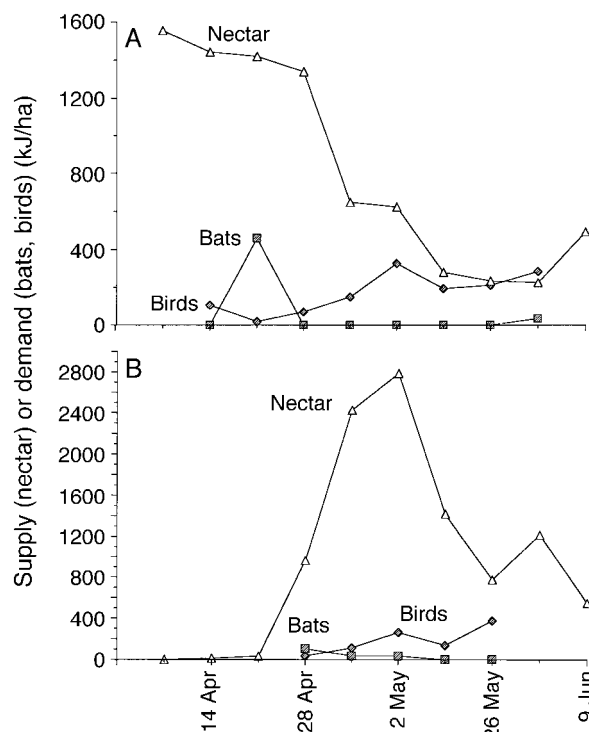


FIG. 6. Relationship between the energy supply in cactus flower nectar and energy demand by cactus-visiting bats and birds at (A) Bahia de Kino in 1996 and (B) Organ Pipe Cactus National Monument in 1997.

eraged $32.6 \pm 3.6\%$ SE (coefficient of variation = 25.0%). Because they visit flowers first, bats likely accounted for most (nearly 100%) fruit set (Table 4). Insects (honeybees) were major contributors to diurnal fruit set. Results of a three-way log-linear analysis indicated that the interaction between year, treatment, and flower fate (aborted or fruit set) was significant as was the interaction between treatment and flower fate (controlling for year) and differences among years (controlling for treatment and flower fate; Table 5).

Fruit set was much higher in saguaro than in cardon and averaged 66% with little variation over five years. Previously reported values of open-pollinated fruit set in saguaro at Saguaro National Monument near Tucson, Arizona, include 60.4% and 53.8% in 1959 and 1960 (McGregor et al. 1962). Combining these data with our data, open-pollinated fruit set in saguaro over seven years averaged $63.6 \pm 2.3\%$ (cv = 9.5%). Open-pollinated fruit set did not differ among our study sites (Table 4). Diurnal visitors to saguaro contributed significantly more to fruit set than nocturnal visitors at both sites, although in 1995 bats contributed more to fruit set than diurnal visitors. Honeybees accounted for ~68% of diurnal fruit set and birds contributed 32% (Table 4). The interaction between year, treatment, and flower fate was significant at BK as was the interaction between treatment and flower fate (controlling for year) and differences among years (controlling for treatment and flower fate; Table 5). Differences in fruit set among

TABLE 4. Percentage fruit set in pollinator exclusion experiments for four species of columnar cacti between 1989 and 1997.

Species	Site, year	N per treatment	Control	Nocturnal	Diurnal	Diurnal insect	Nocturnal as % control†	Diurnal as % control†	Insect as % diurnal
Cardon	BK, 1990	40–75	35.0	31.0	28.0	...	88.6	80.0	...
	BK, 1995	121–125	40.8	47.6	12.9	24.0	100.0	31.6	100.0
	BK, 1996	118	19.5	14.4	9.3	6.8	73.8	47.7	73.1
	Mean		31.8	31.0	16.7	15.4	87.5	53.1	86.6
							(103.3, 51.3–159.0)	(47.0, 27.0–85.8)	
Saguaro	BK, 1989	19–23	74.0	40.0	68.0	43.0	54.1	91.9	63.2
	BK, 1990	44–45	64.0	11.0	66.0	...	17.2	100.0	...
	BK, 1995	76–87	65.5	56.3	43.4	28.9	86.0	66.3	66.6
	BK, 1996	99–105	62.5	13.3	70.3	52.5	21.3	100.0	74.7
	Mean		66.5	30.2	61.9	41.5	44.6	89.6	68.2
Organ pipe	ORPI, 1997	98–102	64.7	12.7	70.3	39.8	19.6	100.0	56.6
							(41.1, 18.0–68.0)	(95.5, 80.2–108.3)	
	BK, 1989	24	21.0	8.0	21.0	4.0	38.1	100.0	19.0
	BK, 1990	44–47	30.0	9.0	18.0	...	30.0	60.0	...
	BK, 1992	65–267	16.0	3.4	11.6	...	21.3	72.5	...
Senita	BK, 1993	33–42	39.0	16.6	22.5	...	42.6	57.7	...
	BK, 1995	94–99	34.0	7.1	23.4	18.1	20.9	68.8	77.4
	BK, 1996	101–112	22.3	5.8	16.8	15.8	26.0	75.3	94.0
	Mean		27.1	8.3	18.9	12.6	29.8	72.4	63.5
	ORPI, 1997	57–68	45.6	40.3	22.8	22.8	88.4	50.0	100.0
Senita							(38.8, 19.7–73.6)	(66.3, 47.6–89.9)	
	BK, 1995	94	46.8	35.1	23.4	...	75.0	50.0	...
	BK, 1996	265–269	44.0	39.8	7.9	...	90.5	18.0	...
	Mean		45.4	37.5	15.7	...	82.7	34.0	...
	ORPI, 1997	361–363	22.6	17.1	6.6	...	75.5	29.2	...
Senita							(86.6, 51.4–128.6)	(29.6, 15.7–59.5)	

Notes: Abbreviations: BK = Bahia de Kino, ORPI = Organ Pipe Cactus National Monument.

† In these two columns the data reported in parentheses include bootstrapped means plus 95% confidence limits with data combined across sites.

TABLE 5. Summary of three-way log-linear analyses of the pollinator exclusion experiments at Bahia de Kino, Mexico, 1989–1996.

Interaction	Species			
	Cardon	Saguaro	Organ pipe	Senita
Y $\times$ T $\times$ F	11.6(4)*	58.4(6)***	3.7(10)NS	12.8(2)***
T $\times$ F given Y	46.8(6)***	138.1(8)***	66.8(12)***	124.2(4)***
Y given T, F	64.7(10)***	65.3(15)***	121.3(25)***	14.9(5)*

Notes: The analyses test for significant interactions between years (Y), treatments (T), and flower fate (F). Treatments include open-pollinated controls, night pollination, and day pollination. Results include *G* values and degrees of freedom (in parentheses).

* $0.05 < P < 0.01$; *** $P < 0.01$; NS, not significant.

treatments at ORPI were significant ($\chi^2 = 85.0$, *df* = 3, $P < 0.001$).

As in cardon, fruit set in organ pipe was relatively low and variable; it averaged 27% in six years at BK (Table 4). Open-pollinated fruit set was significantly higher at ORPI in 1997 (46%) than at BK in 1996 (22%; $\chi^2 = 9.63$, *df* = 1, $P = 0.002$). Fruit set in organ pipe at BK in 1999 was 40.9% (*N* = 115 flowers tagged on 15 plants). In eight years, open-pollinated fruit set in organ pipe averaged $31.1 \pm 3.7\%$ (*cv* = 34.1%). Diurnal visitors contributed more to fruit set than nocturnal visitors at BK; honeybee contribution to diurnal fruit set there averaged 64%. In contrast, bats probably accounted for most fruit set at ORPI. The interaction between year, treatment, and fate at BK was not significant, but the interaction between treatment and flower fate (controlling for year) was significant as were differences among years (controlling for treatment and flower fate; Table 5). Differences in fruit set among treatments at ORPI were significant ($\chi^2 = 9.04$, *df* = 3, $P = 0.029$).

Fruit set in senita averaged 45% in two years at BK, but was half this value at ORPI in 1997 (Table 4). Site differences between open-pollinated treatments (i.e., 1996 vs. 1997) were significant ($\chi^2 = 39.4$, *df* = 1, $P < 0.001$). At two additional sites at ORPI in 1997, open-pollinated fruit set averaged 30.0% (mean of 20 plants) and 29.0% (mean of 13 plants; Holland and Fleming 1999a). Open-pollinated fruit set at BK in 1998 and 1999 was 56.5% (mean of eight plants) and 51.4% (mean of seven plants), respectively (J. N. Holland and T. H. Fleming, unpublished data). In seven population-years, open-pollinated fruit set in senita thus averaged $40.3 \pm 4.9\%$ (*cv* = 32.1%). Contribution of senita moths to fruit set averaged 80% in three years; halictid bees accounted for the remaining fruit set. In 1998–2000 at BK, senita moths accounted for 100% of fruit set (J. N. Holland and T. H. Fleming, unpublished data). The interaction between year, treatment, and flower fate was significant at BK as was the interaction between treatment and flower fate (controlling for year) and differences among years (controlling for treatment and flower fate; Table 5). Differences in fruit set among treatments at ORPI were significant ($\chi^2 = 36.32$, *df* = 2, $P < 0.0001$).

Data from these experiments (Table 4) allow us to quantify year-to-year variability in the contribution of nocturnal and diurnal pollinators to fruit set in cardon, saguaro, and organ pipe. If the bat *L. curasoe* is an unreliable pollinator compared to diurnal pollinators, then the coefficient of variation of its contribution to fruit set should be greater than that of diurnal pollinators. Data summarized in Table 6 indicate that variation in nocturnal (bat) pollination was substantially greater than variation in diurnal pollination in saguaro and organ pipe. Only in cardon was nocturnal pollination less variable than diurnal pollination. *L. curasoe* is a less reliable pollinator for saguaro and organ pipe than it is for cardon.

In addition to differences in fruit set, different pollinators could affect seed production within fruits. Data summarized in Table 7 indicate that, in general, seed production did not differ among pollinator treatments within species. Only in saguaro at ORPI in 1997 was there a significant difference among treatment means with the nocturnal (bat) and diurnal insect means being well below the control value. Despite the absence of significant differences between treatment means, our data suggest that there may be subtle differences among pollinator treatments in seed set. Specifically, visits by nocturnal pollinators resulted in higher seed set than diurnal visits in four out of five cases involving cardon and organ pipe, the two “bat” cacti with the most “nocturnal” flower availability (Table 7). In contrast, visits by diurnal pollinators resulted in higher seed set than nocturnal visits in three out of four cases involving saguaro, which has the most “diurnal” flower avail-

TABLE 6. Year-to-year variation in the relative contribution of nocturnal and diurnal pollinators to fruit set in three species of columnar cacti.

Species	Number of years	Coefficient of variation (%)	
		Nocturnal pollination	Diurnal pollination
Cardon	3	15.0	46.4
Saguaro	7	75.7	15.9
Organ pipe	5	61.8	23.5

Note: Variation is expressed as coefficient of variation of data in columns 8 and 9 of Table 4.

TABLE 7. Number of seeds per fruit produced by visits from different kinds of pollinators during the exclusion experiments.

Species, site, year	Treat- ment	N	Seeds per fruit	χ^2 , df, $P^\dagger$
Cardon, BK, 1990	C	23	1288.1 $\pm$ 91.7	$F_{2,45} = 2.68, P = 0.08$
	N	13	1190.1 $\pm$ 134.0	
	D	12	922.3 $\pm$ 119.0	
Cardon, BK, 1995	C	15	1330.4 $\pm$ 162.2	5.38, 3, 0.15
	N	21	1652.7 $\pm$ 89.9	
	D	2	1182.2 $\pm$ 286.6	
Cardon, BK, 1996	DI	6	1322.2 $\pm$ 254.0	1.18, 3, 0.76
	C	18	1329.1 $\pm$ 141.1	
	N	12	1440.9 $\pm$ 136.3	
Saguaro, BK, 1990	D	8	1483.0 $\pm$ 185.5	$F_{2,42} = 1.05, P = 0.36$
	DI	4	1657.3 $\pm$ 89.7	
	C	15	1358.0 $\pm$ 140.0	
Saguaro, BK, 1995	N	2	750.2	2.87, 3, 0.42
	D	28	1382.8 $\pm$ 127.1	
	C	25	1241.8 $\pm$ 112.7	
Saguaro, BK, 1996	N	18	1464.8 $\pm$ 194.1	6.58, 3, 0.09
	D	16	1148.8 $\pm$ 208.3	
	DI	9	1073.9 $\pm$ 202.6	
Saguaro, ORPI, 1997	C	51	1349.8 $\pm$ 99.3	20.84, 3, 0.001
	N	3	1389.7 $\pm$ 216.4	
	D	54	1628.3 $\pm$ 121.4	
Organ pipe, BK, 1990	DI	3	1389.7 $\pm$ 216.4	$F_{2,36} = 3.12, P = 0.056$
	C	44	1946.7 $\pm$ 131.8	
	N	5	939.6 $\pm$ 264.2	
Organ pipe, BK, 1996	D	42	1863.5 $\pm$ 109.5	4.47, 2, 0.11
	DI	26	1224.8 $\pm$ 135.4	
	C	28	536.9 $\pm$ 101.5	
Senita, BK, 1995	N	3	736.0 $\pm$ 237.1	2.15, 2, 0.34
	D	9	229.7 $\pm$ 36.7	
	C	8	351.3 $\pm$ 77.3	
Senita, BK, 1996	N	1	339	0.06, 1, 0.81
	D	8	172.4 $\pm$ 30.4	
	DI	6	241.2 $\pm$ 73.0	
Senita, ORPI, 1997	C	12	113.3 $\pm$ 13.7	4.56, 2, 0.102
	N	7	136.4 $\pm$ 17.7	
	D	5	108.4 $\pm$ 21.0	
Senita, BK, 1996	C	39	149.6 $\pm$ 8.5	0.06, 1, 0.81
	N	37	150.1 $\pm$ 11.8	
	C	40	157.8 $\pm$ 8.6	
Senita, ORPI, 1997	N	31	134.7 $\pm$ 11.1	4.56, 2, 0.102
	D	6	177.5 $\pm$ 72.5	
	C	40	157.8 $\pm$ 8.6	

Notes: Data are means $\pm$ 1 SE. Study sites include Bahia de Kino, Mexico (BK), and Organ Pipe Cactus National Monument, Arizona (ORPI). Treatments include open-pollinated control (C), nocturnal pollination (N), diurnal pollination (D), and diurnal insects (DI).

† Except for 1990 in which parametric ANOVAs were conducted, the right-hand column reports the results of Kruskal-Wallis ANOVAs testing for differences among treatments within years. The 1990 data are from Fleming et al. (1996).

ability. We tentatively conclude from these results that in terms of seed production, bats may be the most effective pollinators of cardon and organ pipe flowers, whereas diurnal visitors may be the most effective pollinators of saguaro flowers. Further work, however, is needed to confirm this.

In summary, saguaro, which is the most "diurnal" species, had higher and less variable fruit set annually than the other three species, including the highly specialized senita. Bats likely accounted for most fruit set only in cardon (and in saguaro in 1995) at BK and in organ pipe at ORPI in 1997. They were more reliable pollinators than diurnal species only in cardon. Diurnal pollinators, especially honeybees, accounted for most fruit set in saguaro at both sites and in organ pipe at

BK. As expected in a highly specialized pollination mutualism, senita moths accounted for nearly all fruit set in senita.

Is fruit set pollen- or resource-limited?

The four species differed in their response to hand pollination (Table 8). During three years, fruit set in hand-pollinated flowers of females of cardon averaged 74% and was twice as high as open-pollinated fruit set in two years; fruit set in females is strongly pollen limited. In contrast, fruit set in cardon hermaphrodites did not differ among treatments and is resource limited. Fruit set in saguaro was $\geq 64\%$ in both treatments and was resource limited at BK; it was significantly higher in hand-pollinated flowers (88%) than in open-poll-

TABLE 8. Results of the hand pollination experiments at Bahia de Kino, Sonora (BK), and Organ Pipe Cactus National Monument, Arizona (ORPI).

Species	Year and site	N	Percentage fruit set		χ^2 , P
			Hand pollination	Open pollination	
Cardon	1990, BK	40	73.0 (F) [†]	35.0	13.5, 0.0002
	1990, BK	38	29.0 (H)	35.0	0.2, 0.69
	1991, BK	215	76.0 (F)	...	
	1991, BK	139	42.0 (H)	...	
	1996, BK	55	73.0 (F)	30.7	43.6, <0.0001
Saguaro	1996, BK	55	20.0 (H)	18.7	0.02, 0.90
	1990, BK	40	80.0	64.0	1.8, 0.18
	1997, ORPI	40	87.5	64.7	6.2, 0.013
Organ pipe	1990, BK	40	95.0	30.0	35.6, <0.0001
	1997, ORPI	40	85.0	45.6	14.7, 0.0001
	1999, BK	36	94.4	40.9	29.5, <0.0001
Senita				(N = 115)	
	1995, BK	28	46.4	46.8	0.03, 0.86
	1997, ORPI	100	35.0	22.6	5.75, 0.016

Notes: Data for open-pollinated flowers come from Table 4 except for cardon where they come from Fleming et al. (1994) and T. H. Fleming (*unpublished data*), and for organ pipe in 1999 (T. H. Fleming, *unpublished data*). Statistically significant P values are in bold type.

[†] Abbreviations: F = females, H = hermaphrodites

nated flowers (65%) and was weakly pollen limited at ORPI. Fruit set in hand-pollinated flowers of organ pipe was two to three times higher than that of open-pollinated flowers and was strongly pollen limited at both sites (Table 8). Fruit set in senita did not differ between treatments and was resource limited at BK; it was significantly higher in hand-pollinated flowers at ORPI (Table 8). In two other populations at ORPI, however, fruit set in hand-pollinated and open-pollinated fruits of senita did not differ (Holland and Fleming 1999b), nor was pollen limiting in 1998–2000 at BK (J. N. Holland and T. H. Fleming, *unpublished data*).

Pollinator redundancy and complementarity

We used results of our pollinator exclusion experiments (Table 4) to determine whether the four species of cacti have redundant or complementary pollination systems. Based on our calculations, cardon (mean $R = 0.52$, 95% confidence limits (CL) = -0.07 – 1.23) and saguaro (mean $R = 0.35$, CL = 0.07 – 0.68) have partially redundant pollination systems. Only the latter mean differs significantly from zero, probably because of the small sample size (3 yr) for cardon. Resource-limited fruit set occurs in both of these species (hermaphrodites only in cardon). In contrast, organ pipe, whose fruit set is strongly pollen limited, has a complementary pollination system (mean $R = 0.06$, CL = -0.26 – 0.55). As expected in senita, whose fruit set in most years depends nearly exclusively on nocturnal moth pollination, mean R is low (mean $R = 0.14$, CL = -0.30 – 0.73) and does not differ significantly from zero.

Degree of pollinator specialization or generalization in the four species

We also used results of the pollinator exclusion experiments to estimate the degree to which each of the

four species has a specialized or a generalized pollination system. Here we use the terms “specialized” and “generalized” in a relative sense because none of the species is exclusively pollinated by only a single species. By “specialized” we mean that a cactus species is pollinated either by nocturnal or diurnal species, not by both. In each species, nocturnal pollination involves only a single species of pollinator (*Leptonycteris* bats or *Upiga* moths), so nocturnal specialization truly means only one pollinator. Diurnal pollination, in contrast, can involve both birds and insects in cardon, saguaro, and organ pipe, and up to three species of halictid bees in senita. Therefore, “diurnal specialization” has a broader meaning than “nocturnal specialization” in this paper. As stated in the *Introduction*, by “generalized” we mean that a species is effectively pollinated by both nocturnal and diurnal animals.

We used data on mean percentage of control fruit set contributed by nocturnal and diurnal pollinators (Table 4, non-bootstrapped values) to ordinate cactus species and populations in two-phase pollinator specialization space (Fig. 7). Pure nocturnal and diurnal specialists will occupy the lower right-hand and upper left-hand corners of this space, respectively; a pure generalist will occupy the upper right-hand corner. Results indicate that senita is the most nocturnally specialized species, and saguaro is the most diurnally specialized species. Cardon and organ pipe at ORPI are also strongly nocturnal in specialization, whereas organ pipe at BK is strongly diurnal in specialization. Organ pipe is the only species in which significant geographic variation in pollinator specialization occurred (Fig. 7). No species or population was completely specialized or generalized in its use of pollinators.

DISCUSSION

In this study we tested the hypothesis that three species of “bat-pollinated” cacti (cardon, saguaro, and

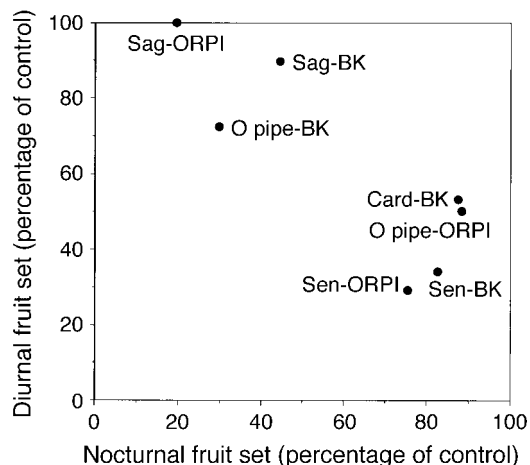


FIG. 7. Estimates of degree of pollinator specialization in four species of columnar cacti based on results of the pollinator exclusion experiments (non-bootstrap mean values in Table 4). Abbreviations for cacti: Card = cardon, O pipe = organ pipe, Sag = saguaro, Sen = senita. Abbreviations for sites: BK = Bahia de Kino, ORPI = Organ Pipe Cactus National Monument.

organ pipe) have more generalized pollination systems than their relatives in southern Mexico because the migratory bat *Leptonycteris curasoae* is an unreliable pollinator in the Sonoran Desert (Valiente-Banuet et al. 1996). We predicted that *L. curasoae* is an unreliable pollinator either because its abundance and contribution to fruit set varies substantially among years and sites, and/or because its abundance is chronically low relative to that of flowers and other potential pollinators. We also tested the prediction that the timing and intensity of flowering in the three “bat-pollinated” cacti exhibit more spatiotemporal variability than that in the senita cactus, which has a highly specialized pollination system involving a nocturnal moth. Unreliable flower resources will favor dietary generalization, and possibly reduced reliability to any one plant, in pollinators. Finally, we used hand pollination and pollinator exclusion experiments to test the prediction that species whose fruit set is limited by resources have redundant pollination systems, whereas species whose fruit set is pollen limited have complementary pollination systems. Before examining our main hypothesis, we will discuss spatiotemporal variability in cactus flowers and their pollinators.

Spatiotemporal variation and interspecific overlap in flowering

Contrary to our prediction, annual variation in the time of peak flowering and intensity of flowering was modest in saguaro and organ pipe. Cardon and senita exhibited substantial annual variation in these reproductive parameters. An unusually cold spring in 1995 delayed the onset of flowering in cardon by ~1 mo, and many individuals had small flower crops that year.

In contrast, flowering in saguaro, which probably is more cold tolerant than cardon given its more northern geographic distribution (Nobel 1982; see also Fig. 1), was not affected by the cold weather. Both timing and intensity of its flowering showed little annual variation. Steenbergh and Lowe (1977) and Haughey (1986) have also documented low temporal variability in the timing and intensity of flowering in saguaro at different sites in Arizona. As in saguaro, the cold weather in 1995 had only a modest effect on the onset of flowering in organ pipe and senita. However, in senita cacti timing of the onset of flowering and the intensity of flowering can be strongly influenced by drought. As water became more limiting between 1995 and 2000, this species delayed the onset and intensity of flowering (J. N. Holland and T. H. Fleming, *unpublished data*). Despite their annual differences in flowering phenology, these plants nevertheless produce relatively reliable floral rewards for their pollinators. Unlike many other desert plants (Turner et al. 1995), their obvious adaptations for drought tolerance enable these cacti to flower and fruit every year (Steenbergh and Lowe 1977, Gibson and Nobel 1986).

The cold spring of 1995 changed the order of blooming in saguaro and cardon and increased the importance of bats as pollinators in saguaro. In most years, cardon begins flowering earlier in the year than saguaro, and because it produces more flowers per night and a greater volume and richer nectar per flower, cardon likely outcompetes saguaro for bat visits (Fleming et al. 1996). Thus, in most years, bats are only about half as important as diurnal species for fruit set in saguaro. In 1995, however, in the absence of cardon flowers, bats visited saguaro flowers heavily and accounted for ~30% more fruit set than diurnal pollinators. Year-to-year variation in the timing of flowering in cardon thus affects the competitive status of saguaro and makes nocturnal blooming worthwhile in this otherwise strongly diurnally dependent species.

Although the flowering seasons of cardon and organ pipe overlap at Bahia de Kino (BK), their flowering peaks differed by nearly two months. As in the case of saguaro, cardon should be a stronger competitor for bat visits than organ pipe because it produces many more flowers per plant per night and substantially richer nectar. Fleming et al. (1996), however, were reluctant to ascribe differences in the timing of peak flowering between cardon and organ pipe to interspecific competition for bat pollinators because they lacked data on geographic variation in time of flowering in organ pipe. Our data on time of peak flowering in organ pipe at Organ Pipe Cactus National Monument (ORPI), where cardon is absent, support the hypothesis that cardon is a superior competitor for bat visits when it co-occurs with organ pipe and saguaro. In the absence of cardon, the flowering peak of organ pipe occurs earlier in the year at ORPI than it does at BK, which results in higher flowering overlap (and potentially stronger competition

for bat visits?) between it and saguaro. Data on flower visitation rates (T. H. Fleming, *unpublished data*) and contribution to fruit set at ORPI (Table 4) suggest that organ pipe is a better competitor for bat visits there than saguaro.

Spatiotemporal variation in the abundance of pollinators

Because it includes a significant number of migratory species, the potential vertebrate pollinator pool for three of the four species we studied varies in size and composition both within and between seasons, a common situation in many (most?) pollination systems. Annual variation can also be substantial in the composition of frugivorous vertebrate assemblages (e.g., Foster 1990, Willson and Whelan 1993, Jordano 1994). The main nocturnal pollinator of cardon, saguaro, and organ pipe is the migratory bat *Leptonycteris curasoae*. Each year, tens of thousands of pregnant females migrate from as far south as coastal Jalisco to give birth to a young bat in mid-May in a few widely scattered maternity roosts in the Sonoran Desert (Cockrum 1991, Wilkinson and Fleming 1996, Ceballos et al. 1997). They remain north, feeding on nectar and pollen produced by columnar cacti and paniculate agaves, and on the pulp of cactus fruit, until late summer (Cockrum 1991, Fleming et al. 1993).

The timing of migration of *Leptonycteris* bats through the Bahia de Kino region of Sonora appears to vary from year to year, apparently in response to annual differences in the onset of flowering in cardon cacti. How the bats adjust the timing of their annual passage through the Bahia de Kino region is unknown, but this temporal variation has an important effect on fruit set in the two cacti whose fruit set is pollen limited (cardon [females only] and organ pipe). We predict that fruit set in these two cacti is correlated with the abundance of this bat. Regardless of the timing of its migration, the density of *Leptonycteris* bats in the Bahia de Kino region is always low in spring, making it a scarce resource for which night-blooming cacti are likely to compete.

Similar seasonal movements characterize some of the major avian visitors to flowers of Sonoran Desert columnar cacti. The White-winged Dove, which is a major pollinator of saguaro flowers, winters from Sinaloa south in Mexico and arrives in the Sonoran Desert, its principal breeding grounds, in early April. In the Cabeza Prieta Wildlife Refuge west of ORPI in southwestern Arizona, peak numbers of this species coincide with peak flowering activity in saguaro (Haughey 1986, Wolf and Martinez del Rio 2000). Likewise, hummingbirds that visit columnar cactus flowers, especially those of organ pipe in May and June, are migrants in our study areas. Costa's Hummingbird breeds at low densities in the Sonoran Desert, principally in March and April. Major periods of migration in this species include early January through mid-March and mid-

April to mid-June (Baltosser and Scott 1996). Our observations in 1995–1999 indicate that its abundance at BK during the latter period is highly variable. At ORPI, it is common only during the ocotillo (*Fouquieria splendens*) flowering season in March and early April (Groschupf et al. 1988). Only woodpeckers, Verdins, and House Finches, among major avian visitors to cactus flowers, are year-round residents in our study areas. Migrant hummingbirds (but not migrant White-winged Doves) probably are less reliable cactus flower visitors than these residents.

Significant spatiotemporal variation in flower production and in the abundance of pollinators results in variation in the supply of and demand for energy in any pollination system. This variation has important implications for the evolution of specialized vs. generalized pollination systems. For example, when supply greatly exceeds demand, as we have documented in this study (Fig. 6), pollinator limitation is likely to occur which can lead to the evolution of pollinator generalization, especially when the abundance of a highly effective pollinator (e.g., *Leptonycteris* bats) is chronically low. Unless alternative pollinators are extremely ineffective, selection should favor changes in flower closing times, nectar production schedules, and/or duration of pollen viability and stigma receptivity to attract diurnal pollinators to an originally nocturnal (bat) pollination system. The addition of diurnal pollinators to a nocturnal pollination system should reduce the intensity of pollinator limitation and increase the match between energy supply and demand.

Are lesser long-nosed bats unreliable pollinators in the Sonoran Desert?

Valiente-Banuet et al. (1996) suggested that generalized pollination occurs at the northern limits of certain columnar cacti because of year-to-year variation in the abundance (and hence reliability) of migratory nectar-feeding bats. In addition, effective pollinators can be unreliable whenever they are chronically less abundant than other potential pollinators. Whenever a plant's effective pollinators are unreliable in space and time, selection should favor traits that increase its range of pollinators or that favor specialization on a more reliable pollinator (e.g., Schemske 1983, Howe 1984, Thompson 1994, Bronstein 1995). Is *L. curasoae* a less reliable pollinator in the Sonoran Desert than in tropical arid habitats?

Our data suggest that there are two reasons why *L. curasoae*, which is a feeding specialist on columnar cacti flowers and fruit in the spring (Fleming et al. 1993), is an unreliable pollinator. First, bat pollination was three to five times more variable than diurnal pollination in organ pipe and saguaro, respectively (Table 6). Only in cardon was bat pollination less variable (by a factor of three) than diurnal pollination. Second, its abundance is chronically low relative to other pollinators, as illustrated by the ratio of energy supply:

energy demand (Fig. 6). Whereas cactus flower densities tend to be high during the spring, densities of *L. curasoe* tend to be low (or zero) except near maternity roosts. The energy supply contained in those flowers appears to exceed the energy demand of pregnant and lactating bats by a factor of at least three to four. The densities of cactus-visiting birds are an order of magnitude higher than those of *L. curasoe*. Based on these density differences, birds are likely to be more frequent (and hence more reliable) visitors to cactus flowers than bats in many parts of the Sonoran Desert.

Our data on annual variation in fruit set as well as low population densities of bats support the hypothesis that *L. curasoe* is an unreliable visitor to cactus flowers in the Sonoran Desert. Is it a more reliable visitor farther south in Mexico? According to Valiente-Banuet et al. (1996) and Rojas-Martinez et al. (1999), the densities of *L. curasoe* and other nectar-feeding bats are also low in tropical arid habitats such as the Tehuacan Valley of southeastern Mexico where these bats are the exclusive pollinators of many species of columnar cacti. The main difference between this site and the Sonoran Desert is that the match between densities of cactus flowers and bats appears to be much closer. Compared with cardon and saguaro, which sometimes bear dozens of open flowers per night, many columnar cacti in the Tehuacan Valley produce only a few (one or two) open flowers per night (A. Valiente-Banuet, *personal communication*; also see Nassar et al. 1997). As a result, despite their low density, bats are able to pollinate nearly 100% of the available flowers in Tehuacan (Valiente-Banuet et al. 1997a, b), whereas they pollinate only a fraction of the available flowers in the Sonoran Desert. But this situation raises a question: Why is flower production in cardon and saguaro (but not in organ pipe) so much higher than that of most tropical columnar cacti? What selective factors have favored the evolution of larger flower crops in certain northern columnar cacti in the face of apparently chronically low densities of nectar-feeding bats (and birds)? One possible explanation for this paradox is that the current densities of cactus-visiting bats and birds in the Sonoran Desert are substantially lower than their historic averages. We have no data bearing on this question, however.

Pollination biology and ecological redundancy

In addition to documenting the consequences for fruit set caused by significant spatiotemporal variation in pollinator abundance, our study addresses concepts of functional redundancy and complementarity in a pollination system. Functional redundancy in pollination systems occurs when only a fraction of the species that pollinate flowers are necessary for full fruit set, perhaps because fruit set is resource limited (fide Lawton 1994). In contrast, complementarity occurs when fruit set is the sum of the contributions of individual pollinators; it is likely to occur whenever fruit set is pollen limited.

The concepts of redundancy and complementarity assume major importance in conservation discussions (e.g., Walker 1992, Bond 1994, Kearns and Inouye 1997, Kearns et al. 1998).

Results of the pollinator exclusion experiments support our prediction that pollinator redundancy is more likely to occur in plants whose fruit set is resource limited than in plants with pollen-limited fruit set. Fruit set in cardon (hermaphrodites only), saguaro, and senita is resource limited, and the former two species have partially redundant pollination systems. In most years, pollination either by bats (cardon) or by White-winged Doves and honeybees (saguaro) alone accounts for most of the open-pollinated fruit set. But, as in saguaro in 1995, redundant pollinators (bats) can sometimes contribute more to fruit set than the main pollinators (diurnal species) can. In senita, partial redundancy occurs only in cool years when its flowers remain open after sunrise and are pollinated by diurnal bees. Otherwise, redundancy in this species is zero, and the senita moth accounts for 100% fruit set (J. N. Holland and T. H. Fleming, *unpublished data*). Likewise, redundancy is zero in organ pipe, whose fruit set is strongly pollinator limited. Maximum fruit set in this species requires the joint contributions of bats, birds, and bees.

The conservation implications of these results are important. Loss of one or more species of pollinators is much more likely to result in a decrease in fruit set in plants with specialized or complementary pollination systems than in those with redundant systems. Because they have partially redundant pollination systems, cardon and saguaro will still suffer some reduced fruit set if one or more of their pollinators disappears, but an equivalent loss of pollinators in organ pipe will result in a much greater reduction in fruit set. Nonetheless, to maximize fruit set in "bat-pollinated" Sonoran Desert columnar cacti, protection of vertebrate visitors to cactus flowers needs to target migratory hummingbirds and White-winged Doves, in addition to the federally endangered bat, *L. curasoe* (Withgott 1999).

Historical biogeography and the evolution of pollinator specialization

Our study system lies at or near the northern geographic limits of columnar cacti in Mexico and the southwestern United States. The species of cacti we studied are derived from arid tropical or subtropical relatives living in south central Mexico (Gibson and Horak 1978). The closest relative of cardon apparently is *Pachycereus grandis* of central Mexico; that of saguaro is *Neobuxbaumia mezcalaensis* of Puebla and Oaxaca; that of organ pipe is *Stenocereus martinezii* of Sinaloa; and that of *Lophocereus schottii* is *Pachycereus marginatus* of central Mexico (Gibson and Horak 1978, Cornejo and Simpson 1997). Three of the southern species are bat pollinated, whereas *P. marginatus* is hummingbird pollinated (Gibson and Horak 1978, Valiente-Banuet et al. 1996, 1997a). The evo-

lutionary legacy of the Sonoran Desert species we studied thus includes adaptations (in terms of flower size and shape, nocturnal flower opening, and nectar and pollen volume) for pollination by bats or birds. These adaptations are still present in cardon, saguaro, and organ pipe (Fleming et al. 1996). They have been modified drastically in senita during its coevolution with a specialized moth pollinator (Fleming and Holland 1998).

In the face of potentially higher climatic variability, at least in terms of winter and early spring air temperatures, and the migratory behavior of some of their potential vertebrate pollinators, to what extent have these three species become more generalized in their pollination biology than their southern relatives? The answer to this question depends on the cactus species. Our data (Fig. 7) suggest that although none of the species is a pure specialist, clear tendencies towards specialization still exist. Thus, as expected, senita is the most nocturnally specialized species followed by cardon (Fig. 7). Saguaro is the most diurnally specialized species followed by the BK population of organ pipe. Neither senita nor saguaro showed strong geographic variation in degree of pollinator specialization. In contrast, such variation apparently exists in organ pipe, which was pollinated primarily by diurnal species at BK but by *Leptonycteris* bats at ORPI.

Evolution towards diurnal specialization in saguaro reflects its status as the northernmost of the three vertebrate-pollinated cacti. Its current range extends well north of the distributional limits of *Leptonycteris* bats (Fig. 1). Although maternity roosts of this bat now exist in several mines in southwestern Arizona, these roosts were not available until recent times (e.g., only since the late 1960s in the case of the maternity roost at ORPI). Historically, major maternity roosts of these bats in the northern Sonoran Desert occurred only at Colossal Cave, ~30 km east of Tucson, Arizona, and in a lava tube in the Pinacate Biosphere Reserve, ~60 km south of ORPI in Sonora (Cockrum and Petyrszyn 1991). Given the scarcity of bats in the northern half of its range, and the presence of a strong competitor for bat visits (i.e., cardon) along coastal Sonora, selection must have been strong for saguaro to switch from complete reliance on nocturnal pollinators to reliance on both nocturnal and diurnal pollinators throughout most of its geographic range. Results of this selection are most evident in saguaro's flower opening and closing times and nectar secretion schedule. Unlike cardon and organ pipe, whose flowers open just after sunset and have a unimodal nectar secretion curve with a peak before 2400, saguaro flowers open well after sunset, and this species has a bimodal nectar secretion curve with one peak occurring at ~0200 and another peak occurring at ~0800 at BK (Fleming et al. 1996). Saguaro flowers close in mid-afternoon, whereas those of cardon and organ pipe usually close before 1200 the next morning.

In conclusion, of the three vertebrate-pollinated species, saguaro and possibly organ pipe have moved the farthest away from an ancestral condition of strong reliance on bat pollination (Fig. 7). Only cardon has retained a strong dependence on bats for most of its pollination. Of the four species, senita has changed the most in its pollinator specialization, perhaps from a diurnal hummingbird specialist to a nocturnal moth specialist. In the Sonoran Desert, climatic variability influences the intensity of interspecific competition between cacti for pollinator visits and causes the relative importance of particular pollinators, especially *Leptonycteris* bats, for fruit set to vary from year to year. Under such conditions, generalized pollination systems (as seen in organ pipe) or shifts from reliance on nocturnal pollinators (as seen in cardon) to reliance on diurnal pollinators (as seen in saguaro) has been favored by selection. Nonetheless, as exemplified by the senita-senita moth system, highly specialized pollination mutualisms can also evolve in this habitat in plants that rely on sedentary insects rather than migratory bats and birds as pollinators.

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