

CONSUMPTION OF PLATYOPUNTIAS BY WILD VERTEBRATES

Eric Mellink and Mónica E. Riojas-López

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Introduction

In arid lands, platyopuntias (prickly pear cacti, also called *nopales* [singular, *nopal*]) often appear as lush, exuberant forage and, during the proper time of the year, bear brightly colored fruits, which, as Gibson and Nobel (1986) indicate, “would be a welcome waterhole and restaurant for animals.” Cladodes and fruits of platyopuntias are indeed consumed by a variety of vertebrates in ways that affect entire ecosystems (Anthony 1954; Janzen 1986).

This chapter presents an overview of the utilization of platyopuntias by wild vertebrates. It also includes a list of the vertebrate species reported to be consumers of platyopuntias. Certainly this list is not complete, as many con-

sumers have not been reported in the formal literature. Because of the natural distribution of platyopuntias, the information about vertebrate consumption is biased toward the deserts of North America and the Galápagos Islands. Most sources indicating consumption of platyopuntias by vertebrates present rather incidental information on the issue; only a few, notably those for the Galápagos Islands, derive from the study of ecological relations involving platyopuntias. Eighty-nine vertebrate species appear in the literature as consumers of platyopuntias: 9 species of reptiles, 26 of birds, and 54 of mammals (Table 7.1). Pads (cladodes) and fruits are the parts most often reported as consumed, although reports on the use of fruits may mask the use of seeds.

TABLE 7.1
A summary of wild, opuntiofagous vertebrates

Species	Part(s) consumed	Reference(s)
<i>Reptiles</i>		
Berlandier's tortoise (<i>Gopherus berlandieri</i>)	Pads, petals, fruits	Auffenberg and Weaver (1969); Rose and Judd (1982)
Galápagos tortoise (<i>Testudo elephantinus</i>)	Pads, fruits	Thorton (1971); Biggs (1990)
Leopard tortoise (<i>Geochelone pardalis</i>)	Fruits	Milton (1992)
Galápagos land iguana (<i>Conocephalus pallidus</i>)	Pads, petals, fruits	Christian et al. (1984)
Galápagos land iguana (<i>C. subcristatus</i>)	Pads, petals	Thorton (1971); Biggs (1990)
Daphne lava lizard (<i>Microlophus albemarensis</i>)	Petals, nectar, pollen	East (1995)
Pinta lava lizard (<i>M. pacificus</i>)	Petals, nectar, pollen, fruits	Schluter (1984)
Whiptail (<i>Cnemidophorus lemniscatus</i>)	Petals	Mijares-Urrutia et al. (1997)
Lagarto Tizón (<i>Gallotia galloti</i>)	Fruits	Valido and Nogales (1994)
<i>Birds</i>		
Ostrich (<i>Struthio camelus</i>)	Fruits	Burt-Davy (1920)
Emu (<i>Dromiceus</i> sp.)	Fruits	Darnell-Smith (1919)
Wild turkey (<i>Meleagris gallopavo</i>)	Fruits	Lehman (1984)
Scaled quail (<i>Callipepla squamata</i>)	Fruits	Lehman (1984); Brown (1989)
Northern bobwhite (<i>Colinus virginianus</i>)	Seeds	Lehman (1984)
White-winged dove (<i>Zenaida asiatica</i>)	Fruits	Lehman (1984); Gonzalez-Espinoza and Quintana-Ascencio (1986)
Galápagos dove (<i>Z. galapagoensis</i>)	Pads, petals, nectar, pollen, fruits, seeds	Grant and Grant (1979, 1981)
Mourning dove (<i>Z. macroura</i>)	Fruits	Lehman (1984)
Greater roadrunner (<i>Geococcyx californianus</i>)	Fruits	Clements and Shelford (1939)
Northern flicker (<i>Colaptes auratus</i>)	Fruits	Clements and Shelford (1939); Gonzalez-Espinoza and Quintana-Ascencio (1986)
Mexican jay (<i>Aphelocoma ultramarina</i>)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Black magpie (<i>Gymnorhina tibicen</i>)	Fruits	Darnell-Smith (1919)
Common raven (<i>Corvus corax</i>)	Fruits	M. Riojas-López (unpublished observations)
Chihuahuan raven (<i>C. cryptoleucus</i>)	Fruits	Lehman (1984); Gonzalez-Espinoza and Quintana-Ascencio (1986)
Little raven (<i>C. mellori</i>)	Fruits	McCulloch (1980)
Curve-billed thrasher (<i>Toxostoma curvirostre</i>)	Fruits	Lehman (1984); Gonzalez-Espinoza and Quintana-Ascencio (1986)
Galápagos mockingbird (<i>Nesomimus parvulus</i>)	Pads, nectar, pollen, seeds	Grant and Grant (1981)
Canyon towhee (<i>Pipilo fuscus</i>)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
House finch (<i>Carpodacus mexicanus</i>)	Fruits	"
Genovesa cactus finch (<i>Geospiza conirostris</i>)	Pads, nectar, pollen, seeds	Grant and Grant (1981, 1989)
Galápagos finch (<i>G. difficilis</i>)	Nectar, pollen, seeds	Bowman (1961); Grant and Grant (1981)
Daphne Major ground finch (<i>G. fortis</i>)	Nectar, pollen, seeds	Grant and Grant (1981); Price (1987); Grant (1996)
Galápagos finch (<i>G. fuliginosa</i>)	Nectar, pollen, seeds	Grant and Grant (1981); Dodd and Brady (1988)
Galápagos finch (<i>G. magnirostris</i>)	Nectar, pollen, seeds	Grant and Grant (1981)
Daphne Major cactus finch (<i>G. scandens</i>)	Pads, nectar, pollen, fruits, seeds	Lack (1947); Bowman (1961); Grant and Grant (1981); Millington and Grant (1983); Grant (1996)

TABLE 7.1 (continued)

Species	Part(s) consumed	Reference
<i>Mammals</i>		
Mexican long-tongued bat (<i>Choeronycteris mexicana</i>)	Nectar, pollen	Dalquest (1953)
Big long-nosed bat (<i>Leptonycteris nivalis</i>)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Baboon (<i>Papio hamadryas</i>)	Fruits	Weed Section (1940)
"Monkeys" (Family Cercopithecidae)	Fruits	Weed Section (1940)
Shasta ground sloth (<i>Nothrotheriops shastense</i>)	Pads, petals, fruits	Long et al. (1974); Hansen (1978); Spaulding and Martin (1979)
European rabbit (<i>Oryctolagus cuniculus</i>)	Fruits	Darnell-Smith (1919)
Desert cottontail (<i>Sylvilagus audubonii</i>)	Pads, fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986); Hoffman et al. (1993)
Nuttall's cottontail (<i>S. nuttallii</i>)	Pads	MacCracken and Hansen (1984)
Antelope jackrabbit (<i>Lepus alleni</i>)	Pads	Vorhies and Taylor (1933)
Black-tailed jackrabbit (<i>L. californicus</i>)	Stems, pads, fruits	Vorhies and Taylor (1933); Timmons (1942); Riegel (1941); MacCracken and Hansen (1984); Hoffmeister (1986); Hoffman et al. (1993); E. Mellink and M. Riojas-López (unpublished observations)
White-tailed jackrabbit (<i>L. townsendii</i>)	Pads	Bear and Hansen (1966); Flinders and Hansen (1972), cited in Dunn et al. (1982)
Harris' antelope-squirrel (<i>Ammospermophilus harrisi</i>)	Fruits, seeds	Hoffmeister (1986)
Spotted ground squirrel (<i>Spermophilus spilosoma</i>)	Pads	Bailey (1931)
Thirteen-lined ground squirrel (<i>S. tridecemlineatus</i>)	Fruits, seeds	Riegel (1941); Lehman (1984)
Rock squirrel (<i>S. variegatus</i>)	Fruits	Hoffmeister (1986)
Ground squirrel (<i>S. sp.</i>)	Seeds	Janzen (1986)
Botta's pocket gopher (<i>Thomomys bottae</i>)	Roots, stems	Hoffmeister (1986)
Mountain pocket gopher (<i>T. talpoides</i>)	Pads	Vaughan (1967)
Bailey's pocket mouse (<i>Chaetodipus baileyi</i>)	Seeds	Hoffmeister (1986)
Hispid pocket mouse (<i>C. hispidus</i>)	Seeds	Blair (1937)
Nelson's pocket mouse (<i>C. nelsoni</i>)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Southern banner-tailed kangaroo rat (<i>Dipodomys phillipsii</i>)	Fruits	"
Banner-tailed kangaroo rat (<i>D. spectabilis</i>)	Pads	Vorhies and Taylor (1922)
Mexican spiny pocket mouse (<i>Liomys irroratus</i>)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Galápagos rice rat (<i>Oryzomys galapagoensis</i>)	Seeds	Thorton (1971)
Rock mouse (<i>Peromyscus difficilis</i>)	Fruits	Dalquest (1953)
Pinyon mouse (<i>P. truei</i>)	Fruits	"
Deer mouse (<i>P. sp.</i>)	Seeds	Janzen (1986)
Hispid cotton rat (<i>Sigmodon hispidus</i>)	Pads	Lehman (1984)
White-throated packrat (<i>Neotoma albigula</i>)	Pads, fruits	Vorhies and Taylor (1940); Dalquest (1953); Gonzalez-Espinoza and Quintana-Ascencio (1986); Rangel and Mellink (1993)
Goldman's packrat (<i>N. goldmani</i>)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Desert packrat (<i>N. lepida</i>)	Pads	Hoffmeister (1986)
Black rat (<i>Rattus rattus</i>)	Seeds	Eliasson (1968)
North American porcupine (<i>Erethizon dorsatum</i>)	Fruits	Hoffmeister (1986)
Coyote (<i>Canis latrans</i>)	Fruits	Lehman (1984); Gonzalez-Espinoza and Quintana-Ascencio (1986); McLure et al. (1995)
Gray fox (<i>Urocyon cinereoargenteus</i>)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
American black bear (<i>Ursus americanus</i>)	Pads, fruits	Hoffmeister (1986); McClinton et al. (1992); Hellgren (1993)
Ringtail (<i>Bassariscus astutus</i>)	Fruits	Leopold (1959); Hoffmeister (1986)

(continued on next page)

TABLE 7.1 (continued)

<i>Mammals</i> (continued)		
Species	Part(s) consumed	Reference
Raccoon (<i>Procyon lotor</i>)	Fruits	Dalquest (1953); Gonzalez-Espinoza and Quintana-Ascencio (1986); Lehman (1984)
White-nosed coati (<i>Nasua narica</i>)	Fruits	Hoffmeister (1986)
North American badger (<i>Taxidea taxus</i>)	Fruits	Gonzalez-Espinoza and Quintana-Ascencio (1986)
Hooded skunk (<i>Mephitis macroura</i>)	Fruits	"
Mammoth (<i>Mammuthus</i> sp.)	Fruits	Davis et al. (1984)
Feral burro (<i>Equus asinus</i>)	Stems, pads	Krausman et al. (1989); Hicks and Mauchamp (1995)
Wild boar (<i>Sus scrofa</i>)	Pads	Baber and Coblenz (1987)
Collared peccary (<i>Pecari tajacu</i>)	Pads, petals, fruits	Dalquest (1953); Eddy (1961); Zervanos and Hadley (1973); Everitt et al. (1981); Bissonette (1982); Sowls (1984); Corn and Warren (1985); Gonzalez-Espinoza and Quintana-Ascencio (1986); Hoffmeister (1986); Janzen (1986); Luévano et al. (1991); Martinez-Romero and Mandujano (1995)
Camel (<i>Camelus dromedarius</i>)	Pads	Janzen (1986)
Mule deer (<i>Odocoileus hemionus</i>)	Pads, fruits	Krausman (1978); Janzen (1986); Krausman et al. (1989)
White-tailed deer (<i>O. virginianus</i>)	Pads, fruits	Quinton and Horejst (1977); Arnold and Drawe (1979); Everitt and Gonzalez (1979); Quinton et al. (1979); Everitt et al. (1981); Gonzalez-Espinoza and Quintana-Ascencio (1986); Hoffmeister (1986); Luévano et al. (1991)
Pronghorn (<i>Antilocapra americana</i>)	Pads, fruits	Russell (1964); Stelfox and Vriend (1977); Sexson et al. (1981); Janzen (1986)
American bison (<i>Bison bison</i>)	Fruits	Janzen (1986)
Bighorn sheep (<i>Ovis canadensis</i>)	Pads, fruits	Hoffmeister (1986); Dodd and Brady (1988); Krausman et al. (1989)
Steenbok (<i>Raphicerus campestris</i>)	Pads	Marais (1939)
Feral goat (<i>Capra hircus</i>)	Stems, pads	Eliasson (1968); Thorton (1971); Hicks and Mauchamp (1995)

Consumption of Vegetative Structures

Four of the nine reptiles that forage on nopales consume their cladodes (pads). These include two tortoises and two land iguanas (scientific names also in Table 7.1). Only 16% of bird species consume the pads, but at least 43% of mammal species, including the Pleistocene Shasta ground sloth and mammoth, do, or did, so. Consumption of vegetative structures is mostly restricted to the pads for mammals, and exclusively so for reptiles (Table 7.2). Only black-tailed jackrabbits, Botta's pocket gopher, and feral burros and goats consume trunks and/or roots. *Opuntia* pads are a staple for only a few species (packrats, rabbits and jackrabbits, javelina, Galápagos tortoise, Galápagos land iguanas, and

occasionally deer), although in some cases they only become a staple under drought conditions. Many of the consumers eat platyopuntias only sporadically.

Cladode Preferences

Most studies reporting nopales in herbivore diets derive their data from fecal analysis, which does not allow for knowledge about differences in preference for different cladodes of the plant. However, a difference in the palatability of young versus old cladodes would be expected. Indeed, Berlandier's tortoise prefers the younger, more tender cladodes that have fewer spines (Rose and Judd 1982). In contrast, rabbits and black-tailed jackrabbits consume the outer cladodes of *Opuntia violacea* var. *macrocentra*

TABLE 7.2

Percentage of animals within each major taxon that consume different parts of platyopuntias

Taxon	Number	Percent						
		<i>Roots</i>	<i>Trunks</i>	<i>Pads</i>	<i>Petals</i>	<i>Pollen and nectar</i>	<i>Fruits</i>	<i>Seeds</i>
Reptiles	9	0	0	44	67	22	67	0
Birds	26	0	0	19	4	35	69	38
Mammals	54	2	7	42	4	2	61	15
Overall	89	1	4	36	10	13	64	20

first, and then progress to the inside of the plants. This process is more as a result of the architectural arrangement of the plant, rather than due to differences in palatability of the cladodes (Hoffman et al. 1993).

When different platyopuntia species are available in the habitat, herbivores apparently prefer some over others. In a test with three platyopuntia species and one cholla species typical of *nopaleras* (nopal communities) in the San Luis Potosí–Zacatecas Plateau, Mexico, white-throated packrats prefer *Opuntia robusta* and *O. streptacantha* over *O. leucotricha* and *O. imbricata* (Rangel and Mellink 1993). *Opuntia robusta* and *O. streptacantha* have the lowest amounts of protein and highest amounts of fiber (Flores Valdez and Aguirre Rivera 1989), so the higher consumption by these packrats is not a response to nutritional quality. Rather, it apparently results from these cacti having fewer spines and glochids, which facilitates their consumption. Collared peccaries prefer one of two different morphs of the same subspecies of *O. phaeacantha*, again favoring the one with fewer spines (Theimer and Bateman 1992). However, in New Mexico, spinescence apparently does not affect grazing intensity by lagomorphs; rather, plant size and grazing history appear to be the factors that most determine grazing intensity; the proportion of grazed pads increases for plants that have more than seven cladodes (Hoffman et al. 1993).

Nopal growers and researchers indicate that some varieties of cultivated platyopuntias are more prone to consumption by wildlife than are others. So, ‘Copena F1,’ a spineless forage nopal, is preferred by rodents and lagomorphs over other spineless varieties in central Mexico (C. A. Flores-Valdés and F. Torres, personal communication). In some cases, lagomorphs can entirely wipe out a commercial orchard of this variety. However, spines are not a requirement for effective mechanical defense. Near Jacumba, California, black-tailed jackrabbits will eat almost anything except *Opuntia basilaris* (A. M. Rea, personal

communication). This species does not have large spines; rather, it is densely covered with fine glochids (small, easily detached spines), a nasty encounter for herbivores.

To determine if white-throated packrats had foraging preferences among different cultivated varieties of *Opuntia ficus-indica*, rows of cultivars ‘Roja,’ ‘Amarilla,’ and ‘Blanca’ were examined at Las Papas de Arriba, Jalisco, Mexico. Packrats clearly prefer to consume cladodes of ‘Roja’ over ‘Amarilla’ and prefer ‘Amarilla’ over ‘Blanca’ (Table 7.3). Packrats build their dens on the ground against and around the trunks of platyopuntias using various materials (e.g., cladodes, twigs, dung, garbage). As there are no differences in the percentage of plants associated with packrat dens among different varieties (Table 7.3), differences in consumption must be attributed to the forage quality of the plants. The higher sugar content of ‘Roja’ presents one logical explanation for packrats’ preference.

Seasonal Effects for Herbivory

In xeric habitats where free water is scarce, cladodes become an important source of water, when they are available. Not unexpectedly, vertebrates increase their use of *Opuntia* cladodes during the dry season, or use them only then. For example, rabbits and black-tailed jackrabbits consume *Opuntia* cladodes during the dry season, or when annuals are scarce and other perennials have not developed new growth (Hoffman et al. 1993). Berlandier’s tortoises consume more cladodes during the summer, as a source of water (Auffenberg and Weaver 1969). Galápagos land iguanas reduce their preference for cladodes from about 32% of bites in the dry season to 5% after the rains (Christian et al. 1984). Even finches, doves, and mockingbirds drink fluids and eat moist pulp from cladodes in the Galápagos Islands (Grant and Grant 1981). Other animals consume platyopuntias under special conditions; e.g., pronghorn antelope feed readily on cladodes after a wildfire has burned off the spines (Stelfox and Vriend 1977).

TABLE 7.3

Differences in feeding by packrats and evidence from packrat dens for adjacent rows of different varieties of *Opuntia ficus-indica* cultivated in Las Papas de Arriba, Jalisco, Mexico

Parameter	Nopal variety		
	'Roja'	'Amarilla'	Statistical significance
Platyopuntias with evidence of feeding by packrats (% of plants)	45	19	< 0.0001
Platyopuntias associated with packrat dens (% of plants)	8	12	n.s.
	'Amarilla'	'Blanca'	Statistical significance
Platyopuntias with evidence of feeding by packrats (% of plants)	20	4	< 0.01
Platyopuntias associated with packrat dens (% of plants)	6	16	n.s.

Unpublished observations of E. Mellink and M. E. Riojas-López.

The white-throated packrat is one of the vertebrates that relies most heavily on platyopuntias for its food (Vorhies and Taylor 1940; Spencer and Spencer 1941; Rangel and Mellink 1993). Although *Opuntia* cladodes are its preferred food, seasonal variations in preference occur. In Arizona, this species exhibits clear peaks in consumption of cladodes in May and November (Vorhies and Taylor 1940), which coincides with the driest period of the year.

The vertebrate most popularized as a cladode eater is the collared peccary. Such fame is not undue, as platyopuntias are one of its most important food resources in arid lands. Indeed, *Opuntia* cladodes are the most common food for the peccary throughout the southwestern United States and northern Mexico (Neal 1959; Leopold 1959; SOWLS 1984; Hoffmeister 1986). Peccaries are not ruminants, but their ruminant-like digestion allows them to use profitably such a high-fiber forage (Langer 1979). Despite their year-round high consumption of platyopuntias, collared peccaries exhibit seasonal variation, consuming them in greater quantities during the summer (Corn and Warren 1985) or fall (Eddy 1961). In northern San Luis Potosi, Mexico, collared peccaries steadily increase the amount of cladodes in their diet from 25% in June to 66% in September (Luévano et al. 1991). Cladode consumption during the summer may be associated with high temperatures, and peccaries as well as white-tailed deer presumably require the water for thermoregulation (Zervanos and Hadley 1973). During drought, a collared peccary must consume at least 2,300 g of succulent plants per day to thermoregulate effectively (Langer 1979).

Deer are not always regarded as consumers of cladodes, but in some arid regions they can rely heavily upon them, at least during certain times of the year. In Big Bend National Park, Texas, *Opuntia engelmannii* makes up 14% of the yearly diet of mule deer and 10% of that of white-tailed deer (Krausman 1978). At other localities in Texas, *Opuntia* cladodes form 30 to over 50% of the white-tailed deer's diet (Everitt and Gonzalez 1979; Quinton and Horejsi 1977). Deer consume the cladodes both for energy and as a source of water for thermoregulation (Arnold and Drawe 1979). Maximum cladode consumption by deer has been reported to occur in the spring (Krausman 1978), summer (Arnold and Drawe 1979), and summer/fall (Quinton and Horejsi 1977). Even within a given season, great month-to-month variation occurs in the amount of *Opuntia* cladodes consumed by deer (Luévano et al. 1991). Differences in the timing of peak consumption reflect water needs by the deer, along with the availability of free water and other succulents that might provide water. Less-studied animals also change their dependence on cladodes during the year, depending on other available resources. For example, the northern pocket gopher consumes cladodes the entire year, but in dramatically higher percentages during the winter, when the land is covered by snow and little other food is available (Vaughan 1967).

Nutritional Qualities of Cladodes

Platyopuntia cladodes make a rather poor forage. Their protein content varies between 3 and 13% (on a dry weight basis), depending on the species, time of the year, whether

the plant bears fruit, the particular cladode, and the age of the plant (Sowls 1984; Retamal et al. 1987; Flores Valdez and Aguirre Rivera 1989; Pimienta-Barrios 1990; Gregory and Felker 1992; Theimer and Bateman 1992). Moreover, while some platyopuntias exhibit variations in protein and phosphorus content associated with cladode age, others do not (Gregory and Felker 1992). Still, at even the highest level, the protein content is generally not sufficient for a substantive diet. For example, when collared peccaries are fed exclusively a cladode diet, they lose weight, but when protein is supplemented, not only do they maintain their weight, but some even gain weight (Sowls 1984). Collared peccaries also demonstrated vitamin B deficiencies when fed only cladodes (Sowls 1984). Regardless of its low nutritional value, the water provided by the cladodes is often critical for the survival of consumers and appears to be more important than any nutritional shortcomings at various times of the year. In any case, vertebrates seldom feed only on platyopuntias, and the inclusion in their diet of other plants with more protein, or invertebrates, prevent them from severe undernutrition.

Not only are *Opuntia* cladodes a less than optimal food for vertebrates, but there are also other risks associated with their consumption. When collared peccaries are forced to consume large quantities of nopales, large amounts of water flow through the digestive system, causing an almost continuous diarrhea (Sowls 1984), which can have serious consequences in arid lands. Probably the best known negative consequence of feeding on platyopuntias comes from the high levels of the oxalates in them (Hodgkinson 1977; Sowls 1984; Gibson and Nobel 1986). Dietary oxalates bind calcium (Ca), magnesium (Mg), sodium (Na), and potassium (K) as highly insoluble compounds and, in sufficiently high doses, commonly leads to hypocalcemia (James 1972; Hodgkinson 1977; Sowls 1984; Gibson and Nobel 1986). The binding with Ca and Mg is likely the strongest (E. Ezcurra, personal communication). Ill effects of high oxalic acid intake by mammals include nephritis and respiratory failure (Hodgkinson 1977; Sowls 1984). Although calcium oxalate crystals may cause mechanical damage to the digestive system (James 1972), those of *Opuntia* cladodes are rather rounded, as opposed, for example, to crystals in agaves, and may not be sufficiently abrasive to be a major problem (E. Ezcurra, personal communication).

However, herbivores that have intestinal or ruminal microflora capable of digesting cellulose can also degrade calcium oxalate and absorb the calcium, if given enough time for their digestive microbiota to adapt (Allison and Cook 1981; Justice 1985). This appears to be the case with packrats and other rodents (Shirley and Schmidt-Nielsen

1967; Justice 1985). This ability is provided by the adaptability of the digestive microflora itself, and does not represent an evolutionary adaptation of the herbivores (Justice 1985). Herbivores cope with dietary oxalates in at least one other way. Collared peccaries select inner cladodes that have lower levels of oxalates (although lower spininess seems to be also involved in this selection), but because these cladodes also have less protein and more lignin, the peccaries sacrifice diet quality (Theimer and Bateman 1992). Nopales also contain high quantities of alkaloids (Meyer et al. 1980; Gibson and Nobel 1986). These substances could harm consumers of platyopuntias, but not enough is known about them and their potential effects on herbivores.

Spine Effects on Herbivory

Spines can potentially inflict wounds that can become infected (Anthony 1954). Several vertebrates, e.g., the collared peccary (Theimer and Bateman 1992) and white-throated packrats (Rangel and Mellink 1993), feed less on the more spiny cladodes. In the Galápagos Islands, spines effectively prevent young arborescent platyopuntias from being consumed by tortoises (Biggs 1990). However, Berlandier's tortoises feeding on cladodes are not hindered much by spines, as several individuals with large spines in the masseter muscles on both sides of the neck have been observed (Auffenberg and Weaver 1969).

In addition to selecting cladodes that are less spiny, vertebrates often scrape the spines off. For example, collared peccaries sometimes bite through the entire cladode, but most commonly they step on it, peel the skin (epidermis plus hypodermis) off one side, and then eat the pulp (Sowls 1984). Captive Galápagos land iguanas fed cladodes often scrape the surface with a front foot to remove the spines before biting into the pad (Carpenter 1969). In platyopuntia orchards in Jalisco, desert cottontails discard the areoles and spines along with little pieces of cuticle when feeding on cladodes. This explains the abundant pieces of cuticle found at the bases of platyopuntias, together with cottontail rabbit fecal pellets. Platyopuntias that have only jackrabbit pellets and no cuticle pieces suggest that the jackrabbits handle the spines in a different manner. White-throated packrats, in addition to selecting less spiny plants, most often gnaw across the cladode, beginning somewhere along its edge, and then work their way inward, possibly discarding the spines and glochids along the way (Fig. 7.1A). At other times they feed by scraping the pulp from the side of the cladode (Fig. 7.1B). In spite of the hazards that might be involved, the animals that rely on *Opuntia* cladodes for an important part of

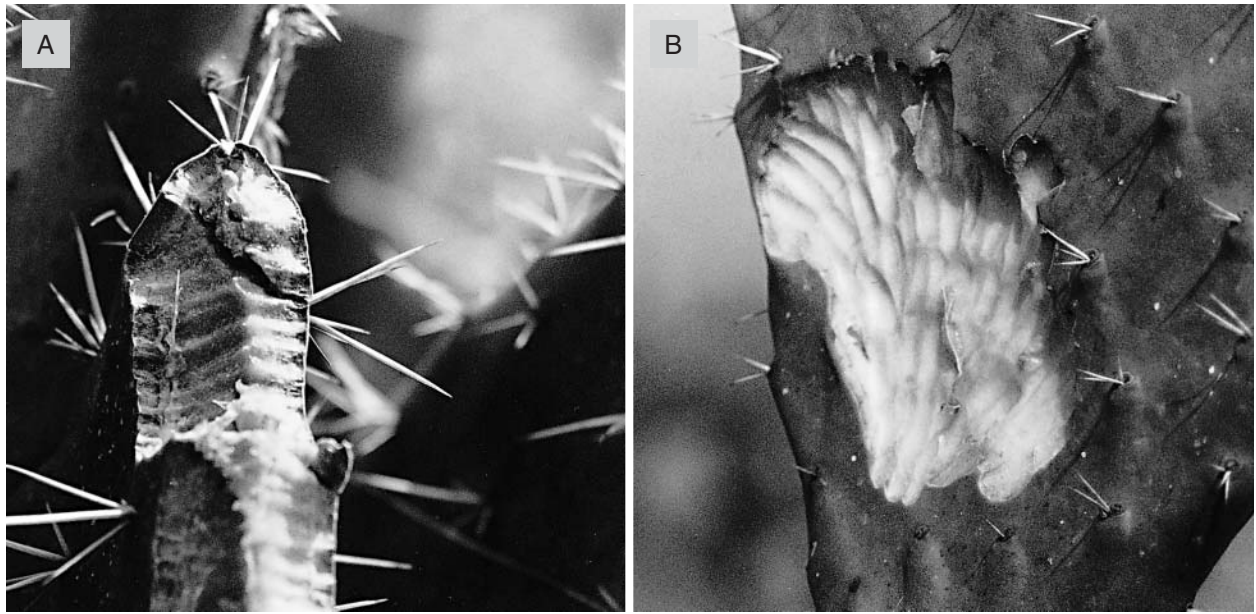


Figure 7.1. Cladodes exhibiting signs of feeding by packrats near Las Papas, Jalisco, Mexico: (A) feeding on the edge and (B) feeding on the side.

their diet are able to cope with this resource, and death induced by such consumption in free-ranging conditions is rather uncommon.

Consumption of Reproductive Structures

The reproductive structures of platyopuntias, especially fruits and seeds, are the major source of attraction to consumers. All the reptilian and bird consumers eat them, as do most of the mammalian consumers (Table 7.1). Actually, given a chance, all mammals that consume vegetative platyopuntia structures may readily eat flowers and fruits as well. Flowers and fruit are available seasonally, but the seeds can be available all year, because fruits ripen asynchronously, and because seeds can remain on the ground for long periods.

Consumers of reproductive structures are of three foraging types: (1) primary foragers—those that directly reach the flowers or fruits to feed on them; (2) secondary consumers—those that feed on flowers or fruits once they have been made available by a previous consumer; and (3) tertiary consumers that feed on seeds, including those of platyopuntias that are in the feces of other consumers, e.g., kangaroo rats, pocket mice, and canyon towhees, among others (Gonzalez-Espinoza and Quintana-Ascencio 1986). A primary consumer may open a fruit, allowing a secondary consumer to reach its interior, or it may cause petals, fruits, or seeds to fall to the ground. Once a fruit has been pried open by a primary consumer, such as a packrat, a host of other users might eventually feed on it. These

secondary consumers will include not only insects—ants, bugs, wasps (Fig. 7.2)—but also birds and rodents (Gonzalez-Espinoza and Quintana-Ascencio 1986).

Flower Consumption

Flowers provide more energy for herbivores than do the cladodes or the fruits but only modest amounts of protein (Christian et al. 1984). So the nutritive quality does not seem to explain the “enthusiasm with which the iguanas scramble for a newly fallen flower, nor does it demonstrate the willingness of the iguanas to travel from tree to tree to consume fallen flowers of *Opuntia*” (Christian et al. 1984). Indeed, two-thirds of the reptiles that consume platyopuntias specifically eat the flowers (Table 7.2). Pollen and nectar contained in the flowers might be part of the explanation for such a preference.

Some bird species on the Galápagos Islands consume pollen and nectar during the dry season, switching to fruits, seeds, and arthropods during the rainy season (Grant and Grant 1979, 1981; Millington and Grant 1983). During the dry season when other foods are scarce, the cactus finch on Daphne Major relies almost exclusively on pollen and nectar, which seem to provide sufficient nutrients for pre-rain breeding. This is an advantage because pairs of this finch that start breeding before the rains produce more offspring (Grant 1996). This finch is a true cactus specialist. To some extent, it excludes the other finches from feeding on pollen and nectar of platyopuntias, defending larger territories year-round, which is in contrast



Figure 7.2. Nopal fruit used as food source by a wasp after a primary consumer has pried it open, near Las Papas, Jalisco, Mexico.

with other finches on Daphne Major, who defend smaller territories and only for part of the year (Grant and Grant 1981; Grant 1996). Indeed, the ground finch on Daphne Major consumes much lower amounts of nopal pollen and nectar, and the onset of its breeding season is after the rains (Grant 1996).

Doves on the Galápagos Islands feed on *Opuntia* flowers, possibly first removing the stamens and nectar, and then tearing and eating the petals. This seems to be a rather unusual feeding habit—not often observed and not exhibited by all dove populations (Grant and Grant 1979). Lava lizards on Pinta Island climb up platyopuntias and tear the petals to obtain the pollen. In contrast, the lava lizard on Daphne Major does not climb platyopuntias but obtains pollen opportunistically by eating the pollen-impregnated petals that fall when the Daphne Major cactus finch feeds (East 1995). The lizards probably obtain an important portion of protein from the pollen, especially as the onset of *Opuntia* flowering occurs during the dry season when arthropods are in short supply (East 1995). Even the Lagarto Tizón, an omnivorous lizard of the Canary Islands, Spain, feeds on platyopuntia pollen (Valido and Nogales 1994).

Pollen has variable levels of protein. Notably, pollen from bat-pollinated cactus flowers has a high protein content, e.g., up to 44% in the saguaro, but pollen of the non-bat-pollinated *Opuntia versicolor* has only 9% protein (Howell 1974). In addition to their protein content, pollen

grains are valuable because they contain essential amino acids and vitamins (Howell 1974; Grant and Grant 1981; Millington and Grant 1983; Richardson et al. 1986; Grant 1996). Galápagos finches digest over 90% of the pollen they consume (Grant 1996). The physiology of such high digestibility has not been clarified, but either the Galápagos finches and lava lizards (which also exhibit a high digestion of pollen) are especially efficient, or platyopuntia pollen is quite easy to digest (Grant 1996). Several paths are theoretically possible in the digestion of pollen; for a small, pollen-eating marsupial (*Tarsipes rostratus*), pollen seems to be digested directly through the pores in its exine coat (Richardson et al. 1986). Consuming nectar along with pollen, in addition to providing energy, may also help the ingested pollen germinate, facilitating its digestion (Grant 1996).

Fruit Consumption

Opuntia fruits are a valuable food resource for animals and are readily eaten when available. Over 60% of platyopuntia consumers in any taxa eat the fruits. Platyopuntia fruits (tunas) have 9 to 18% sugar and large quantities of vitamin C (Pimienta-Barrios 1990). Fruits of *Opuntia lindheimeri* from southern Texas have 7% protein, 0.15% phosphorus (P), 2.5% Ca, 0.93% Mg, 3.4% K, and 0.02% Na (Everitt and Alaniz 1981). Vertebrates may consume fruits as a “gourmet” food, when they encounter them, as the Shasta ground sloth did (Hansen 1978). On the Canary Islands, the endemic Lagarto Tizón consumes fruits of *Opuntia dilenii* during May (Valido and Nogales 1994). As different platyopuntia species bear fruits of different sizes, color, and spininess, foraging preferences of vertebrates differ (Janzen 1986).

The seeds are used by at least 13 vertebrate herbivores, mostly birds (Table 7.2). They are also an important resource for many rodents (González-Espinoza and Quintana-Ascencio 1986). Such seeds are rich in oils and proteins (Pimienta-Barrios 1990). Although seeds may be available year-round, certain vertebrates eat them only when other resources are in short supply. In the Galápagos Islands during the dry season, seed consumption by the Daphne Major cactus finch declines as flower feeding increases (Millington and Grant 1983).

Evolutionary and Ecological Context

Past and Present Herbivory Pressures

In arid and semiarid lands, platyopuntias often constitute one of the most conspicuous elements of the landscape, and it is easy to find relationships among them and some

vertebrates. *Platyopuntias* provide protein, carbohydrates, and water to vertebrates, and these vertebrates in turn act as pollinators and dispersers (Grant and Grant 1979; Gonzalez-Espinoza and Quintana-Ascencio 1986; Biggs 1990; East 1995). However, these relationships do not explain the evolution of the traits currently exhibited by *platyopuntias* and their fruits. Rather, *platyopuntias* on continental America are the ghosts of past interactions that involve currently extinct megaherbivores (Janzen and Martin 1982; Gonzalez-Espinoza and Quintana-Ascencio 1986; Janzen 1986). On the Galápagos Islands, the evolutionary pressures, which are still operational, are different.

According to Janzen (1986), not only did Pleistocene megaherbivores shape the form and anatomy of *platyopuntias*, but they also could have dispersed them from South to North America, or vice versa, after the closure of the Central American bridge. In addition to being long-distance dispersers in Pleistocene communities, some megaherbivores probably munched their way through dense patches of *platyopuntias*, creating clearings that would be colonized by other plants and, perhaps, small mammals, reptiles, and invertebrates. After most of the megaherbivores of the Americas vanished at the end of the Pleistocene, *platyopuntias* have maintained most of the traits developed under the pressure of their former consumers. Certainly, important changes in distribution and abundance resulted from the absence of their principal dispersers, but the species survived. In a few cases, erosion of anachronistic traits (*sensu* Janzen and Martin 1982) seems to be occurring; e.g., some *platyopuntia* species have “spiny” fruits that are not eaten by herbivores and which are mostly sterile (Anthony 1954).

Although they might have contributed little to the past shaping of *platyopuntias*, the extant opuntiofagous vertebrates do currently serve as dispersers of seeds. Birds remove only modest amounts of seeds—less than 5% of the total crop (Janzen 1986)—but rodents can remove more seeds from the fruits once they fall to the ground (Gonzalez-Espinoza and Quintana-Ascencio 1986). Rodent caches often become the source of new *platyopuntias* away from the mother plants. The seed shadows produced by extant vertebrate dispersers are surely much different—and at smaller geographical scales than from those that can be presumed for Pleistocene megaherbivores (Janzen 1986). Nonetheless, these extant vertebrates may substantially increase the cover of *platyopuntia* communities, especially when patterns of competition among different plants is altered by the introduction of alien grazers, such as cattle or sheep (Riegel 1941; Timmons 1942). The effects of direct removal of *platyopuntia* parts by extant species on the system

are difficult to assess. For example, collared peccaries can remove 2 to 5% of the cladodes (Bissonette 1982). As *platyopuntias* are well armored against grazing, direct removal of large parts of their vegetative structure is unlikely (and probably was unlikely even during the Pleistocene), except during severe drought.

Galápagos Islands

Nowhere is the association between *platyopuntias* and vertebrates as intense as on the Galápagos Islands. The morphology of nopales on different islands is a clear adjustment to avoid herbivory on vegetative structures (Thornton 1971; Biggs 1990; Hicks and Mauchamp 1995). Arborescent *platyopuntias* predominate on specific islands of the Galápagos that support, or have supported, tortoise and land iguana populations. These plants have large scaly trunks (> 60 cm in height), bearing rounded compact crowns with lower cladodes strongly armored with spines and the upper cladodes almost spineless. When young, spines protect these nopales from grazing by tortoises. On islands that have never supported tortoises or iguanas, the plants are decumbent and have weak or no spines, some cladodes bearing only tufts of glochids (Biggs 1990). During the rainy season, some cladodes of arborescent *platyopuntias* become heavy, turgid with water, and break off from the mother plants, falling to the ground. There they maintain a high water content, even through the following dry season, when they are the main food source for land iguanas and tortoises (Biggs 1990).

A particularly strong relationship exists between birds and *platyopuntias* in the Galápagos Islands. In its simplest form, differences in size and hardness of *platyopuntia* seeds may be a partial response to predation by finches. Conversely, the size and shape of the beaks of finches may reflect an adjustment to forage efficiently for pollen and nectar, as well as the ability to break seeds (Grant and Grant 1989). Some finches contribute significantly to the cross-pollination of *platyopuntias*, transporting pollen from plant to plant. Such transport is important, as flowers that receive pollen from flowers of the same plant produce significantly fewer seeds than those that receive pollen from more distant plants (Grant and Grant 1981). Consequently, these finches promote larger seed crops.

However, this pollinating service is not without negative repercussions. When feeding on flowers, the finches often snip off the styles, presumably to facilitate access to the pollen, which prevents fertilization of the ovules. As a result, by obtaining energy and protein from nectar and pollen, the finches benefit by having an early onset of their



Figure 7.3. Feral burro eating the fruit of *Opuntia* aff. *megacantha* near Las Papas, Jalisco, Mexico.

breeding season, but, in doing so, threaten the seed supply for their dry-season feeding (Grant and Grant 1981). The negative effect of snipping styles might be only partial: the later the style is snipped, the greater the chance that the pollen has already reached the stigma and some ovules are fertilized (Grant and Grant 1981). Despite their overall value as pollinators, finches sometimes cause damage to platyopuntia trunks and young cladodes when pecking into them to drink fluid, eat storage tissues, and take insect larvae (Grant and Grant 1981). As a result, the damaged pads are vulnerable to infection by bacteria and fungi, eventually leading to necrosis.

The preceeding is a highly simplified picture of the relationships that have shaped the Galapagos Islands platyopuntias and their communities. The real picture is more complex and involves variations at different time scales. Regrettably, the conditions that promoted the evolution of the local relationships have not remained intact. The land reptiles have been hunted, sometimes to extinction, and alien species have been introduced (Thornton 1971; Hicks and Mauchamp 1995). These events have already affected the permanence of such relationships and probably will cause others that might be detrimental to the conservation of the entire platyopuntia-associated system.

Alienized Relations

Whenever platyopuntias have been introduced to other parts of the world, they have been readily accepted by local vertebrates. Ten animals have been reported to consume introduced platyopuntias (Leopard tortoise, Lagarto Tizón, ostrich, emu, black magpie, little raven, baboon, “monkeys,” camel, and steenbok; Table 7.1), but there are probably many more unreported consumers. Frequently, native vertebrates may become dispersers of alien platyopuntias, which is the case for the Lagarto Tizón (Valido and Nogales 1994) on the Canary Islands, the black magpie in Australia (Darnell-Smith 1919), and primates and birds in South Africa (Weed Section 1940). Other native vertebrates that consume alien platyopuntia fruits may also disperse seeds. Alien vertebrates may also disperse alien platyopuntias, as demonstrated by feral European rabbits in Australia (Darnell-Smith 1919). The roster of opuntiofagous vertebrates in areas where platyopuntias are alien is surely much larger than what has been reported so far (Table 7.1), and it is unlikely that it will ever be fully reported.

The other side of the coin in alienized relations is that of the impact of alien vertebrates on native platyopuntias. Four alien species currently consume cladodes in the wild in the Americas (black rat; feral burro, Fig. 7.3; wild boar;

and feral goat). When cattle and horses roamed wild two centuries ago, they likely also engaged in cladode consumption, as domestic individuals of these species do today. In continental America, the introduction of large domestic vertebrates (namely, cattle and horses) restored functions interrupted by the extinction of megafauna at the end of the Pleistocene (Martin 1975; Janzen 1986), although this view is not always accepted. In insular contexts, however, the introduction of alien herbivores or omnivores often causes conservation hazards, if not mass extinction, even for well-protected species, such as platyopuntias.

Three alien vertebrates threaten platyopuntias on the Galápagos Islands. Goats feed on the pads of nopal (Hicks and Mauchamp 1995). They munch through the trunks of arboreal platyopuntias, up to 50 cm in diameter, causing them to fall (Eliasson 1968). Medium and large platyopuntias are subject to a higher grazing pressure, because they are less spiny, and this selection can seriously impair platyopuntia populations, as it leads to the killing of the plants before they reach reproductive age (Hicks and Mauchamp 1995). Fallen cladodes can produce new trees, but the goats eagerly eat the pads before any rooting takes place (Hicks and Mauchamp 1995). Burros have also affected the distribution of platyopuntias on the Galápagos Islands (Van der Werff 1982; Hicks and Mauchamp 1995). In the case of seedlings, their heavy spiny armour can prevent grazing by native reptiles but does not prevent goats from considering them a “favorite” (Schofield 1989). While not evident at first consideration, mice (probably *Mus musculus*) are also a threat to platyopuntias on the Galápagos Islands (Snell et al. 1994). They burrow among and into the roots, weakening their hold on the soil. The effect of such activities and the success of prevention programs in the long run is difficult to predict.

Concluding Remarks

Platyopuntia cladodes offer not only food and water, but also protective cover, den anchorage, and den building materials to wild vertebrates. Several species are closely associated with platyopuntias: Berlandier’s tortoise, white-throated packrat, collared peccary, and deer, as well as finches, land iguanas, and tortoises on the Galápagos Islands. Other vertebrates rely on cladodes for survival during critical periods such as drought. Still other species, although not using the cladodes themselves, use the native platyopuntia nopaleras as habitat.

Despite the fact that several relationships between platyopuntias and vertebrates exist, there has been a paucity in the efforts to understand them, except for the highly creative studies on the Galápagos Islands. For the

continental Americas, the advances in understanding platyopuntia-vertebrate interactions notably include the proposal of Janzen (1986) on the evolution of platyopuntias, their communities, and their dispersal in North America as well as the work of González-Espinoza and Quintana-Ascencio (1986) on *Opuntia* seed dispersal for nopaleras in the Mexican plateau. Most other work has focused on the role of cladodes in the diet of selected vertebrates, especially the collared peccary. Clearly, much research remains to be done to understand the function of nopaleras in the continental Americas. If such an understanding is to be generated, action should be taken soon, as nopaleras are being modified at accelerated rates to raise agricultural products or livestock, or as an inevitable side effect of human population growth.

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Literature Cited

- Allison, M. J., and H. M. Cook. 1981. Oxalate degradation by microbes of large bowel of herbivores: The effect of dietary oxalate. *Science* 212: 675–676.
- Anthony, M. 1954. Ecology of the Opuntiae in the Big Bend region of Texas. *Ecology* 35: 334–347.
- Arnold, L. A., Jr., and D. L. Drawe. 1979. Seasonal food habits of white-tailed deer in the south Texas plains. *Journal of Range Management* 32: 175–176.
- Auffenberg, W., and W. G. Weaver. 1969. *Gopherus berlandieri* in southern Texas. *Bulletin of the Florida State Museum* 13: 141–203.
- Baber, D. W., and B. E. Coblenz. 1987. Diet, nutrition, and conception in feral pigs on Santa Catalina Island. *Journal of Wildlife Management* 51: 306–317.
- Bailey, V. 1931. Mammals of New Mexico. *North American Fauna* 53: 1–412.
- Biggs, A. L. 1990. Coevolution in the Galápagos. *American Biology Teacher* 52: 24–28.
- Bissonette, J. A. 1982. Ecology and social behavior of the collared peccary in Big Bend National Park. *National Park Service Scientific Monograph* 16: 1–85.
- Blair, W. F. 1937. The burrows and food of the prairie pocket mouse. *Journal of Mammalogy* 18: 188–191.
- Bowman, R. I. 1961. Morphological differentiation and

- adaptation in the Galápagos finches. *University of California Publications in Zoology* 58: 1–302.
- Brown, D. E. 1989. *Arizona Game Birds*. University of Arizona Press, Tucson.
- Burt-Davy, J. 1920. Utilizing prickly pear and spineless cactus. *South African Journal of Industry* 3: 1001–1011.
- Carpenter, C. C. 1969. Behavioral and ecological notes on the Galápagos land iguanas. *Herpetologica* 25: 155–164.
- Christian, K. A., C. R. Tracy, and W. P. Porter. 1984. Diet, digestion, and food preferences of Galápagos land iguanas. *Herpetologica* 40: 205–212.
- Clements, F. E., and V. E. Shelford. 1939. *Bio-Ecology*. Wiley, New York.
- Corn, J. L., and R. J. Warren. 1985. Seasonal habits of the collared peccary in south Texas. *Journal of Mammalogy* 66: 155–159.
- Dalquest, W. W. 1953. Mammals of the Mexican state of San Luis Potosí. *Louisiana State University Studies, Biological Sciences Series* 1: 1–112.
- Darnell-Smith, G. P. 1919. Animal aids to the spread of prickly pear. *Agricultural Gazette of New South Wales* 30: 125–127.
- Davis, O. K., L. Agenboard, P. S. Martin, and J. I. Mead. 1984. The Pleistocene blanket of Bechan Cave, Utah. *Special Publication of Carnegie Museum of Natural History* 8: 267–282.
- Dodd, N. L., and W. W. Brady. 1988. Dietary relationships of sympatric desert bighorn sheep and cattle. *Desert Bighorn Council Transactions* 1988: 1–6.
- Dunn, J. P., J. A. Chapman, and R. E. Marsh. 1982. Jackrabbits. In *Wild Mammals of North America* (J. A. Chapman and G. A. Feldhamer, eds.). Johns Hopkins University Press, Baltimore, Maryland. Pp. 124–145.
- East, K. T. 1995. Pollen digestion in Galápagos lava lizards. *Noticias de Galápagos* 55: 8–14.
- Eddy, T. A. 1961. Foods and feeding patterns of the collared peccary in southern Arizona. *Journal of Wildlife Management* 25: 248–257.
- Eliasson, U. 1968. On the influence of introduced animals on the natural vegetation of the Galápagos Islands. *Noticias de Galápagos* 11: 19–21.
- Everitt, J. H., and M. A. Alaniz. 1981. Nutrient content of cactus and woody plant fruits eaten by birds and mammals in south Texas. *Southwestern Naturalist* 26: 301–305.
- Everitt, J. H., and C. L. Gonzalez. 1979. Botanical composition and nutrient content of fall and early winter diets of white-tailed deer in south Texas. *Southwestern Naturalist* 24: 297–310.
- Everitt, J. H., C. L. Gonzalez, M. A. Alaniz, and G. V. Latigo. 1981. Food habits of the collared peccary on south Texas rangelands. *Journal of Range Management* 34: 141–144.
- Flores Valdez, C. A., and J. R. Aguirre Rivera. 1989. *El Nopal como Forraje*, 2nd ed. Universidad Autónoma Chapingo, Chapingo, Mexico.
- Gibson, A. C., and P. S. Nobel. 1986. *The Cactus Primer*. Harvard University Press, Cambridge, Massachusetts.
- Gonzalez-Espinoza, M., and P. F. Quintana-Ascencio. 1986. Seed predation and dispersal in a dominant desert plant: *Opuntia*, ants, birds, and mammals. In *Frugivores and Seed Dispersal* (A. Estrada and T. H. Fleming, eds.). W. Junk, Dordrecht, The Netherlands. Pp. 273–284.
- Grant, B. R. 1996. Pollen digestion by Darwin's finches and its importance for early breeding. *Ecology* 77: 489–499.
- Grant, B. R., and P. R. Grant. 1981. Exploitation of *Opuntia* cactus by birds on the Galápagos. *Oecologia* 49: 179–187.
- Grant, B. R., and P. R. Grant. 1989. Natural selection in a population of Darwin's finches. *American Naturalist* 133: 377–393.
- Grant, P. R., and K. T. Grant. 1979. Breeding and feeding ecology of the Galápagos dove. *Condor* 81: 397–403.
- Gregory, R. A., and P. Felker. 1992. Crude protein and phosphorus contents of eight contrasting *Opuntia* clones. *Journal of Arid Environments* 22: 323–331.
- Hansen, R. M. 1978. Shasta ground sloth food habits, Rampart Cave, Arizona. *Paleobiology* 4: 302–319.
- Hellgren, E. C. 1993. Status, distribution, and summer food habits of black bears in Big Bend National Park. *Southwestern Naturalist* 38: 77–80.
- Hicks, D. J., and A. Mauchamp. 1995. Size-dependent predation by feral mammals on Galápagos *Opuntia*. *Noticias de Galápagos* 55: 6–17.
- Hodgkinson, A. 1977. *Oxalic Acid in Biology and Medicine*. Academic Press, New York.
- Hoffman, M. T., J. D. James, G. I. H. Kerley, and W. G. Whitford. 1993. Rabbit herbivory and its effects on cladode, flower and fruit production of *Opuntia violacea* var. *macrocentra* (Cactaceae) in the northern Chi-

- huahuan Desert, New Mexico. *Southwestern Naturalist* 38: 309–315.
- Hoffmeister, D. F. 1986. *Mammals of Arizona*. University of Arizona Press, Tucson.
- Howell, D. J. 1974. Bats and pollen: Physiological aspects of syndrome of chiropterophily. *Comparative Biochemistry and Physiology, Series A* 48: 263–276.
- James, L. F. 1972. Oxalate toxicosis. *Clinical Toxicology* 5: 231–243.
- Janzen, D. H. 1986. Chihuahuan Desert nopaleras: Defaunated big mammal vegetation. *Annual Review of Ecology and Systematics* 17: 595–636.
- Janzen, D. H., and P. S. Martin. 1982. Neotropical anachronisms: The fruits the gomphotheres ate. *Science* 215: 19–27.
- Justice, K. E. 1985. Oxalate digestibility in *Neotoma albigula* and *Neotoma mexicana*. *Oecologia* 67: 231–234.
- Krausman, P. R. 1978. Forage relationships between two deer species in Big Bend National Park, Texas. *Journal of Wildlife Management* 42: 101–107.
- Krausman, P. R., B. D. Leopold, R. F. Seegmiller, and S. G. Torres. 1989. Relationship between desert bighorn sheep and habitat in western Arizona. *Wildlife Monographs* 102: 1–66.
- Lack, D. 1947. *Darwin's Finches*. Cambridge University Press, Cambridge, England.
- Langer, P. 1979. Adaptational significance of the fore stomach of the collared peccary, *Dicotyles tajacu* (L. 1758) (Mammalia: Artiodactyla). *Mammalia* 43: 235–245.
- Lehman, V. W. 1984. *Bobwhites in the Rio Grande Plains of Texas*. Texas A&M University Press, College Station, Texas.
- Leopold, A. S. 1959. *Wildlife of Mexico*. University of California Press, Berkeley.
- Long, A., R. M. Hansen, and P. S. Martin. 1974. Extinction of the shasta ground sloth. *Geological Society of America Bulletin* 85: 1843–1848.
- Luévano E. J., E. Mellink, E. García M., and R. Aguirre R. 1991. Dieta y traslapo dietario del venado cola blanca, jabalí de collar, cabra y caballo, durante el verano en la Sierra de la Mojonera, Vanegas, S.L.P. *Agrociencia, serie Recursos Naturales Renovables* 1: 105–122.
- MacCracken, J. G., and R. M. Hansen. 1984. Seasonal foods of blacktail jackrabbits and Nuttall cottontails in southeastern Idaho. *Journal of Range Management* 37: 256–259.
- Marais, J. G. 1939. Spineless cactus and old-man saltbush for sheep. *Farming in South Africa* 1939: 99–100.
- Martin, P. S. 1975. Vanishings, and future, of the prairie. *Geoscience and Man* 10: 39–49.
- Martinez-Romero, L. E., and S. Mandujano. 1995. Habitats alimentarios del pecarí de collar (*Pecari tajacu*) en un bosque tropical caducifolio de Jalisco, Mexico. *Acta Zoologica Mexicana* 64: 1–20.
- McClinton, S. F., P. L. McClinton, and J. V. Richerson. 1992. Food habits of black bears in Big Bend National Park. *Southwestern Naturalist* 37: 433–435.
- McCulloch, E. M. 1980. Little raven *Corvus mellori* eating fruit of prickly pear *Opuntia* sp. *Australian Bird Watcher* 8: 248.
- McLure, M. F., N. S. Smith, and W. W. Shaw. 1995. Diets of coyotes near the boundary of Saguaro National Monument and Tucson, Arizona. *Southwestern Naturalist* 40: 101–105.
- Meyer, B. N., A. H. Mohamed, and J. L. MacLaughlin. 1980. β -phenethylamines from the cactus genus *Opuntia*. *Phytochemistry* 19: 719–720.
- Mijares-Urrutia, A., B. Colvée, and A. Arend R. 1997. Sauria: *Cnemidophorus lemniscatus* (NCN). Herbivory. *Herpetological Review* 28: 88.
- Millington, S. J., and P. R. Grant. 1983. Feeding ecology and territoriality of the cactus finch *Geospiza scandens* on Isla Daphne major, Galapagos. *Oecologia* 58: 76–83.
- Milton, S. J. 1992. Plants eaten and dispersed by adult leopard tortoises *Geochelone pardalis* (Reptilia: Chelonii) in the southern Karoo. *South African Journal of Zoology* 27: 45–49.
- Neal, B. J. 1959. A contribution on the life history of the collared peccary in Arizona. *American Midland Naturalist* 61: 177–190.
- Pimienta-Barrios, E. 1990. *El Nopal Tunero*. Universidad de Guadalajara, Zapopan, Mexico.
- Price, T. 1987. Diet variation in a population of Darwin's finches. *Ecology* 68: 1015–1028.
- Quinton, D. A., and R. G. Horejsi. 1977. Diets of white-tailed deer on the rolling plains of Texas. *Southwestern Naturalist* 22: 505–509.
- Quinton, D. A., R. G. Horejsi, and J. T. Flinders. 1979. Influence of brush control on white-tailed deer diets in north-central Texas. *Journal of Range Management* 32: 93–97.
- Rangel, M. G., and E. Mellink. 1993. Historia natural de la rata maguayera en el Altiplano Mexicano. In *Avances*

- en el Estudio de los Mamíferos de México (R. A. Medellín and G. Ceballos, eds.). Asociación Mexicana de Mastozoología, Mexico City. Pp. 173–183.
- Retamal, N., J. M. Duran, and J. Fernandez. 1987. Seasonal variation of chemical composition in prickly pear (*Opuntia ficus-indica* [L.] Miller). *Journal of the Science of Food and Agriculture* 38: 303–311.
- Richardson, K. C., R. D. Wooller, and B. G. Collins. 1986. Adaptations to a diet of nectar and pollen in the marsupial *Tarsipes rostratus* (Marsupialia: Tarsipedidae). *Journal of Zoology* 208: 285–297.
- Riegel, A. 1941. Some coactions of rabbits and rodents with cactus. *Transactions of the Kansas Academy of Sciences* 44: 96–101.
- Rose, F. L., and F. W. Judd. 1982. Biology and status of Berlandier's tortoise (*Gopherus berlandieri*). In *North American Tortoises: Conservation and Ecology* (R. B. Bury, ed.). Wildlife Research Report 12. United States Fish and Wildlife Service, Washington, D.C. Pp. 57–70.
- Russell, P. T. 1964. *Antelope of New Mexico*. New Mexico Department of Fish and Game, Santa Fe.
- Schluter, D. 1984. Body size, prey size and herbivory in the Galápagos lava lizard, *Tropidurus*. *Oikos* 43: 291–300.
- Schofield, E. K. 1989. Effects of introduced plants and animals on island vegetation: Examples from the Galápagos Archipelago. *Conservation Biology* 3: 227–238.
- Sexson, M. L., J. R. Choate, and R. A. Nicholson. 1981. Diet of pronghorn in western Kansas. *Journal of Range Management* 34: 489–493.
- Shirley, E. K., and K. Schmidt-Nielsen. 1967. Oxalate metabolism in the pack rat, sand rat, hamster, and white rat. *Journal of Nutrition* 91: 496–502.
- Snell, H. L., H. M. Snell, and P. Stone. 1994. Accelerated mortality of *Opuntia* on Isla Plaza Sur: Another threat from an introduced vertebrate? *Noticias de Galápagos* 53: 19–21.
- Sowls, L. K. 1984. *The Peccaries*. University of Arizona Press, Tucson.
- Spaulding, W. G., and P. S. Martin. 1979. Ground sloth dung of the Guadalupe mountains. *National Park Service Proceedings* 4:259.269.
- Spencer, D. A., and A. L. Spencer. 1941. Food habits of the white-throated wood rat in Arizona. *Journal of Mammalogy* 22: 280–284.
- Stelfox, J. G., and H. G. Vriend. 1977. Prairie fires and pronghorn use of cactus. *Canadian Field Naturalist* 91: 282–285.
- Theimer, T. C., and G. C. Bateman. 1992. Patterns of prickly-pear herbivory by collared peccaries. *Journal of Wildlife Management* 56: 234–240.
- Thornton, I. 1971. *Darwin's Islands; a Natural History of the Galápagos*. American Museum of Natural History, Garden City, New York.
- Timmons, F. L. 1942. The dissemination of prickly pear seed by jack rabbits. *Journal of the American Society of Agronomy* 34: 513–520.
- Valido, A., and M. Nogales. 1994. Frugivory and seed dispersal by the lizard *Gallotia galloti* (Lacertidae) in a xeric habitat of the Canary Islands. *Oikos* 70: 403–411.
- Van der Werff, H. 1982. Effects of feral pigs and donkeys on the distribution of selected food plants. *Noticias de Galápagos* 36: 17–18.
- Vaughan, T. A. 1967. Food habits of the northern pocket gopher on shortgrass prairie. *American Midland Naturalist* 77: 176–189.
- Vorhies, C. T., and W. P. Taylor. 1922. Life history of the kangaroo rat *Dipodomys spectabilis spectabilis* Merriam. *Bulletin of the United States Department of Agriculture* 1091: 1–40.
- Vorhies, C. T., and W. P. Taylor. 1933. The life histories and ecology of jack rabbits, *Lepus alleni* and *Lepus californicus* ssp., in relation to grazing in Arizona. *University of Arizona College of Agriculture Technical Bulletin* 49: 471–587.
- Vorhies, C. T., and W. P. Taylor. 1940. Life history and ecology of the white-throated wood rat, *Neotoma albigula albigula* Hartley, in relation to grazing in Arizona. *University of Arizona College of Agriculture Technical Bulletin* 86: 455–529.
- Weed Section [South African] Department of Agriculture and Forestry. 1940. Opuntias in South Africa. I: Some naturalized species with special reference to prickly pear, and methods for its eradication. *Farming in South Africa* 15: 119–125.
- Zervanos, S. M., and N. F. Hadley. 1973. Adaptational biology and energy relationships of the collared peccary (*Tayassu tajacu*). *Ecology* 54: 759–774.

BIODIVERSITY AND CONSERVATION

Thomas H. Boyle and Edward F. Anderson

Introduction

Biodiversity of Cacti

*Biodiversity of Natural Communities of Cacti**Genetic Diversity in Wild Cacti**Breeding Systems and Sexual Expression in the Cactaceae**Biodiversity of Cultivated Cacti*

Conservation of Cacti

*Why Cacti Are Threatened**Determination of Threatened Cacti**Conservation of Specific Cacti**Importance of Artificial Propagation**CITES**The Convention on Biological Diversity**In situ and ex situ Conservation*

Conclusions and Future Prospects

Literature Cited

Introduction

Cacti have been exploited since pre-Columbian times. Many cacti have fruits that are eaten raw, cooked, or fermented into alcoholic beverages. Stems of some cacti are cooked as a vegetable, used as an emergency source of water, or fed to domestic animals as forage or fodder. Dried woody stems of some large columnar cacti are gathered for building material or firewood. Some species produce substances of pharmaceutical or industrial interest (e.g., cochineal dye extracted from the dried bodies of a scale insect [*Dactylopius coccus*] collected from many species of prickly-pear cacti), whereas other cacti are consumed to induce visual hallucinations for religious or recreational

purposes. Last but not least, cacti are prized for their diverse forms and beautiful flowers and are cultivated worldwide as ornamentals. Unfortunately, habitat destruction and collection of wild cacti has threatened the very survival of some species, and attention now must be focused on their protection.

The conservation of biodiversity is one of the major issues facing humankind today and is of paramount importance for the long-term survival of cacti as well as other organisms. This chapter examines the biodiversity of both wild and cultivated cacti, and discusses contemporary and long-term issues pertaining to conservation of cacti. Factors affecting biodiversity of cacti and the estimation of genetic diversity in wild and cultivated cacti are considered