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Col. illus

drawings by
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Col. illus
& Swilley,
Manabai Saito



blossom of the saguaro contains 3,000 stamens and produces
mendous amount of pollen. Bats, birds, bees, and moths
ze this cactus, which may tower 50 feet above the desert.
bu Saito's painting of saguaro blossoms is three-fifths life size.

Life on a tall cactus

by RUTH KIRK

C ACTI COME IN ALL SIZES, shapes, and colors. Saguaro stand fifty feet high, proportioned like living candelabra. Barrel cacti sit squat and cylindrical, armor-plated with stout curving thorns the color of rusted iron. The oval pads of prickly-pear are a soft green, lightly spined with thorns the color of straw. Night-blooming cereus grows as an unpromising stick half an inch in diameter and a yard long, seeming more dead than alive; then one June night it unfolds long petals of shining white and wafts an exquisite fragrance into the hot darkness. The bloom has an unexpected, almost disproportionate glory, bursting from such singularly plain parentage, although cacti outdo the rainbow with the color of their flowers. Every possible red, pink, orange, and yellow is represented, and even greens and browns. Petals are luminous and saturated in hue, as though endowed with structural color like tropical fishes instead of the pigment of ordinary flowers.

Thorns vary widely. They come as hairs, hooks, and bristles; as short spines, straight spines, curved spines, long spines. As Father Johann Jakob Baegert, one of the early-day desert Jesuits, wrote: "Thorns... are surprisingly numerous, and there are many of frightening aspect. It seems as if the curse of the Lord, laid upon the Earth after the fall of Adam, fell especially hard on [Baja] California and had its effect." He counted the thorns on a section of organpipe cactus the length of his handspan, and found "no less than 1,680... It is easy to see that, according to my calculation, a single one of these shrubs carries more than a million thorns." The padre also comments on the usefulness of thorns as toothpicks: "One of them will serve for many years without repointing or resharpening." And he marvels that "the always barefoot and very careless California Indians, especially the children, do not get hurt every day... This gives me cause to admire the vigilance of their Guardian Angel."

For the cactus, thorns serve several purposes. In species

such as barrel cactus and pincushion, they shade one-quarter of the plant at a time, acting as a built-in lathhouse and preventing overheating. They also reduce the drying effect of wind. You realize this when camped with sleeping bags spread at the base of a saguaro or organpipe cactus. If the night is a usual one with the air astir, wind will whisper among the thorns as a lullaby, or rise to a wild sibilance, its hiss as fierce as the gusts that race along the crest of a mountain ridge. By breaking the force of the air's rush, thorns lessen demand for the moisture hoarded within the plant.

It is possible that thorns directly affect the water regimen of cacti, although the theory rates as a bizarre one among many botanists. The idea is based on plants' tendency to build an electrical charge greater than that of surrounding earth or air—the charge coming from free ions in the water, absorbed by the roots and carried to the branches and leaves. With cacti, thorns act something like reverse lightning rods, discharging the built-up electricity from their tips. This helps raise water within the plant in a sort of pumping action. The concept, if true, may help to explain the lifting of water by giant cacti such as saguaros and cardons, which are so tall that capillarity alone scarcely seems adequate. For most plants the transpiration of leaves creates an enormous suction to which roots respond. But cacti have no leaves, and the cuticle encasing trunk and branches is waxy and serves to minimize the loss of moisture. Consequently, the mechanics of lifting water from roots to highest branch tip has been difficult to explain. Thorns may be part of the answer—and any desert traveler who has cursed the bother of thorns can take comfort in the possibility of this compensating usefulness.

When it comes to pain, no thorns surpass those of cholla. Desert hikers carry pliers specifically for pulling cholla from boots, elbows, and fingers; and this is all to the good so far as the plant is concerned. The thorns anchor easily into

much as fifty feet high with two to six uplifted branches. Cardons reach about the same height and look much like saguaros except for being coarser and more branched. They grow only in Mexico, whereas saguaros are familiar on both sides of the international line (and in fact are so abundant and beloved in Arizona that the saguaro blossom is the state flower). A third, also found only in Mexico, appears to be about halfway between a saguaro and a cardon, and bears odd spiny fruit the size of a baseball. Yaqui and Mayo Indians used the fruits as brushes, hence the name of the plant, "hairbrush cactus," or *Pachycereus pectenaboriginum* in Latin, literally, "Indian comb."

Four other species of giant cactus are found in the Sonoran Desert, all of them the type that branch profusely at the ground. Organpipe and senita grow in Arizona, Sonora, and Baja California; agria and sina belong only in Mexico. These four grow with as many as twenty or thirty clumped upright arms, which give the plant the look of a strangely massive shrub ten or fifteen feet high. Actually, Arizona can barely claim this form of cactus. If the boundary were five miles farther north there would be no senita in the United States; eighty miles north, and there would be no organpipe.

Woody ribs support all of the giant cacti; and within the wood, xylem and phloem transport water and nutrients between roots and stems, the same as in other woody plants. The ribs come in two styles. Saguaro, cardon, and hairbrush cactus have circlets of twelve to twenty slender rods that run the length of the trunk and branches. In organpipe, senita, agria, and sina a woody core like a three-inch pipe supports each branch. Both the circlets of individual ribs and the pipelike cores are filled with pith and are surrounded by cortex in the living plants. When the cacti die both stand like gaunt wooden skeletons. Desert peoples prize them as building material: long, straight, and lightweight, the rods and cores become fences and roofs. They are greatly valued in this dry land where there is little to choose from other than the crooked branches of mesquite and ironwood trees, or pines too far distant in the mountains to be practicable.

Like all plants, cacti need water. Some botanists feel that they may even need proportionately more water than other types of plants despite their ability to live on inner reserves alone. The succulence of cacti equalizes desert conditions, bridging from those rare times of abundant water to the far more common and prolonged periods of drought. Succulence hoards water; but it does not produce water. Wherever succulence occurs—and it is not limited to cacti—its effect is an emergency extension of the plant's capacity for life. The stored moisture may provide the margin needed for new shoots, and for blossoming and setting fruit to start the next generation on its way to life. Sedum, a noncactus succulent, has flowers that will set seed even

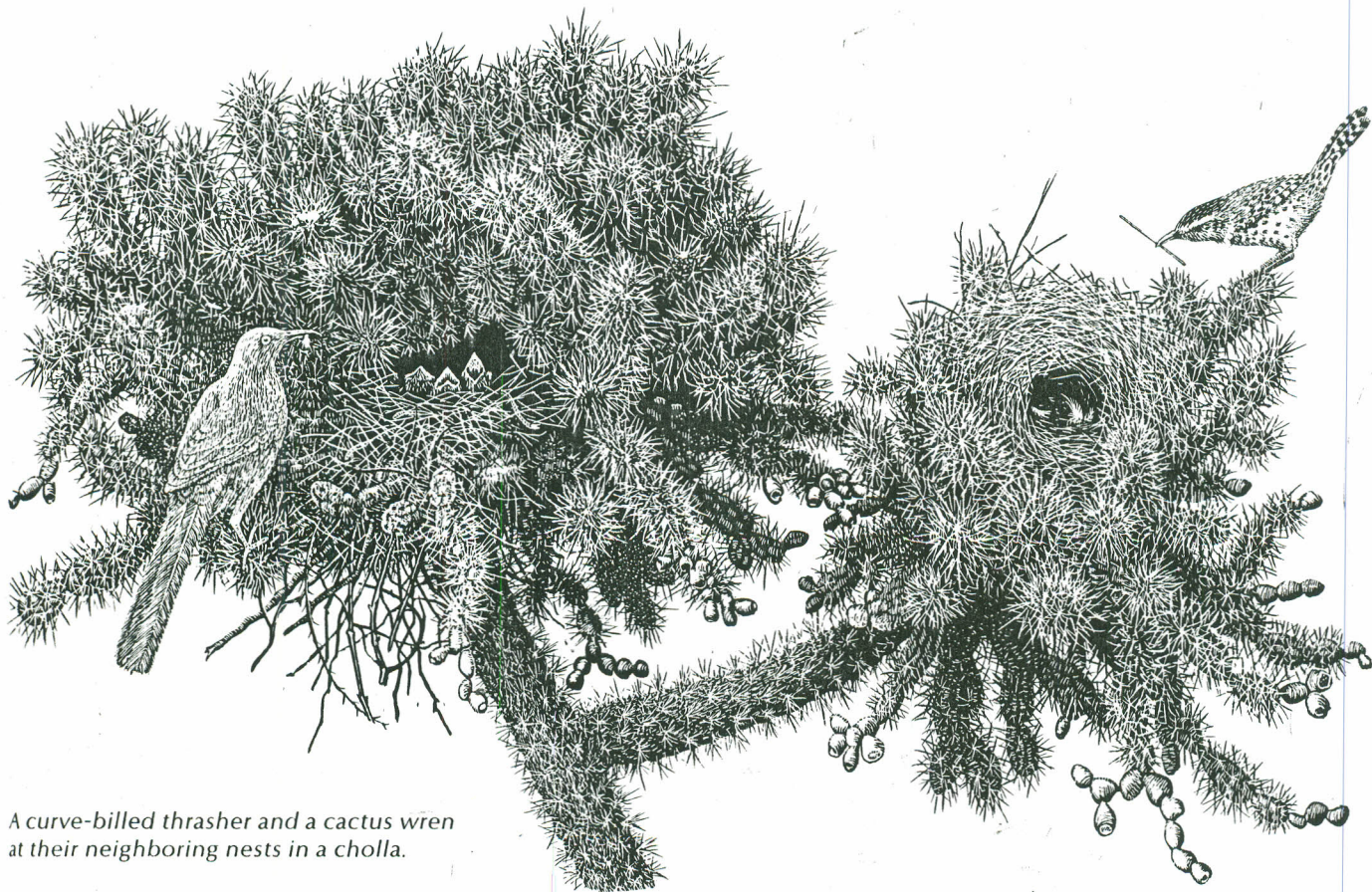
Ruth Kirk's revealing story of saguaro ecology is a chapter from her new book, Desert: The American Southwest, which Houghton Mifflin will publish this fall as part of its Naturalist's America series. Mrs. Kirk's husband, Louis, has been a ranger-naturalist in Death Valley and Organ Pipe Cactus national monuments. Her books include Exploring Death Valley and The Olympic Rain Forest, and she is a frequent contributor to Audubon and other national magazines.

after they have been severed from the plant and placed in a collector's press to dry. A stem from another kind of succulent, *Ibervillea sonorae*, stored in a museum cupboard for eight years, formed new growth each summer while its weight slowly shrank to half of what it was when brought in from the field. Applied on the scale of a saguaro or a cardon, succulence involves a considerable volume of water. Cardons weigh twelve to fifteen tons; saguaros, with fewer arms, weigh about eight tons. Close to ninety percent of this is water; it is a reservoir that for each cactus about equals the moisture supplied by two years of rain.

THE WAYS CACTI OBTAIN and keep moisture reveal remarkable specializations. With saguaros and other giants in the genus *Cereus*, fleshy roots radiate near the soil surface, assuring the best possible chance to soak up rainwater before it can run off, evaporate, or percolate beyond reach. Even so, according to studies at the University of Arizona, saguaros do not absorb water from rain showers of less than 0.20 inches. Below this amount the rain is wasted so far as saguaros (and most other desert plants) are concerned. It evaporates before it can seep into the soil, although temperature, humidity, wind, soil conditions, and other factors determine exactly what happens. To speed absorption, special "rain roots" grow out immediately after a rain, whether a gentle shower or a torrential downpour. The new moisture stimulates their growth, and so long as it lasts these lengthy hairlike roots suck it up thirstily. When the soil dries, they drop off and the root system returns to the minimum network needed to hold a topheavy cactus upright.

Aboveground, the accordion-pleat structure of trunks and branches allows swelling and contracting, according to actual moisture supply. In fact, the diameters of the cacti are a fair gauge of current conditions. If the pleats are deeply folded you can know that it has been a long time since rain last fell, and that the plant is slowly spending its inner reserves. But let there be a thunderstorm, and cacti quickly become plump, their pleats expanded to accommodate the fresh swelling of the water-storage tissue. Occasionally the roots of a saguaro will draw up more water than the cells can hold, and a cactus will burst. Usually the ruptures heal without serious injury, although sometimes infection sets in.

Once moisture has been taken up, the next need is to safeguard it. All plants lose water to the air by transpiration. The process is for them like breathing for animals: a gas exchange absolutely necessary, no matter what the cost in moisture. Cacti have evolved various means of regulating the loss, thereby suiting themselves to life in the desert. One of the chollas, *Opuntia versicolor*, has minute moisture-proof tubes that channel the flow of carbon dioxide and oxygen from the atmosphere into the plant and back out again, a system that minimizes water loss. The tubes are present in mature joints, but not in new joints. On the contrary, water is transpired flagrantly from the new joints of these chollas and also from the half-inch, cylindrical leaves that appear at the onset of the first summer rains. Experiments show that the leaves give off water at triple the rate of mature stems, and their presence coincides with the fleeting days of abundant water. When the rainy period passes, the leaves wither and fall. Their only



A curve-billed thrasher and a cactus wren at their neighboring nests in a cholla.

purpose seems to be to step up transpiration; to squander water and thereby stimulate growth. Prickly-pear cactus also sprouts short-lived leaves that stud the edges of the pads for a time, then dry and fall.

In saguaros, as in all dicot plants, growth takes place at the tip of trunks and branches, the most water-saturated part of the plant. The growing period begins as soon as the summer rains arrive in mid-July, and it continues until they taper off a month or six weeks later—the wettest time of the desert year, and also the hottest. The combination works well. Water is readily available, and the high temperatures reduce the viscosity of both soil moisture and plant juices, providing optimum flow. Furthermore, the warmth steps up the metabolic activity of the cactus, helping to fit needed growth into the briefly favorable time.

The densest stands of saguaros often are on the hottest slopes, which face south and southwest and catch the full force of the sun. The position is not a matter of needing maximum heat, despite the link between optimum growth and summer; the comparatively moderate temperatures of other slopes would be hot enough, and the greater moisture would be an advantage. The largest known individual saguaros are found in moist canyon bottoms. It is winter cold that augurs against slopes facing north. Saguaros also are essentially nonexistent west of the Colorado River or north of the Gila; the California desert is too dry and northern Arizona is too cold.

Various aspects of cold affect plants differently. Some Arctic species survive even when ice forms in their cells, providing they can thaw slowly. If the thaw comes suddenly, they die. For other plants the crucial factor may be the minimum temperature reached in winter, or the length

of winter from first frost to last. It may be how long individual freezes last without relief; or the cumulative total of frost regardless of how many consecutive hours there are. For saguaro, which is more cold-tolerant than any other giant cactus, the deciding factor seems to be how long a freeze lasts. Forrest Shreve, a pioneer in desert botany, potted young saguaros and subjected them to mild freezing. They survived readily when given only six to fifteen hours of freezing at a time, but with an increase to thirty hours or more wholesale fatalities ensued.

By inserting thermometers into mature saguaros growing near the Carnegie Desert Laboratory, Shreve found a remarkable response to changes in air temperature. The temperature of the outside inch or two of cactus tissue consistently fluctuated more widely than that of the surrounding air, often warming above air temperature by day and dropping lower at night. Heat absorbed from sunshine during the day would be lost by reradiation at night, and transpiration would add to the nighttime chilling. From his data, Shreve realized that weather alone does not tell the story of the temperatures a cactus actually is experiencing. In winter the outer layers of tissue may be subjected to more hours of freezing than a weather-station reading indicates; or conversely, since the sun nearly always breaks through the clouds at least briefly even on cold days, the warmth of its rays may raise cactus-skin temperatures above freezing while ice still crusts in rain puddles and thermometers register 32°.

As might be expected, internal temperatures vitally affect plant functions, such as flowering. Saguaros bloom in Arizona from late April through June, with as many as two or three hundred buds ringing the tips of main trunks and

crowning branches. Some stems produce a series of ten to fifteen concentric rings of buds, rising one after another from the areoles. However, the number of buds does not accurately indicate the number of flowers there will be, for less than one-third open. Some years, a full half of the buds are killed by larvae of the beetle *Carpophilus longiventris*. Attacks come while the buds are still marble-sized, causing them to shrivel and turn to blackened nubs. Cactus wrens and other birds also destroy buds when seeking insects to feed on (although buds infested enough to attract birds might be doomed in any case).

Insects and birds are not the complete explanation of flowers that fail to open: many buds wither without discernible reason. Investigating, Duncan Johnson, an early-day ecologist, noticed that flowering success followed a definite pattern around the stem, beginning with buds on the east and southeast. Why? Temperature. Morning sun warms the east side of the cactus three or four degrees above the rest of the plant and gives buds there a head start. By late afternoon the sun swings around and heats the stem's west side, but little time is left before sundown and the cooling of night. As a result, west-side buds may never open, and those on the north may stay mere nubbins.

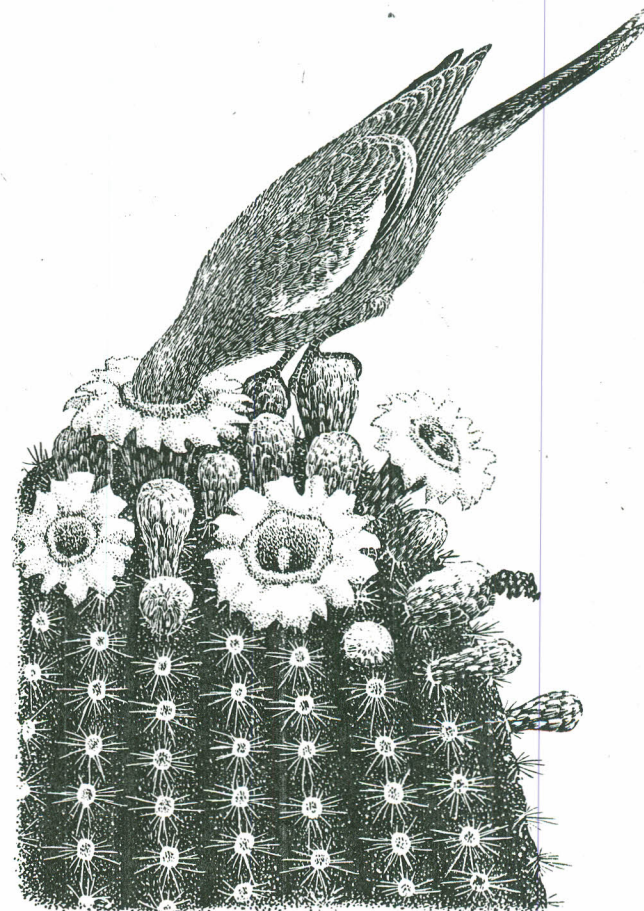
With flowering so uneven because of temperature, it can fairly be asked how stems stay symmetrical. The answer seems to be that saguaro tips receive equal sunshine on all sides. The tips are blunt and slightly cupped, and this shape allows the entire rim of growing tissue to receive the sun. The temperature within the cup is effectively averaged, and a matting of cottony hair helps to hold the warmth. Thus saguaro tips do not actually experience the erratic temperatures of the rest of the cactus, and the stems retain symmetry.

On a typical saguaro about one hundred flowers succeed in getting beyond the bud stage, spreading their bloom over a four-week period. Petals open between sunset and midnight, and close the following afternoon. During these few hours pollination must take place, and it must be cross-pollination not only from one blossom to another but at least from one branch to another. Three thousand stamens stud each blossom, producing an enormous amount of pollen. The grains are too large to be carried by the wind, and this indicates that other means of fertilization must take place. Honeybees are attracted to saguaro flowers in great numbers, for good reason. Each individual blossom produces about 125 beeloads of nectar, an exceptionally rich supply that totals a sixth of an ounce per flower. But, honeybees were not introduced into the Southwest until 1872, and consequently cannot explain the earlier growth of the cactus forest, whatever their effect is currently. Furthermore, bees tend to visit one flower repeatedly without stopping at adjoining ones, or at those on other arms or on other saguaros, and this pattern would not be conducive to cross-pollination. One investigator watched an easily recognized dark bee for three hours as it made trips back and forth between a certain blossom and the hive. He clocked it at seven minutes per trip, and it never varied this time or sampled another blossom. A test then was set up using flowering saguaros in mesh cages where potential pollinators could be introduced and checked, one kind at a time. Bees proved effective cross-pollinators despite their habit of visiting single flowers, perhaps because hive-living involves a great amount of

body contact and inadvertent exchange of particles. In any case, about half the flowers in the cage set fruit, which is the same proportion as under natural conditions.

Even so, there remained the historical impossibility of domestic bees being responsible for saguaro reproduction. There had to be other pollinators, and Samuel E. McGregor and Stanley M. Alcorn of the U.S. Department of Agriculture desert experiment station decided to continue the cage experiments, testing doves and bats as candidates for the role. They collected forty branches with buds, largely from windthrown saguaros (working under special permit, since the species is protected by law on state, Indian, and federal land). They knew from previous work that by cutting stems one to three feet long, normal blossoming would continue, drawing on stored moisture and nutrients.

White-winged doves were tested first. Several saguaro arms were placed in the cage, which measured 12 by 24 by 9 feet and had its bottom edges well buried to keep out mice and rabbits and peccaries. The doves were thought to be likely pollinators because their range from near the Mayo River in Mexico northward to the Arizona borderlands coincides with that of saguaro. Furthermore, the spring migration pattern of whitewings duplicates the progression of saguaros' blooming. They arrive in the Tucson region just as the flowers are beginning to open, and are a common sight as they dip into the blossoms, and emerge with their foreheads powdered. In the cage the doves went readily to the flowers and perched for ten seconds at a time with their heads inside the petals.



A white-winged dove feasts on saguaro nectar.

Evidently they were drinking nectar, or at least their throat motions were the same as when drinking at a waterhole. Toward the end of their feeding period at sunrise, the doves seemed to feed also on the lower, nectar-soaked anthers or on other flower parts. In this test there had been forty-two flowers; in time, half of them set fruit. This equaled the pollination rate of the bees.

Yet doves could not be the prime pollinators of saguaro because they are active only by day, and substantial pollinating was known to occur at night. McGregor and Alcorn had previously experimented with controlling the precise hours that flowers are available for pollination. They fitted drinking straws over the styles of blossoms and folded the ends shut, then opened them on a controlled basis to provide access. The hours between midnight and sunrise proved the most productive time for pollination, the same period that the style is at its longest, lifted well above the stamen. Such an arrangement prevents accidental self-pollination and simultaneously allows the style to receive a brush of pollen as visitors first arrive. Later the style shrinks. These predawn hours are therefore the flowers' most receptive time.

For a nighttime pollinator, longnose bats seemed the likeliest. Different from most bats, which feed on insects, this species has a diet of nectar; and, like the doves, it arrives in Arizona from Mexico at the time saguaros are starting to bloom. Small and brown, with short round ears and a long nose, these bats are well suited to life among the flowers. They have bristly tongues about a quarter as long as their entire body, ideal for lapping nectar. Nine female bats and four young were released into the test cage. They alternately hovered at a blossom and fed quickly, then clambered like clumsy mice among blooms ringing a stem. Nearly two-thirds of the flowers tested with the bats set fruit, more than in the tests with doves or bees.

The three species investigated were picked because they seemed the easiest to work with. Others may contribute to pollination as significantly. Gila woodpeckers alight in the tops of blooming saguaros as commonly as white-winged doves, and they dip slowly and delicately into the blossoms like tomboys remembering teatime manners—a drastic contrast to their usual raucous chasing of one another. Thrashers, cactus wrens, and gilded flickers also are probable major pollinators in the Tucson region. So are various native bees, moths, and hognose bats, relatives of longnose bats and similarly equipped with long tongues.

On an average, 37 days pass from the time a saguaro flower opens until the figlike fruit ripens, its pulp a spectacular scarlet studded with nearly 2,000 shiny black pin-head seeds. The seeds are the object of mystery: What happens to them? Around 15 to 20 mature saguaros per acre are the average in the cactus forests near Tucson. Each produces about four flowers per day for 30 days, or 120 flowers per plant. Now, botanists reason, if half of these blossoms were to set fruit, as experiments indicate is usual, there would be two million seeds per acre per year. If a single seedling from this vast production established itself every five years, a saguaro forest could maintain itself—a regeneration that is occurring in most locations, although not in the case of the widely publicized population decline in the lowlands of Saguaro National Monument.

The rest of the seeds disappear by the millions into the gullets of insects, birds, rodents, and man. Papago Indians



The longnose bat is a nocturnal visitor to saguaro flowers.

relied on saguaro fruits so much in the old days that they began their calendar year with *Navaita*, the time of the saguaro harvest. They utilized juice, pulp, and seeds. Susie Wilson, a Shoshoni Indian woman who taught me basketry in Death Valley, spoke of traveling to the Colorado River to trade for ripe saguaro fruit and join in the harvest. It was a trip she had made only a time or two, and one that possibly dated no farther back than the transportation convenience of automobiles; yet her experience indicates the widespread importance attached to saguaro fruit by the aboriginal people of the desert. Among wildlife, birds gorge on fruit still clinging to saguaro branches, and packrats, coyotes, and a host of other species scurry to feed on it after it falls. Harvester ants may deplete the supply of seeds most of all. Seeds swallowed by birds and animals tend to pass through their digestive tracts unharmed and are given a second chance at germination; but ants gather millions of these seeds and take them into their labyrinthine nest chambers, far too deep to sprout.

Warren Steenbergh, a research biologist at Saguaro National Monument, decided to find out exactly what happens to the seeds. He patiently separated 50,000 seeds from the sticky pulp of a basketful of saguaro fruits and scattered them onto test plots, 1,000 seeds per plot. In just an hour's time, harvester ants had carried off every seed from one plot. Other plots failed to germinate for different reasons. Sprouting requires a precise combination of light, moisture, and temperature; and seeds will hold over for years until these conditions occur if necessary. Steenbergh found that

rain has to fall twice within five days if seeds are to germinate, and must be enough to let the seeds directly contact free water. Mere moisture won't do. Light also is crucial. In a separate test more than 8,000 seeds were supplied with every condition known to be necessary for germination except that they were kept in darkness. Only thirteen sprouted. The experiment was repeated using daylight, and half the seeds grew.

In nature, saguaro seeds probably germinate best lying at the surface of the soil or in a crevice well exposed to light. Temperatures should be in the 70s or 80s. In reality, temperatures at the soil's surface swing far above and below this optimum, but the fluctuation seems of no consequence so long as the seeds receive enough cumulative hours at an ideal temperature. If highs stay persistently below 60°, or if they climb above 95° for several consecutive days, few seedlings will appear. Conversely, brief exposures at extremes as great as several degrees below freezing or at 180° seem to cause no harm, at least under laboratory conditions. Rocky soils are a boon. They trap moisture, and their coarseness helps to anchor saguaro roots. They provide camouflage, which hides seeds from the eyes of rodents and protects against pulverization beneath the feet of grazing cattle. The roughness of the soil also breaks the force of wind and creates eddies of calm air that pose less of a threat to the frail moisture supply of tiny seedlings.

"Nurse" trees are a help too. More than a century ago men on a border survey along the Arizona-Sonora line commented in reports that young saguaros inevitably seemed to be growing beneath mesquite or paloverde trees, although nobody then knew why. The effect of the trees is now understood: they act like parasols. Daytime shading may be crucial during practically the first decade of a saguaro's life. In fact, decreasing nurse vegetation in the eastern unit of Saguaro National Monument is believed to be the main cause of the saguaro loss there—a loss so marked that all saguaros will be gone from that particular area by the year 2000 unless something reverses the trend.

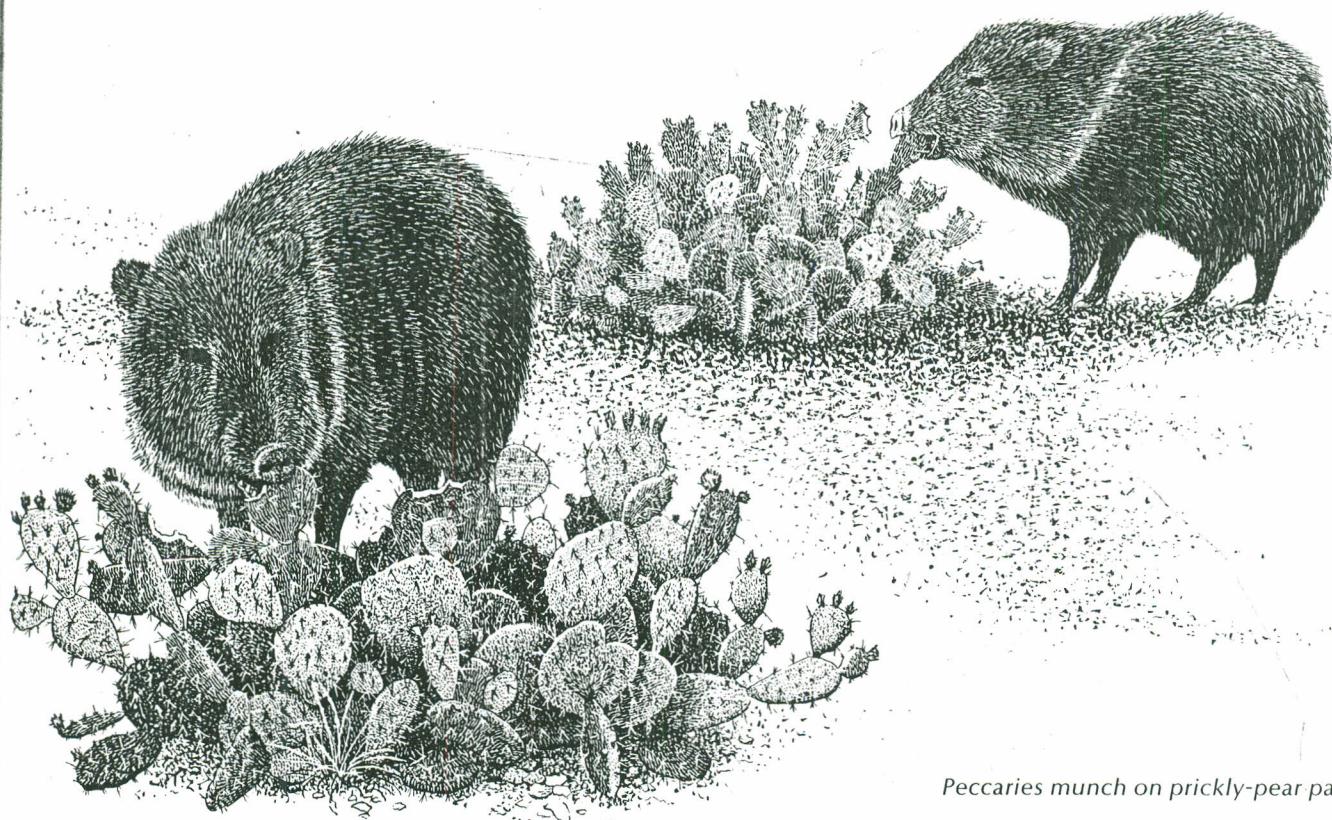
Little seems to go right for saguaro seedlings, all factors considered. If the number of germinations seems minute in view of the prodigious quantity of seeds produced, the ratio shrinks still further when it comes to establishment among those that do sprout. Here results often approach zero. Of 800 seedlings set out in unfenced plots in one test, only 14 were still alive after six months. In another year and a half, those particular 14 were dead and so were 770 seedlings from a second planting of 800. Rodents, probably packrats, destroyed practically all the plants that were lost. Cacti provide nearly half of the food eaten by these animals the year round, and in May the amount jumps to 90 percent. In the laboratory, packrats live indefinitely on nothing more than saguaro seedlings and water, whereas the same diet is quickly spurned by kangaroo rats and other common rodent species. In this regard, too, man's war against coyotes and other predators has often been blamed for allowing rodent populations to increase, thereby hampering saguaro regeneration. However, this cannot be substantiated. There is no real indication that rodent populations have increased in cactus forests; more likely the number of predators is controlled by the rodent population available as food, and not the reverse.

Desert weather is another factor affecting saguaro seed-

lings—not just heat and dryness and cold but also rain. Rain supplies needed moisture; and it also offsets summer soil temperatures that otherwise might climb disastrously high. The mid-July onset of the rains coincides with the period of greatest heat, and their cooling effect has been measured as deep as twelve inches beneath the surface of the soil. The importance of this is apparent from the high death rate among seedlings that survive their first summer but perish during the hot foreshadow of the following year, before the rains bring their cooling. These tiny cacti have inherently small water-storage capacities and large evaporative surfaces; they are exceedingly vulnerable and may be saved only by rain. A few may also be lost because of it, for rain has a detrimental effect as well as a beneficial one. Saguaros have no protection against washing out in a rainstorm. Their roots are shallow to permit a quick absorption of moisture, but success in this direction at times proves fatal in another direction. Storm waters rip young plants from their holds and sweep them to destruction, and even mature saguaros fall victim to torrential rains, their roots undercut and loosened and unable to support the plant if wind accompanies the rain. They crash to earth, the victims of rain.

SURVIVAL IS FURTHER COMPLICATED by an unusually prolonged period of vulnerability. Saguaros are extraordinarily slow growing. After two years a seedling will stand only one-quarter of an inch high; in 15 years it barely reaches one foot, and by 40 years it won't measure more than 10 feet. Not until it is 60 or 70 years old, and two or three times the height of a man, will the cactus finally have passed most of the dangers likely to befall it. About this time, prickly balls will begin to appear near the top of the plant, the first buds of branches. By 150 years of age, saguaros reach full size, standing 35 to 50 feet tall and with branches that commonly number from two to seven or eight. Another 50 or 60 years of life will remain for these mature specimens—and perhaps this longevity is a pivotal factor in the case of stricken saguaro populations such as that of Saguaro National Monument. It may be perfectly normal for several decades to pass in a particular locality without producing conditions ideal for saguaro germination. A marked decline may appear within a saguaro forest and continue for a period that seems long to man but is actually of little real consequence. Such declines do not necessarily doom the future of even that particular forest, let alone the species, since abundant seeds will still be available so long as even a single saguaro continues to flower and set fruit. Sites reported 60 years ago by Shreve as lacking young saguaros now support healthy stands, despite his bleak remark that "plants less than one decimeter in height are so rare, or inconspicuous, that nine botanists who have had excellent opportunities to find them report they have never done so." Man's patience and perspective is often out of step with nature's, and the dilemma of threatened saguaro forests may belong at least partially in this category.

Perhaps one saguaro out of every thousand will develop an odd crested growth called a cristate. Nobody really knows the cause of these. They may be genetic; or possibly a response to injury, such as insect damage. Maybe they result from radioactivity in the soil, or from a cancerlike



Peccaries munch on prickly-pear pads.

multiplication of cells. Whatever the reason, cristates seem benign: they bring no harm to saguaros, or to organpipes on which they also sometimes form.

In the case of necrosis, a disease similar to the common rot of carrots or to fire blight in peas and apples, the story is different. There may be very real harm. Necrosis was first noticed and identified in saguaros in 1899, but nobody even yet knows what to do about it. Some investigators believe the disease directly explains saguaro die-off; others feel that the disease merely starts the decomposition of tissue already fatally damaged by other causes. A bacillus carried in the digestive tract of the larvae of a drab nocturnal moth (*Cactobrosis fernaldialis*) is the cause of the trouble. Adult moths live only three nights, just long enough to mate and lay eggs and thereby affect the future of the particular saguaros in which their larvae will feed. Sometimes a cactus will manage to wall off an infected area with a corklike seal; if this fails the rot may spread even to the roots, and once infected that far the cactus is likely to topple in the next wind. Several species of cactus are affected by the necrosis, which is carried by fruit flies as well as the moths; but no other is as damaged as saguaro. Decay from the disease ruptures saguaro skin and sends a suppurating black ooze trickling down the trunk, darkening the soil for a five- or six-foot radius. This contamination ends the life of any cactus seedlings near the parent plant, and it spreads the disease to other mature saguaros. Windblown dust carrying bacilli may also infect open wounds, and root injuries provide avenues of infection within the soil.

Gila woodpeckers and gilded flickers are the saguaros' vigilante committee. They tunnel after *Cactobrosis* moths in the saguaro forests of the desert as readily as their relatives work over the pine and fir forests of the rest of the world. Sometimes they also seem to peck open a

saguaro trunk to "drink" from the watery pulp, an action that may be incidental to searching out insects but often seems intentional. Either way, the habit rids the cactus of at least some future trouble and at the same time benefits other birds unable to pierce the rough outer covering of a saguaro for themselves. Juices soon coagulate and seal the wound, although before they do the cactus offers accessible moisture and may be visited by several species. While studying birds at Organ Pipe Cactus National Monument, Max Hensley noticed a Gila woodpecker chipping vigorously at the top of an eighteen-foot saguaro and showering the ground with green chunks of cactus, a sure indication that it had dug beneath the outer skin to the moist pulp within. When the woodpecker flew off, a thrasher quickly replaced it and began to make characteristic drinking motions, dipping in its bill, then raising its head and swallowing.

More common by far than "drinking holes" are cavities deliberately excavated in saguaros and cardons as nest sites. A brief visit in any part of the giant cactus forest reveals several of these—round holes three or four inches in diameter, gaping black and inviting. Woodpeckers and flickers chisel them out, usually about the size and shape of a football, and a surprising variety of desert creatures use them. The excavators themselves use a hole only one year, pecking a new one each spring. The cactus secretes callus tissue a quarter- to a half-inch thick to wall off the holes, a process that remains a puzzle. One researcher cut an imitation woodpecker cavity into a saguaro and found after sixty days that it had a shell only three sixty-fourths of an inch thick. This rate suggests that the linings may continue to form for at least a year, and ties in with observations of woodpeckers hollowing out cavities several months ahead of nesting time. Chemically, however,

the callus is still a puzzle, for although it contains a considerable proportion of lignin (the woody substance found in cactus ribs and in the wood of all trees) none of this substance is present in cortex tissue, which is where the wound occurs. So far there is no explanation.

Many features enhance the value of saguaro holes as nests, with evaporative cooling perhaps the most important of all, since nesting in the desert often depends more on keeping eggs cool than on warming them. A hole deep within a living cactus solves this. The temperature of the desert air may hover around 110° or 115°, yet be only 90° inside a nest hole because of the evaporation of moisture, according to work by Robert Krizman of the University of Arizona. At night the situation is conveniently reversed, with the inner part of cactus as much as 12 degrees warmer than the air. Nest holes have a further advantage in holding relative humidity five or ten percent higher than that of the outside air. This significantly lessens the drain on birds' body moisture and is a particular advantage for nestlings.

There are other effects as well. Among birds nesting in the open, eggs usually are camouflaged by color and a speckled pattern, but those of hole-nesters tend to be nearly white. This difference probably developed through long centuries of evolution as the need of camouflage disappeared for eggs laid inside holes. Or it may be that the light color of nest-cavity eggs is not so much a loss of camouflage as a means of guiding adults settling into the darkness of the hole: white eggs show up better, and

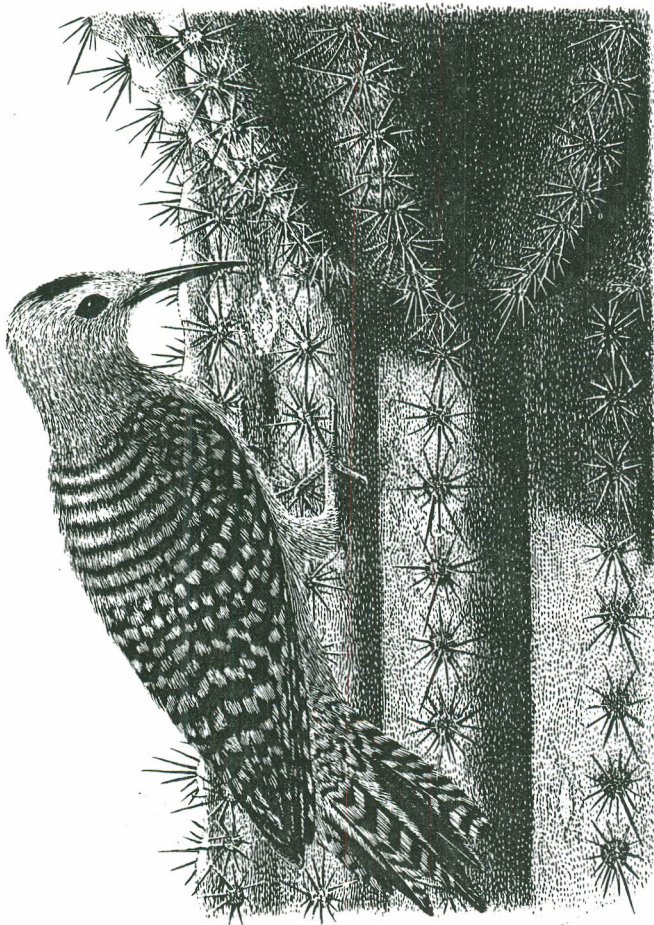
the parent birds are more sure to find them immediately and sit on them. This matter of seeing within the dim light of the cavities also affects feeding. The beak nodes of hole-nesting infants generally are white, an advantage since hatchlings tend to wait until an adult taps them on the node before they open their mouths for food. After the first few days this gaping pattern becomes triggered simply by the darkening of the nest entryway instead of by a tap on the beak; the young open their mouths and stretch their rubbery necks even before the parent bird has clawed down inside the hole to reach them.

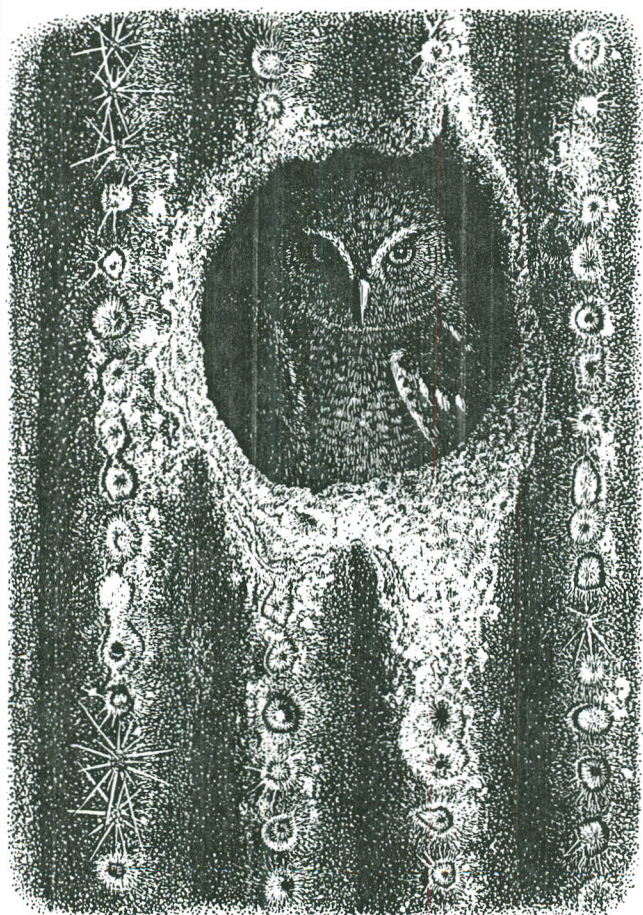
Nesting in a hole affects courtship, too—drastically so. In locations where the branches of one tree or bush are about as acceptable as those of another for a nest, birds will first claim their territory and after that will select a building site. Where a hole is needed for nesting, the priorities are reversed. The nest site itself must be found first, and then the territory can be worked out. This is because an area with adequate food cannot necessarily be counted on also to have a hole available, but the chances are that any place where a male bird with rising hormones finds a tempting hole he can also find food. (Studies of fish corroborate this order of selection: those with definite nesting requirements pick that site first and then secure a territory around it, whereas species not choosy about nest requirements pick a general territory first and then decide where to lay.)

Nest holes are so much in demand that beginning in April competition for them becomes keen. A male bird finding a hole does not dare stray far from it. Rather than go in search of a mate and risk losing the hole, he may use a special "advertising" song to lure a female into range. When a female responds and comes close, the hopeful bachelor will pop in and out of his prized hole, hoping to stimulate her urges to the same pitch as his. For some species the number of available nest cavities almost surely limits population more than the availability of food does, and in various locations springtime fights over holes cause a higher mortality than comes from predators or any other cause. Yet the value of a hole is great enough to warrant struggle. Polygamy is much more common among species that nest in holes than among those that nest in the open: with the young relatively safe inside a nest cavity, the male can leave the major responsibility of defense and feeding to the female and devote part of his attention to seeking a second mate and starting a second brood, thereby benefiting the species.

A much higher percentage of young birds survive in nest holes than in open nests—and this affects the number of eggs laid. Some sparrows increase clutch size by 50 percent. Birds that nest in the open have a pressing need to get their young fledged and on their own as quickly as possible; consequently they lay few eggs. Fewer mouths to fill means a faster development of each individual nestling. In contrast, among birds using holes prolonged vulnerability is relatively safe. These species can afford more gaping mouths and the added days it takes to bring insects and lizards and fruit enough for the transformation into feathers and wings and functioning nervous systems. At least sixteen species of birds are known to use saguaro holes abandoned, or left unguarded, by their original makers. These are the elf owl, screech owl, pygmy owl, sparrow hawk, Bendire's thrasher, cactus wren, ash-throat-

A Gila woodpecker tunnels in a saguaro.





An elf owl peers from its nest hole in a saguaro.

ed flycatcher, Wied's crested flycatcher, western kingbird, Lucy's warbler, purple martin, bluebird, house finch, English sparrow, lark bunting, and starling. Without the cool moist microclimate within cactus, it is doubtful whether these species could endure desert conditions. Their presence depends directly on holes in saguaros.

Working on a master's thesis at the University of Arizona, Oscar Soule found that of the sixteen, only starlings and house finches carry nesting materials into the holes; the other species nest on the bare floor. Probably evolution explains this difference, since starlings and finches have only recently started to use saguaro holes. The finches normally build rather compact nests in brush or cholla, and evidently they carry over the urge when they nest in saguaros, because they will nearly fill a hole with grass and twigs, then settle into a depression scooped into the top of the pile. The approach offsets much of the advantage of the hole's moderate temperature and deep concealment, and persistence of the habit suggests that these finches have not yet had time to develop complete efficiency as hole-nesters. A saguaro cavity is a finished nest in itself; no additional lining is needed. Starlings, on the other hand, come closer to utilizing the full advantage of the holes. They first appeared in the desert only about 1950 but already have adapted so fully that they take only token strands of grass into a nest hole—vestigial behavior left over from other conditions and already an urge they barely heed. The starlings are a surprising sight in the desert however at home they now have become. The species was

unknown in America until 1890, when a flock of 80 was brought from Europe and set free in Central Park, New York. An additional 40 starlings were imported the following year. Now the descendants of these original 120 birds range corner to corner across the continent, from Hudson Bay to Mexico, adapted even to the theoretically difficult habitat of the desert.

Mammals also use saguaro holes. Brown bats frequently roost within them throughout the summer, and packrats and cactus mice occasionally take over holes as much as twenty feet above the ground. They gnaw spiral corridors up to such nests, feeding on saguaro pulp as they go. Or, if they choose, they can climb by the thorns and ribs alone without fashioning a special passageway. As for smaller creatures, Soule found thirteen species of insects in saguaro holes, one nematode, three spiders, and a pseudoscorpion. One of the insects, a mosquito, apparently is limited only to saguaro holes (a fairly typical restriction for mosquitoes, since some of them belong specifically to the tiny pools of water that collect against the internodes of tropical bamboo and others to the pools held by pitcher plants in northern bogs). Even so, a "saguaro mosquito" seems incongruous: a dryland plant as host to a wet-habitat insect. It is possible, given suitable angle and exposure, because rainwater runs readily into saguaro holes and provides the pools needed by mosquito larvae.

Few detailed observations have been made of such water sources. A saguaro near Gates Pass, west of Tucson, was found with nearly four inches of water in a hole even though two months had passed since the last rain, and it had been little more than a light shower. A sample of the water from the hole quickly filmed over in the laboratory, covered by oily scum plus bits of callus tissue, bird feathers, insect wings, and animal debris. Such films probably help to reduce evaporation and underwrite the chance for mosquitoes to complete their cycles.

According to work by Dr. Anthony Ross, while at the University of Arizona, the mosquitoes lay eggs within the tissue of the cactus during the winter, and these stay dormant until summer rains and rising temperatures initiate hatching. Larvae then progress into adulthood with exceptional rapidity, as if aware of the essentially fragile quality of aquatic life inside desert cactus. Some of the pools that the mosquitoes use must last nearly year-round since they serve as water sources for birds. It is not unusual to see a flicker or woodpecker flying from hole to hole, looking in, ultimately finding one with water, and drinking.

Various wasps and bees also are among the parade of species that rely on saguaro holes. Sometimes buzzing within a saguaro can actually be heard from a distance of twenty feet, so active are the bees swarming inside. Flies breed in saguaros too, probably feeding on springtails, small primitive insects that abound in the holes; grasshoppers and katydids often retreat into cactus holes to escape daytime heat and radiation.

Saguaros have long been the symbol of the Sonoran Desert, and appropriately so. They stand as romantic sentinels for humans, and as refuge and entire world for various desert creatures. Perhaps nowhere else is the dependence of the animal kingdom on the plant kingdom more dramatically evident. Saguaros and other tall cacti must first win the battle against desert drought; then birds and animals and insects dependent on them also can claim victory. ■