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Elisabet V. Wehncke, José Rubén Lara-Lara,
Saúl Álvarez-Borrego, and Exequiel Ezcurra

EDITORS

POLLINATION BIOLOGY OF SONORAN DESERT SUCCULENTS AND THEIR POLLINATORS: EVOLUTION AND CO-EVOLUTION AT A BIOGEOGRAPHIC BOUNDARY

Theodore H. Fleming,[1] J. Nathaniel Holland,[2] and Francisco Molina-Freaner[3]

The pollination biology of six species of Sonoran Desert columnar cacti and two species of paniculate agaves falls along a continuum from extreme specialization (as seen in the moth-pollinated *Pachycereus schottii*) to generalization involving bats, birds, and insects in two cacti (*Carnegiea gigantea*, *Stenocereus thurberi*) and one agave (*Agave subsimplex*). Two species (*Pachycereus pringlei*, *Agave angustifolia*) rely heavily on the nectar-feeding bat *Leptonycteris yerbabuenae* for pollination. Low pollinator reliability (which occurs most strongly in *Stenocereus eruca*) is thought to favor pollinator generalization in these plants, which are among the most charismatic species in this region. Unusual reproductive characteristics, including a trioecious breeding system in *P. pringlei*, the ability to use a different cactus species' pollen to set fruit in *S. thurberi*, and active pollination in *P. schottii*, occur in these species. Most of the vertebrate pollinators of these plants are migratory and have special conservation concerns. Continued reproductive success in these Sonoran Desert succulents depends strongly on habitat conservation both within and outside of this region.

1. INTRODUCTION

In the spring, the floral landscape of the Sonoran Desert is dominated by the color yellow. The yellow flowers of brittlebush and desert marigold stand out at ground level while among trees, the yellow flowers of whitethorn acacias, palo verdes, and mesquites predominate. To be sure, other colors such as the red flowers of ocotillo and lavender flowers of desert ironwood provide some relief in this sea of yellow, but yellow clearly is the color of choice for the flowers of many Sonoran Desert plants. Knowing that this habitat harbors one of the highest diversities of bees in

the world makes it easy to understand why yellow is the preferred flower color. Bees are the most important pollinators of plants in this and many other habitats worldwide, and bee flowers are often yellow in color. But not all Sonoran Desert plants are bee-pollinated, and, as indicated above, not all of its plants produce yellow flowers. Hummingbirds, for example, are common in the Sonoran Desert and are the principal pollinators of plants with red tubular flowers such as species of ocotillo and the gracile columnar cactus *Stenocereus* (*Rathbunia*) *alamosensis*. Among night-blooming plants pollinated by moths or bats, white is the most common flower color.

Although relatively few Sonoran Desert plants are pollinated by birds and bats, these plants and their flowers are among the most charismatic and ecologically important members of this region. To many people familiar with this region, the strange and stately saguaro (*Carnegiea gigantea*), cardon (*Pachycereus pringlei*), and organ pipe (*Stenocereus thurberi*) cacti alone define the Sonoran Desert. In this chapter we review the pollination biology of these cacti and some of their close relatives as well as certain members of the Agavaceae, another group of succulent plants that often share pollinators with columnar cacti. Motivating questions that we address include: (1) to what extent do these plants depend on bats for pollination; how diverse are the pollination systems of Sonoran Desert columnar cacti and agaves; (2) what, if anything, is novel about the reproductive and pollination systems of these plants; and (3) how finely tuned or co-evolved are these plants and their pollinators? Before addressing these questions, we will briefly review the evolutionary history and biogeography of these plants and their chiropteran pollinators.

2. THE EVOLUTIONARY HISTORY AND BIOGEOGRAPHY OF SONORAN DESERT COLUMNAR CACTI, AGAVES, AND THEIR POLLINATORS

Located between latitudes 25° and 35° N in southwestern Arizona (and a small part of adjacent California), coastal Sonora, and most of Baja California, the Sonoran Desert lies at the northern boundary of the geographic ranges of vertebrate-pollinated columnar cacti and other arid-adapted succulents and their pollinators. The evolutionary origins of these organisms lie farther south in arid and semiarid regions of the Neotropics. Subfamily Cactoideae of the Cactaceae, for example, likely first evolved in the central Andes at least 30 million years ago (Arakaki *et al.* 2011). From there different tribes of Cactoideae migrated south (Trichocereeae, Notocacteae), east (Cereeae), and north (Hylocereeae, Leptocereeae, Cacteae, Pachycereeae) with two main lineages (Pachycereeae in Greater Mexico and the Browningieae-Cereeae-Trichocereeae [BCT] clade in South America) giving rise to the bulk of the 'giant'

or columnar cacti (Wallace 2002, Yetman 2007). Of the approximately 130 currently recognized species of columnar cacti, at least 60 occur in Mexico and about 40 occur in Brazil. Most of these plants are pollinated by vertebrates.

Tribe Pachycereeae contains two currently recognized subtribes (Pachycereinae and Stenocereinae) and at least 10 of its genera and 70% of its species are primarily or exclusively bat-pollinated. Genera notable for their species richness in this tribe include *Stenocereus* (with 19+ species) in the Stenocereinae, and *Neobuxbaumia* (9+ species), *Pachycereus* (9 species, including two *Lophocereus*), and *Cephalocereus* (5 species) in the Pachycereinae; the monotypic genus *Carnegiea* (saguaro) also occurs in subtribe Pachycereinae (Yetman 2007). The closest relatives of saguaro, cardon, and organ pipe are thought to be *Neobuxbaumia mezcalaensis* of Puebla and Oaxaca, *Pachycereus grandis* of central Mexico, and *Stenocereus martinezii* of Sinaloa, respectively (Gibson and Horak 1978, Cota and Wallace 1997). Senita (or sinita), *Pachycereus schottii* (formerly *Lophocereus schottii*), is a moth-pollinated columnar that often co-occurs with the three larger species in much of the Sonoran Desert. Its closest relative is the hummingbird-pollinated *Pachycereus marginatus* of central Mexico (Hartmann *et al.* 2002). Hartmann *et al.* (2002) speculate that the shift from bat pollination to hummingbird and moth pollination in *P. marginatus* and *P. schottii*, respectively, represents a single evolutionary event (cf. two independent events). Selective pressures favoring these shifts have not yet been studied. To judge from its very low level of cytoplasmic and chloroplast DNA variation, *P. schottii* is a recently derived species (Hartmann *et al.* 2002). It may have evolved in southern Baja California where its highest genetic diversity occurs (Nason *et al.* 2002).

In contrast to the above estimates of species richness and taxonomy, Arias and Terrazas (2009) suggest that *Pachycereus* contains only five species (*P. grandis, P. pringlei, P. weberii, P. pecten-aboriginum*, and *P. tepamo*) and that *Lophocereus* should contain *P. marginatus* as well as *L. schottii*. Classification and phylogenetic relationships within tribe Pachycereinae are clearly still in a state of flux, and we will adhere to Yetman's (2007) treatment of these cacti in this chapter.

Molecular data suggest that the Agavaceae, which is narrowly defined here to include only New World taxa (Heywood *et al.* 2007), arose 21–26 mya (Good-Avila *et al.* 2006). *Yucca* (with about 49 species) and *Agave* (which in the broad sense includes *Manfreda*, *Polianthes*, and *Prochynanthes* contains about 210 species; *Agave sensu stricto* contains about 166 species) are the family's two largest genera. Good-Avila *et al.* (2006) suggest that the genus *Agave* (*sensu stricto*) evolved in Mexico in the Miocene (9–10 mya) and that it underwent two periods of rapid speciation 6–8 and 2.5–3 mya. *Agave* (*s.s.*) contains two well-defined subgenera (*Littea* and *Agave*), and glossophagine phyllostomid bats, especially species of *Leptonycteris*,

are important pollinators of species in both subgenera (Rocha *et al.* 2006). Species of *Agave* (*s.s.*) are generally not as well-adapted to extreme aridity as cacti and tend to be distributed in moister upland sites in the Sonoran Desert. Nonetheless, about 40 of the 150 North American species occur in this region (Dimmitt 2000; Rocha *et al.* 2006). Good-Avila *et al.* (2006) and Rocha *et al.* (2006) suggest that the presence of large, arid zone bat-pollinated cacti set the stage for the evolution of tall *Agaves* (*s.l.*) that produce nectar-rich flowers attractive to bats. Production of a large, energetically expensive paniculate inflorescence in *Agave* (*s.s.*), in turn, selected for a monocarpic 'suicidal' life history, which is a derived condition in this family.

Members of the endemic American leaf-nosed bat family Phyllostomidae are pollinators of columnar cacti and paniculate agaves throughout the Neotropics. This family contains about 150 species and evolved about 36 mya; its crown groups arose in the late Oligocene, 26–28 mya (Jones *et al.* 2005; Teeling *et al.* 2005). Insectivory is the ancestral diet in the family, but its current dietary diversity is substantial and includes blood-feeding, vertebrate carnivory, nectarivory, and frugivory. The main clade of nectar-feeding phyllostomids (subfamily Glossophaginae *sensu lato*) evolved about 12 mya and contains about 38 species (Davalos 2004, Simmons 2005). Although several species of nectar- and fruit-eating phyllostomids visit and presumably pollinate flowers of columnar cacti, members of one glossophagine genus, *Leptonycteris*, which contains three species, are the primary pollinators of columnar cacti and agaves in Greater Mexico (*L. yerbabuenae* and *L. nivalis*) and northern South America (*L. curasoae*) (Fleming and Nassar 2002; Simmons and Wetterer 2002).

Leptonycteris yerbabuenae (formerly *L. curasoae*) is the main chiropteran cactus and agave pollinator in the Sonoran Desert. Its population biology is complex and includes migratory and resident populations and two reproductive schedules in Mexico (Fleming and Nassar 2002). Females living in the Pacific coastal region of south-central Mexico mate in November and December and migrate north to the Sonoran Desert to have their babies in mid-to-late May. Several substantial maternity roosts containing tens of thousands to over one hundred thousand adult females are known in the Sonoran region (Wilkinson and Fleming 1996, Fleming and Nassar 2002, Peñalba *et al.* 2006). These roosts disband in late summer with some females and young moving into the uplands of southern and southeastern Arizona to feed on the nectar and pollen of *Agave palmeri* (which includes *A. chrysantha)* while others begin to migrate toward southern Mexico. Populations of *L. curasoae* living in Baja California appear to be year-round residents there, and several maternity roosts are known on the Baja mainland and surrounding islands (Wilkinson and Fleming 1996, W. Frick, pers. comm.). Spring births also occur in these populations. In contrast, populations living in southern Mexico mate in the

summer and give birth in December and January when bat-pollinated tropical trees are in peak bloom.

3. POLLINATION BIOLOGY OF SONORAN DESERT COLUMNAR CACTI

Flowering is a spring and early summer event in the four main columnar cacti that we treat in this chapter. Peak flowering in cardon and saguaro usually occurs in late April through mid-May whereas peak flowering in organ pipe occurs in June. Flowering in senita occurs in several pulses between April and July. Fruit set in cardon (females only in this trioecious species; see below) and organ pipe is pollen-limited but is resource-limited in saguaro, senita, and hermaphrodites of cardon (Fleming *et al.* 1996, 2001).

Although saguaro, cardon, and organ pipe produce classic bat flowers (*i.e.*, they are large and white in color with nocturnal anthesis and copious amounts of nectar and pollen), pollinator exclusion experiments indicate that bats are relatively minor pollinators of saguaro (about 45% of fruit set) and organ pipe (about 30% of fruit set) but account for about 90% of fruit set in cardon (Fleming *et al.* 2001). Diurnal pollinators such as birds and bees account for more fruit set than bats in the former two species. White-winged doves are especially important pollinators of saguaro flowers whereas hummingbirds are important pollinators of organ pipe flowers. As a result, these Sonoran Desert columnar cacti have more generalized pollination systems involving both nocturnal and diurnal vertebrates and insects than their relatives farther south in Mexico and Venezuela, many of which rely exclusively on bats for pollination (Fleming 2002).

Our research has revealed two novel aspects about the pollination biology of these columnar cacti. First, cardon does not have a hermaphroditic breeding system as found in most Cactaceae (*e.g.*, saguaros, organ pipes, etchos [*Pachycereus pecten-aboriginum*], and senita). Instead, it has a *trioecious* breeding system in which hermaphroditic (bisexual) individuals co-occur with male and female (unisexual) individuals in some populations. This complex breeding system varies geographically with male plants being absent from the southern portion of cardon's range in coastal Sonora and in the northern portion of its range in Baja California (Fleming *et al.* 1998). Populations that lack males but which contain hermaphrodites and females are called *gynodioecious*. Initially, it was thought that this geographic variation reflected, and was caused by, geographic variation in the abundance of cardon's main pollinator, the bat *L. yerbabuenae*, but recent research has refuted this hypothesis (Fleming *et al.* 1998, Molina-Freaner *et al.* 2003).

Although we currently do not know what factor(s) is/are responsible for geo-
graphic variation in the form of cardon's breeding system, we do know why cardon
has an odd (and extremely uncommon) breeding system. Unlike other members
of *Pachycereus* (and most other cacti) that are diploid (*i.e.*, all chromosomes occur
as pairs in individuals), *P. pringlei* is tetraploid (*i.e.*, all chromosomes occur in sets
of four), a condition that often results in the loss of self-incompatibility barriers in
flowering plants (Levin 1983). Most diploid columnar cacti in the Sonoran Desert
(and elsewhere) are self-incompatible and must receive pollen from another indi-
vidual for successful fertilization and seed production. In contrast, hermaphrodites
of cardon are self-compatible, and individuals can fertilize their own ovules. Self-
fertilization in many plants leads to the production of inferior offspring that suf-
fer from inbreeding depression (the loss of fitness through the deleterious effects
of recessive mutations). Self-compatibility and inbreeding depression, in turn, can
select for mechanisms that promote out-crossing (genetic exchange between dif-
ferent individuals), and one of these mechanisms is the production of unisexual
individuals (*i.e.*, separate males and females) through the occurrence of genetic
mutations causing male or female sterility. Male sterile individuals are females that
transmit their genes from one generation to the next only via seeds whereas female
sterile individuals are males that transmit their genes only via pollen. Hermaphro-
dites, in contrast, possess both male and female sex functions and can transmit their
genes via both pollen and seeds.

Knowing that hermaphrodites have a two-fold advantage in reproduction over
unisexual individuals, we can ask, how do males and females persist in populations
with hermaphrodites? One way they could do this is if the cost of inbreeding in her-
maphrodites was very high, so that their inbred offspring were much less competi-
tive than the outcrossed offspring of females. But through a series of observations
and experiments, we know that this is not likely to be true: inbred seedlings of her-
maphrodites survive and grow just as well as those of females both in the field and in
the lab, at least during their first two years of life (Sosa and Fleming 1999). Another
way by which females and males can successfully compete with hermaphrodites is
by outproducing them in terms of seed and pollen production. Intuitively, we might
expect females to produce twice as many seeds and males to produce twice as much
pollen per season as hermaphrodites if they are to remain in the evolutionary game.
Data on seed and pollen production in several cardon populations in Sonora over
several years indicate that females and males indeed outproduce hermaphrodites in
both seed and pollen production by factors of 1.6–9.3 (Fleming *et al.* 1994, Molina-
Freaner *et al.* 2003), which helps to explain why they are able to coexist with bisexual

individuals, even in the face of apparently low levels of inbreeding depression in seedlings of hermaphrodites.

The second novel aspect of the pollination systems of Sonoran Desert columnar cacti occurs in organ pipe, *S. thurberi*. As indicated above, peak flowering in this cactus occurs in June, after the flowering peaks of cardon and saguaro, but observations of marked plants indicate that some individuals (about 25% at Bahía de Kino, Sonora) routinely begin flowering in early April, well before the bulk of the population. Early-flowering organ pipes are faced with strong competition for bats and other pollinators from cardon and saguaro and are highly likely to receive heterospecific, rather than conspecific, pollen from bat visits. In most plants, receipt of heterospecific pollen causes flowers to abort, but this does not happen in organ pipe. Carefully controlled hand pollination experiments indicate that when cardon pollen is placed on organ pipe stigmas, fruit set is nearly as high (74%) as when conspecific pollen is placed on their stigmas (84%); cardon flowers abort when they receive organ pipe pollen (Fleming 2006). Compared with fruit from flowers receiving conspecific pollen, heterospecific fruit develop more slowly, are smaller at maturity, and contain fewer and smaller seeds. Most importantly, seeds in heterospecific fruits lack embryos and hence are sterile. Comparison of the growth rates of open-pollinated fruits with those of conspecific or heterospecific fruits indicate that between early April and mid-May, most fruits are derived from heterospecific pollination.

These observations and experiments indicate that, unlike cardon and saguaro, organ pipe can use heterospecific pollen to produce fruits that mature but contain sterile seeds. This fruit retention is odd and raises the question, why hasn't selection eliminated early flowering in this species? One explanation for the existence of early flowering in coastal Sonora is that it has positive selective value at sites that lack cardons (*i.e.*, in much of *S. thurberi's* range in Sonora; see Figure 1) because it enables individuals to attract migrating populations of nectar-feeding bats and hummingbirds (Fleming 2006). Levels of between-population gene flow, mediated by strong-flying *Leptonycteris* bats, are known to be high in organ pipe (as well as in cardon and saguaro; Hamrick *et al.* 2002) which might make it difficult for selection to remove early flowering genes from coastal populations.

In Sonora, *S. thurberi* apparently has a geographic 'refuge' from a strong competitor, *P. pringlei*, but what about in Baja California, where the ranges of organ pipe and cardon overlap completely (see Figure 1)? Based on the results from Bahía de Kino, we might expect early flowering in organ pipe to be much less common in Baja than in Sonora, but this apparently is not the case. In the area around Loreto, Baja California Sur, between 18–22 April 2009, the frequency of early flowering in
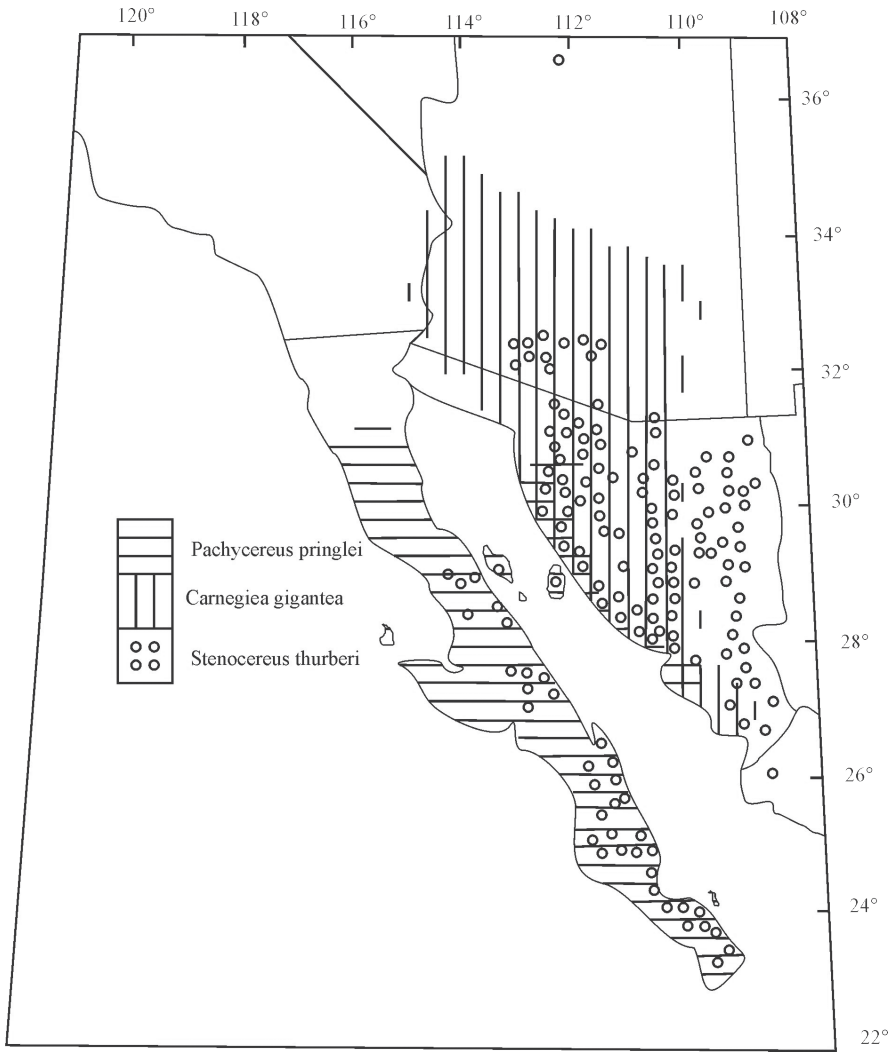
FIGURE 1. Map of the distribution of three species of Sonoran Desert columnar cacti: cardon (*Pachycereus pringlei*), organ pipe (*Stenocereus thurberi*), and saguaro (*Carnegiea gigantea*).

two populations of organ pipe was 14% (n = 56 plants) and 38% (n = 37), values that are similar to those reported for Sonora at a similar time of the year (Fleming 2006, unpubl. data). Early flowering is thus not uncommon in southern Baja. What was different about flowers of Loreto organ pipes compared with those is Sonora is that

they were open by mid-afternoon rather than opening after sunset, and their tepals were erect rather than reflexed, making their corollas more tubular in shape. The Loreto flowers were being visited by two species of hummingbirds in the afternoon as well as by *Leptonycteris* bats at night; they closed early the next morning as they do in Sonora (T. Fleming, pers. obs.). Although a detailed study of the pollination biology of *S. thurberi* in Baja California needs to be done, these preliminary observations suggest that this species has shifted from a strongly nocturnal/weakly diurnal flowering pattern as occurs in Sonora to a more balanced diurnal/nocturnal flowering pattern with a greater emphasis on hummingbird pollination in Baja. Timing of anthesis, pattern of nectar production, and flower form all seem to differ in Baja compared with Sonora. The net result of these differences is potentially lower competition for pollinators between organ pipe and cardon and reduced loss of fitness as a result of heterospecific pollination in Baja.

A similar shift away from nocturnal pollination toward diurnal pollination has also occurred in saguaro, the columnar cactus with the most northern distribution in North America (see Figure 1). Compared with cardon and organ pipe, flowers of saguaro open later at night and close much later the next afternoon (Fleming *et al.* 1996). Whereas rate of nectar production has a single peak before midnight in cardon and organ pipe, nectar production in saguaro has two peaks, one at about 0200 and another at 0800. Saguaro has clearly moved from the strongly nocturnal/weakly diurnal flowering pattern seen in most bat-pollinated columnar cacti to a weakly nocturnal/strongly diurnal pattern, probably because of the low density or absence of *Leptonycteris* bats in much of the northern part of its geographic range (Fleming *et al.* 2001, Fleming 2002).

The fourth species of Sonoran Desert columnar cactus studied by Fleming, Holland, and their associates is senita, *Pachycereus schottii*. Producing relatively small white or pink actinomorphic (radially symmetrical) flowers that open just after sunset and offer little or no nectar reward, this cactus clearly is insect-pollinated. Rather than being pollinated by hawkmoths, which occasionally visit bat-pollinated cacti, however, the pollinator of senita is a small pyralid moth, *Upiga virescens* (the senita moth), whose entire life cycle is physically associated with this cactus (Fleming and Holland 1998, Holland and Fleming 1999a). During the day, adults of this species rest in the long, bristle-like spines located at the tops of branches. As soon as flowers open at night, they are visited by female senita moths which rub their abdomens over the anthers, collecting pollen on elongated abdomenal setae and scales. Females then fly off to find another individual of this self-incompatible species to pollinate. When they arrive at another plant, females climb onto the stigma of a flower and

rub pollen on it in an act of *active pollination* (cf. passive pollination as practiced by bats, birds, and bees as they seek a tongueful of nectar). Active pollination is very uncommon in plant-pollinator interactions and is best documented in the yucca/yucca moth and fig/fig wasp pollination mutualisms. In these well-studied interactions, females oviposit one or more eggs in a flower's ovary before or after pollination, and their larvae eat and destroy seeds. A similar situation obtains in the senita/senita moth interaction because after pollinating a flower, females lay a single egg on the tips of flower petals or among anthers in the corolla. After the eggs hatch, larvae chew into the ovary and eat developing seeds. They then chew out of the fruit, causing it to abort, and pupate in the stem beneath the areole supporting that fruit. Not all larvae survive long enough to destroy seeds and fruit, and pollination by female moths produces about four to five times more mature fruit than are destroyed by their larvae (Holland and Fleming 1999b). Thus, like the yucca/yucca moth and fig/fig wasp interactions, the senita/senita moth interaction has a net positive effect on plant reproductive success and should be considered mutualistic rather than parasitic. Finally, on warm nights, senita flowers close before sunrise, making *U. virescens* their sole pollinator. On cold nights, flowers remain open for a short time after sunrise and are visited by halictid bees, which are legitimate pollinators (Holland and Fleming 2002). The vast majority of senita fruits, however, result from pollination by female senita moths, and this pollination interaction is thus much more specialized than the pollination systems of saguaro, cardon, and organ pipe.

In addition to *S. thurberi*, the pollination biology and population structure of two other species of *Stenocereus* that occur in Baja California have been studied in detail (Clark-Tapia and Molina-Freaner 2003, 2004, Molina-Freaner and Clark-Tapia 2005). These two closely related species include *S. gummosus*, which can be considered to be a small columnar cactus reaching only a couple of meters in height, and *S. eruca*, which is a prostrate cactus called the 'creeping devil' (Yetman 2007). Both species flower in the summer and fall, and both are self-incompatible hermaphrodites (Clark-Tapia and Molina-Freaner 2004). Although flowers of both species are mostly nocturnal and are pollinated by sphingid moths and native bees, the relative importance of sexual vs. asexual reproduction differs strongly between them. Flowers of *S. gummosus* are reliably visited by moths, and fruit set is similar (40–60%) to that of other Sonoran Desert columnar cacti in most years. In contrast, pollinator visitation in *S. eruca* is highly erratic, and fruit set is very low (3–15%) in good years and 0% in bad years. As a result, clonal propagation is much more important for regeneration in *S. eruca* than in *S. gummosus*. Not surprisingly, populations of *S. eruca* contain less genetic variation and are much more structured genetically (*i.e.*, genotypes are strongly clumped) than those of *S. gummosus* (Molina-Freaner and

Clark-Tapia 2005). Pollinator unreliability has likely favored an emphasis on clonal rather than sexual reproduction in *S. eruca*.

Pollinator unreliability resulting from (1) outright absence of ancestral pollinators (as in *C. gigantea*), (2) strong year-to-year variation in the abundance of sedentary insect pollinators (as in *S. eruca*) or migratory vertebrate pollinators (as in *C. gigantea*, *P. pringlei*, and *S. thurberi*), or (3) strong competition for pollinators from other cacti (as in *S. thurberi*) has had a strong effect on the pollination and reproductive biology of Sonoran Desert columnar cacti. Of the species that we have studied, only senita (*P. schottii*) has evolved a highly specialized relationship with a single species of pollinator, the senita moth. The other species rely on a variety of species, including both nocturnal and diurnal vertebrates and insects in the case of the large columnars, for pollination. In this respect, these plants are no different from flowering plants in many other habitats and regions. Generalization, rather than narrow specialization, characterizes the relationships between many plants and their pollinators, particularly in extra-tropical regions (Waser *et al.* 1996). Do we see a similar emphasis on pollinator generalization in Sonoran Desert agaves, whose reproduction relies on the same suite of potential pollinators?

4. POLLINATION BIOLOGY OF SONORAN DESERT AGAVACEAE

As indicated above, relatively few species of *Agave* inhabit lowland portions of the Sonoran Desert, and the pollination biology of only two species has been studied in detail. These species include *A. subsimplex*, which occurs in a few small colonies in coastal Sonora, and *A. angustifolia*, which is widely distributed in the coastal lowlands to mid-elevations of Mexico and Central America (Gentry 1982). Both species are self-incompatible hermaphrodites that flower in late winter and spring in central Sonora (Molina-Freaner and Eguiarte 2003). Observations of pollinator visitations indicate that bats, birds (hummingbirds, orioles, and woodpeckers), and insects (moths and introduced and native bees) visit flowers of both species, but pollinator exclusion experiments indicate that the bat *L. yerbabuenae* is the only effective pollinator of *A. angustifolia* whereas both nocturnal and diurnal pollinators are effective in *A. subsimplex*. Molina-Freaner and Eguiarte (2003) concluded that *A. angustifolia* resembles tropical Mexican agaves in its strong dependence on bats for pollination and that *A. subsimplex* resembles extra-tropical *Agave*s (*e.g.*, *A. palmeri/chrysantha* in southeastern Arizona; Slauson 2000) by having a more generalized pollination system. These results are similar to the situation in Mexican columnar cacti in which extra-tropical species have more generalized pollination systems than bat-pollinated tropical species (Fleming *et al.* 2001, Fleming 2002).

5. SYNTHESIS AND CONCLUSIONS

Available data on the pollination biology of Sonoran Desert columnar cacti and paniculate agaves indicate that these systems fall along a continuum between strong specialization and total generalization (*fide* Waser *et al.* 1996) with pollinator reliability being a strong determinate of where particular species fall on this continuum. The senita/senita moth interaction is clearly the most specialized of these pollination systems. Indeed, because of active pollination, it is one of the most specialized pollination systems in the world. While we generally expect to find most highly specialized mutualistic interactions to occur in the tropics because of its perceived climatic stability and year-round growing season, it is interesting to note that two of the world's most specialized and coevolved pollination systems —the yucca/yucca moth and senita/senita moth systems— occur in extra-tropical and often strongly arid, climatically variable habitats. We conclude from this that climatic stability is not a *sine qua non* for the evolution of highly specialized pollination systems. In the case of the yucca and senita systems, it has been postulated that nocturnal anthesis, self-incompatibility, and resource-limited fruit set, rather than climatic stability or pollen-limited fruit set, have been particularly important factors in the evolution of these systems (Pellmyr *et al.* 1996, Fleming and Holland 1998).

The next most specialized pollination systems include *Stenocereus gummosus* and *S. eruca*, which are pollinated by sphingid moths, and *Pachycereus pringlei* and *Agave angustifolia*, which are pollinated by *Leptonycteris* bats. Although these plants rely heavily on particular nocturnal animals for pollination, their pollinators are not nearly as restricted and visit a variety of different flowers for nectar and pollen. As a result, these systems represent asymmetrical mutualisms in which the plants are more dependent on particular kinds of pollinators than their pollinators are on particular kinds of plants. Over an entire annual cycle, for example, *L. yerbabuenae* is known to feed on the flowers of many species of columnar cacti as well as spicate and paniculate agaves and a variety of tropical trees and shrubs (Fleming and Nassar 2002, Rocha *et al.* 2006). Similarly, the hawkmoth *Hyles lineata*, which pollinates *S. gummosus* and visits many other cactus and non-cactus flowers, has a broad diet (Alarcón *et al.* 2008). Finally, the most generalized pollination systems include those of *Carnegiea gigantea* and *Stenocereus thurberi* and *Agave subsimplex*. Both diurnal and nocturnal vertebrates as well as diurnal insects are known to effectively pollinate these plants. It is tempting to postulate that generalized pollination systems have evolved in these species because of a combination of (1) their geographic distributions (*C. gigantea*, *A. subsimplex*) and/or (2) their reduced attractiveness to nectar-feeding bats when they co-occur with a superior competitor (*C. gigantea*, *S. thurberi*).

A northern distribution or restricted distribution reduces the exposure of *C. gigantea* and *A. subsimplex* to chiropteran pollinators, respectively. Because of its high density and greater number of open flowers per night, *P. pringlei* likely is a superior competitor for bat visits, to judge from its higher flower visitation rates, than *C. gigantea* and *S. thurberi* when all three species co-occur at the same site (Fleming *et al.* 1996). Again, as we discussed above, reliability of particular kinds of pollinators, especially *Leptonycteris* bats, has played an important role in the evolution of the pollination systems of several species of Sonoran Desert succulents.

In addition to detailed studies of the pollination systems of Sonoran Desert columnar cacti and agaves, our research has revealed new complexities in the reproductive biology of some of these plants. Totally unexpected was the trioecious breeding system of cardon, which is one of the world's largest cacti. Such a complex breeding system in a long-lived plant is unexpected. Other plants with trioecious breeding systems (*e.g.*, wild thyme, *Thymelea hirsuta*) are small, relatively short-lived species. As discussed by Murawski *et al.* (1994) and Fleming *et al.* (1994), a ploidy event in which *P. pringlei* doubled its chromosome number autonomously from a haploid number of 11 that occurs in most cacti to 22 set the stage for the successful invasion of unisexual individuals into populations of hermaphrodites. According to Levin (1983), such ploidy events are not unusual in plants living in extreme environments.

Also unexpected was organ pipe's ability to set seed with heterospecific pollen. Neither cardon nor saguaro has the ability to do this (Alcorn *et al.* 1962, Fleming 2006). Whether other species of *Stenocereus* can do this is presently unknown. This ability likely has negative fitness consequences for *S. thurberi* because it wastes resources through the production of sterile fruits weighing ≥ 50 g. We cannot think of a reason why this ability might have positive selective value in a desert setting.

In conclusion, Sonoran Desert columnar cacti and paniculate agaves living at the northern limits of their clades' geographic distributions have had to adapt to physiologically and biologically challenging environments. In terms of their pollination biology, their biggest challenge has been to adapt to significant spatial and temporal variation in the abundance of their pollinators. Virtually all vertebrate pollinators in this region are migratory, and their numbers at particular sites vary substantially from year to year (Fleming *et al.* 2001). Less is known about year-year fluctuations in the abundance of moth and bee populations in this desert, but to judge from the high annual variation in fruit set in *Stenocereus eruca* in Baja California, some insect populations are also likely to be highly variable in size. Bat pollination is likely to be ancestral in the Pachycereeae, but because *Leptonycteris* bats are migratory in the Sonoran Desert, two of three ostensibly bat-pollinated columnar cacti and one of two paniculate agaves there rely less on them for pollination than their southern

relatives. An extreme response to pollinator unreliability —giving up sexual reproduction altogether— occurs in the prostrate cactus *S. eruca*, which evolved from *S. gummosus* in the dunes of west-central Baja California (Molina-Freaner and Clark-Tapia 2005). Vegetative, rather than sexual, reproduction is much more important in *eruca* than in *gummosus*.

Our final conclusion deals with the conservation implications of the pollination biology of Sonoran Desert columnar cacti and agaves. Sexual reproduction is important, at least at times, in the lives of virtually all of the large northern cacti and agaves, and vertebrate and insect pollinators are intimately involved in this process. Anything that has a negative effect on populations of these pollinators will also have a negative effect on the reproductive success and demography of their food plants. Many of the most important Sonoran Desert vertebrate pollinators, including *Leptonycteris* bats, certain hummingbirds, and white-winged doves, are only seasonal residents in this region (see chapters in Nabhan 2004), and their lives are particularly vulnerable to disruption in a number of different ways. Loss of habitat containing food resources and safe nesting and roosting sites is probably the greatest threat to most migratory animals (Fleming and Eby 2003, Fleming 2004). Mesquite bosques, for example, are an important nesting habitat for white-winged doves, and loss of this habitat has had a profound effect on certain populations of this dove (Martinez de Rio *et al.* 2004). Similarly, *Leptonycteris* bats use a limited number of caves as traditional mating and maternity roosts in Mexico and southern Arizona. When Colossal Cave east of Tucson was commercialized in the 1960s, *L. yerbabuenae* lost one of only four known maternity roosts in Arizona (Cockrum and Petryszyn 1991). Further loss of such roosts would have a devastating effect on this species at the northern limits of its geographic range. Likewise, Fleming (2004) estimated that females of *L. yerbabuenae* need to make at least two stopovers for replenishing their fat reserves when migrating from mating roosts in Jalisco to maternity roosts in the Sonoran Desert. Flowers of columnar cacti (*e.g.*, *Pachycereus pecten-arboriginum*) are an important food (fuel) source during this migration. Anything that disturbs their stopover roosts or food supplies in tropical dry forest and thornscrub along Mexico's Pacific coast will endanger this migration and, ultimately, the reproductive success of Sonoran Desert plants that depend on these bats for pollination. Similar concerns hold for *Leptonycteris* bats and their food plants in Baja California and for habitats, roosts, and food plants used by these bats during their southward fall migration in mainland Mexico. The bottom line is this: the reproductive success and persistence of many charismatic Sonoran Desert plants are now being threatened by factors both within and outside of this region. Within this region habitat conversion and bufflegrass (*Pennisetum ciliare*) invasion threaten or destroy populations of columnar

cacti and agaves (Morales-Romero and Molina-Freaner 2008). Similar forces in western Mexico as far south as Jalisco pose a similar threat. Habitat conservation throughout the Pacific coast of Mexico is critical for the health of populations of charismatic Sonoran Desert plants and their animal pollinators.

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[1*] Emeritus Professor, Department of Biology, University of Miami, Coral Gables, FL, USA, tedfleming@dakotacom.net

[2] Department of Biology and Biochemistry, University of Houston, Houston, TX, USA.

[3] Departamento de Ecología de la Biodiversidad, Instituto de Ecología, UNAM, Hermosillo, Sonora, México.

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