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Seed Dispersal in Yucca Brevifolia (Agavaceae)-Present and Past, With Consideration of the Future of the Species

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ABSTRACT

Earlier descriptions of the fruit of *Yucca brevifolia* are reviewed. It is here shown that the fruit is a fleshy, sugar-rich berry that later becomes a hard, dry, spongy body. At no time are seeds released from the fruits without the exertion of an outside force. Various animals that might release seeds from the dry fruits are considered, as is wind that may disperse entire fruits. The question is introduced as to why *Y. brevifolia* Engelm. would expend large amounts of energy and resources to create a product for which there is no market. The appeal that the fruits may have had for now extinct megaherbivores is addressed. Finally, the possible future of the species is considered.

INTRODUCTION

The Joshua tree is as universally recognized as a symbol of the Mojave Desert as is the sahuaro (*Carnegiea gigantea* Brit. & Rose) of the Sonoran Desert (Fig. 1). Its present distribution as determined by Rowlands (1978) is shown in Fig. 2. The species occurs at elevations of ~600 to 2100 m (Merriam 1893; Webber 1953; Munz and Keck 1959; Vasek 1973; Rowlands 1978). Although found in a wide variety of plant communities it attains its greatest size in the desert savanna (Kornoelje 1973; Leary 1977) or in desert grassland or shrub-steppe (Rowlands 1978) at elevations from ~1200 to 1400 m. It is most often found on level flats or gentle slopes (0–10%) (Rowlands 1978). The Joshua tree tolerates a broad range of temperatures, from −25° to 51° C, and annual precipitation from 98 to 268 mm. During the late Wisconsin (~25.0–12.5 kya) the species occurred in southern Arizona (Van Devender 1990). As I shall later show, during the late Miocene (23.3–5.2 mya) an arborescent *Yucca,* the fossil equivalent of *Y. brevifolia* or a related species, was growing in northwestern Nevada near the Oregon border, the two sites separated by ~9° latitude. (Note: Unless otherwise indicated, geological ages are from Harland et al. 1990).

TAXONOMY

Engelmann described *Yucca brevifolia* in 1871, and in 1935, McKelvey established *Y. brevifolia* var. *jaegeriana.* Jones (1935) proposed *Y. wolfei* for the same plants, however McKelvey's name has priority (by five days). Webber described *Y. brevifolia* forma *herbertii* in 1953, and in 1958, Munz changed the status to *Y. brevifolia* var. *herbertii.* Hochstätter (2001) created the new combinations *Y. brevifolia* ssp. *jaegeriana* and *Y. brevifolia* ssp. *herbertii.* Hess and Robbins (2002) do not recognize infraspecific taxa. Rowlands (1978) recognized *Y. brevifolia* var. *brevifolia* and *Y. brevifolia* var. *jaegeriana.* Following extensive field studies, and based of morphology and distribution, I follow Rowlands except that I employ subspecies rather than varieties.

In view of the fact that the dispersal mechanism is the same for all, unless otherwise indicated, the term *Y. brevifolia* will be used here.

THE FRUIT

Until now the nature of the fruit has received little consideration and botanists have described them in a multiplicity of ways. Engelmann (1871) wrote, "Fruit indehiscent, at last dry." Trelease (1893) recognized the "thin endocarp enveloping the seeds, which in turn was surrounded by a thick exocarp that on maturity became pulpy." Parish (1891) wrote that the fruits were dry with a somewhat "spongiose pericarp." In 1896, Sargent described the fruits as "indehiscent showing a tendency to split with the outer coat sometimes a quarter of an inch thick, spongy and closely investing the case-like inner coat." Jepson (1925) referred to the fruits as capsules. McKelvey (1938), in her typical profuseness, reported the fruits "plump throughout . . . first green eventually reddish-brown or nearly black; exocarp smooth to slightly granular." Kearney and Peebles (1964) referred to the fruit as "semicapsular, soon becoming dry, spreading." Munz and Keck (1959) and Munz (1974), describe them as "plump, drying in age." Simpson (1975) wrote "[Fruits] indehiscent, dry and spongy . . . partially septicidally dehiscent." Cronquist et al. (1977) and Welch

Fig. 1. *Yucca brevifolia* ssp. *brevifolia*. Joshua Tree National Park, California. Photograph by author.

et al. (1987) characterize them as "capsules ellipsoid, dry and rather spongy." According to McKinney and Hickman (2002) the fruits are "spreading to erect." Hess and Robbins (2002) describe them as "pendant, capsular, indehiscent . . . dry and spongy." These conflicting accounts are the result of a failure to recognize the true nature of the fruit.

The fruit of *Y. brevifolia* is a berry (*sarcocarpium*) as interpreted by Esau (1953), Roth (1977), Fahn (1982) and Mauseth (1988) or a *bacca* as defined by Spjut (1994) who acknowledges berry as a synonym. Members of *Yucca* section *Yucca* are known as fleshy- or baccate-fruited species. In these species, the pericarp consists of a thin to thick exocarp, a fleshy mesocarp, and a parchment-like endocarp that functionally separates the six cylinders of seed from the mesocarp. In tropical species, the endocarp is absent (Simpson 1975; Lenz pers. obs.). Fruits of *Y. brevifolia* are borne in tightly congested clusters at the ends of branches with the masses often weighing >4 kg. The smooth, broadly ovoid to elliptical fruits, as much as 9 cm long and 6 cm wide, frequently weigh >250 g. The fruits are never malformed. On reaching their ultimate size they are grayish-green in color and are individually detached from the branches of the cluster with considerable difficulty. On the other hand, individual lateral branches with one to four fruits are easily detached by pulling down sharply on the branch.

Fruits and the seeds they contain mature synchronously and fruit maturity is considered the stage when seeds are capable of germination (Fahn 1982). At maturity, fruits of *Y. brevifolia* have a moisture content of ~86%. The fleshy mesocarp tastes somewhat sweet, very sweet according to Simpson (1975), but has an exceptionally unpleasant aftertaste. The sugar (su-

crose) content of the mesocarp was determined in the field by means of a Misco Brix Refractometer model 10430VP. Sections ~1 cm thick were taken from near the center of the fruit, the exocarp removed and portions of the mesocarp placed in a small hand-held press. A drop of expressed liquid was placed on the refractometer sensor and the sugar content read in degrees Brix. Inasmuch as Brix degrees are equivalent to percent sugar, we will use the latter term. In 20 randomly selected fruits, collected in early June in the Antelope Valley, Los Angeles County, California, the sugar content averaged 11.6% (10–15%). By early July, a collection of 25 fruits from the same locality had an average sugar content of 14.5% (11–25%). Fruit-to-fruit variation may be explained on the basis that once the fruits have reached their ultimate size, it is visually impossible to recognize their state of maturity; as a result the randomly selected fruits examined represented a collection of mixed maturity. It appears reasonable to assume that liquid expressed from fully ripened *Y. brevifolia* fruits may have a sugar content of more than 20 per cent.

By the time the fruits are ripe, i.e., have reached their maximum sugar content, they have softened due possibly to enzymatic breakdown of cell walls. Although still firm to the touch, the thin exocarp is readily broken by slight pressure and liquid exudes from the breaks. At this stage, the endocarp is green, to some extent comparable to the flesh of a kiwi fruit (*Actinidia chinensis* Planch). The seeds are mature and capable of germination beginning within 24 hours. Later the green fleshy endocarp becomes granular and is changed into a mealy white mass. Standard tests for starch proved negative. Macerated in water, the mealy material tested positive for a small amount of sugar. At this stage, I regard the fruits as having reached a state of *post-maturity*. As fruits age, they continue to soften, often partially splitting along carpel lines and cracks appear in the exocarp, both facilitating release of moisture. Eventually the fruits become hard, dry, spongy, grayish-green to tan or brown-colored bodies described by Trelease (1893) as possessing large bulk and low specific gravity. *The fruits never open spontaneously for the release of the enclosed seeds* (Fig. 3).

SEED DISPERSAL—PRESENT

Numerous explanations of seed dispersal in *Y. brevifolia* have been advanced. Parish (1891) was of the opinion that birds opened the fruits most likely in search of the yucca moth larvae [*Tegeticula synthetica* Riley]. Trelease (1893) referred to them as "tumble fruits" . . . disseminated over the dry sands of the desert by the aid of the strong winds that prevail there, the seeds being liberated ultimately by the breaking of
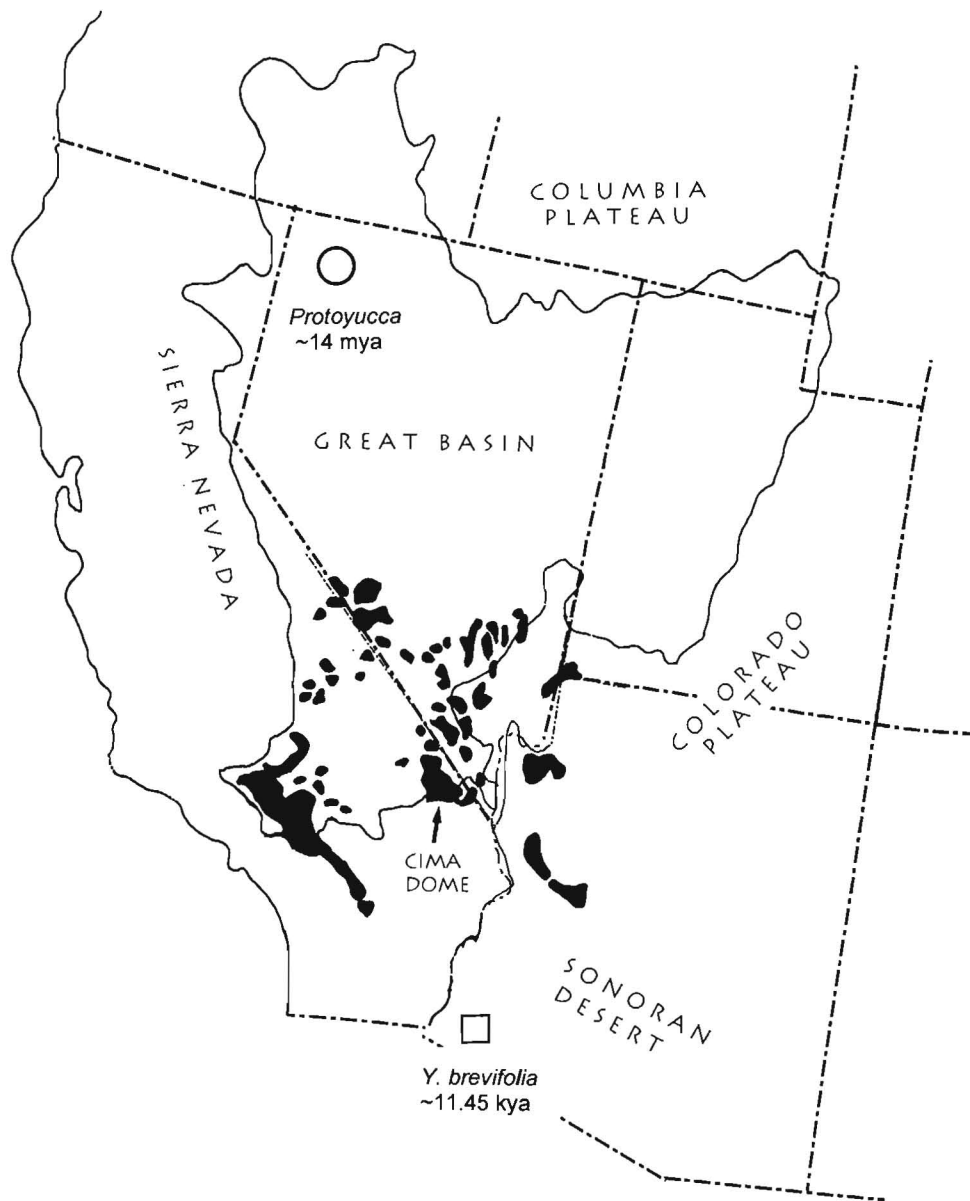
Fig. 2. Distribution of *Yucca brevifolia*. Redrawn from Simpson, 1975. Open circle, distribution of *Protoyucca shadishii,* open square, earlier distribution of *Yucca brevifolia*. Limits of the Great Basin are shown in outline.

the fragile pericarp." Simpson (1975) wrote, "Like the tumbleweed, the fruits may be blown about in the wind." Another author wrote, "Many of the viable seeds are still left [not destroyed by yucca moth lar-vae] to shake free of their papery husks and scatter across the arid earth." The author continued, "viable seeds are blown upon hot, dry winds or are carried afar and dropped by some desert rodent" (Keith 1985). Still another author wrote, "Seeds are dispersed chief-ly by wind, carried by animals or water" (Tirmenstein 1989). According to Simpson (1975) the fruits are clearly adapted for wind dispersal.

In considering seed dispersal, Pijl (1972) formulated a scheme of ecological dispersal classes, a modified portion is shown in Table 1.

Ornithochory

Birds.—Over a hundred years ago H. J. Webber (1895) provided a detailed account of mockingbirds in Florida dispersing the seeds of *Y. aloifolia* L. (NOTE: Where available, common names of animals will be used. Scientific names are shown in Appendix I). In California, foraging Scott orioles utilize Joshua trees for nesting sites and obtain food and moisture from the fleshy fruits (Miller and Stebbins 1964). In Baja California, hooded orioles and ladder-backed wood-peckers feed on the fleshy fruits of *Y. capensis* Lenz. The birds puncture a hole in the thick exocarp and proceed to remove the fleshy pulp with their tongues but do not disturb the cylinders of seed protected by

Fig. 3.   Dried post-mature fruits of *Yucca brevifolia* ssp. *brevifolia*.

Table 1.   Ecological dispersal classes (adapted from Pijl 1972).

Class			Agent
Abiotic			
	Anemochory		Wind
Biotic	Ornithochory		Birds
	Mammaliochory		
		Flying mammals	
			Bats
		Terrestrial mammals	
			Ungulates
			Rodents
			Other

the parchment-like endocarp. There is no evidence that birds disperse seeds of *Y. brevifolia*.

Mammaliochory

Bats.—In the New World, members of the Phyllonycterinae are known dispersing agents of the seeds of many plants (Pijl 1957; Janzen 1983a; Stiles 2000). There are however, no frugivorous bats at present native to the Joshua tree area (Hall 1981; Katherine Hinman pers. comm.).

Ungulates.—From the nature of the fruit of the Joshua tree, it is reasonable to assume that frugivorous or omnivorous terrestrial mammals might be seed vectors. Owing to the size of the fruits, Simpson (1975) proposed that they might be adapted for consumption by large animals. Native ungulates within the geographical range of the Joshua tree include bighorn sheep and mule deer. The fruits of *Y. baccata* Torr. are reported to be a favorite food for bighorn sheep and it seems possible that they would consume fruits of the Joshua tree that were within their reach. The mule deer is the only member of the Cervidae found within range of the Joshua tree and they have been reported as eating the fruits (Keith 1982, 1985).

Introduced ungulates include horses, burros, domestic cattle and goats. Seeds of many species pass through the intestinal tract of horses and remain viable (Korsmo 1911; Janzen 1982, 1983a; Barlow 2000) and horses and burros have been reported as feeding upon Joshua tree fruits (Cronquist et al. 1977). According to a rancher in San Bernardino Co., California, cattle are very fond of the fruits and consume large quantities (Wolf 1945). Cattle are known seed vectors (Janzen 1983b) and it seems reasonable to assume that they (and horses) may at times distribute seed of *Y. brevifolia*. However,

none of the present day ungulates is of a size that would permit them to reach any but the lowest clusters of fruits of *Y. brevifolia*. At present there appears to be no large mammal that may be considered a prime candidate for dispersing seeds of *Y. brevifolia*. As an alternative, consideration must be given to small mammals such as rodents and carnivores.

Rodents.—Sciuridae. Five species of sciurid rodents occur within the geographical range of the Joshua tree. (1) *Mojave ground squirrels* are endemic to four counties in southern California and according to Jameson and Peeters (1988) the fruits of the Joshua tree are its favorite food, with fruiting trees attracting concentrations of the animals. According to Zembal and Gall (1980) the Mojave ground squirrels climb to the top of the tallest Joshua trees, spending daylight hours harvesting the seeds that they then store in deep burrows. (2) *White-tailed antelope squirrels* are widely distributed from Idaho to the tip of Baja California, east to Colorado and New Mexico and northern Arizona. In northwestern Arizona, they are not found south or east of the Colorado River. The animals are omnivorous (Karasov 1982; Belk and Smith 1991) and are known to consume the seeds of *Y. baccata* Torr., *Y. brevifolia* and *Y. schidigera* Roezl ex Ortgies (Bradley 1968). Antelope squirrel store food in deep underground chambers (Bartholomew and Hudson 1961), in crevices or under rocks (Novak and Paradiso 1983; Lenz pers. obs.). The seeds are carried in cheek pouches and Grinnell and Dixon (1919) reported that one animal had seventeen yucca seeds in its pouch. Mojave ground squirrels and antelope squirrels may work the same Joshua tree at the same time. There was, however, never more than a single Mojave ground squirrel in a single tree, but at the same time, there could be up to seven antelope squirrels (Zembal and Gall 1980). According to these authors, in one small area of 0.39 km^2 containing 30 Joshua trees there were 16 Mojave squirrels and 27 antelope squirrels. (3) *California ground squirrels* occur along the Pacific coast from Washington to central Baja California but at present occur only marginally in the range of the Joshua tree.

Although reported to be a ground dwelling species (Jameson and Peeters 1988), the squirrels readily climb to the top of Joshua trees and in some areas destroy large quantities of fruit, consuming both the fleshy pulp and seeds (Lenz pers. obs.). (4) *Round-tailed ground squirrels* are native to eastern California and adjacent parts of Nevada, Arizona and western Sonora where they occupy sandy arid areas. In Arizona, its distribution overlaps that of *Y. brevifolia*. Omnivores, their diet includes a wide range of foods varying from season to season according to availability (Bailey 1931). The squirrels are known to climb trees and are reported to cut peduncles of pine cones allowing them to fall to the ground where the squirrels extract the seeds (Bailey 1931). In some areas, the round-tailed squirrel is sympatric with both the white-tailed and Harris antelope squirrels (Ernst and Mares 1987). (5) *Rock squirrels* are found in southern Arizona, Sonora, and the species reaches its western limit in the Providence Mountains of California. It is widely sympatric with the round-tailed squirrel (Best et al. 1990). Rock squirrels are reported to eat a variety of fruits and seeds, including those of *Yucca* (Bailey 1931) and are known to store acorns, walnuts, and seeds of peaches, plums and apricots (Vander Wall 1990). Normally they do not climb trees (Hoffmeister 1986).

Of the five species, the white-tailed antelope squirrel is the most widely distributed. They are larder-hoarders and wasteful seed predators. At the time they are gathering seeds, the post-mature fruits are dry with a thin brittle exocarp that is easily shattered. The seeds, which a writer from Nevada has likened to small black poker chips, are stacked singly in six cylinders within the dry porous fruits, each cylinder protected by a tough, parchment-like endocarp. As the squirrels gnaw the dry fruits and break the endocarps, seeds are liberated, and those not taken by squirrels are released to fall to the ground, or to be carried by the wind. Examination of soil under and around trees reveals abundant remains of broken fruits as well as many seeds (Lenz pers. obs.).

Rodents.—Cricetidae. Two species of wood rat are found in the geographical range of *Y. brevifolia*; the white-throated wood rat, and the desert wood rat. Both species feed on a wide range of plant species, especially cacti from which they obtain water (Jameson and Peeters 1988). In Baja California Sur desert wood rats readily climb mature plants of *Yucca capensis* and consume the fleshy mesocarp that probably serves as both a source of water and nutrients, however, the animals leave the cylinders of seed intact (Lenz pers. obs.). This same behavior might be expected of the wood rats in the range of the Joshua tree. There appears to be no substantial evidence that wood rats distribute seeds of the Joshua tree.

Rodents are remarkably versatile ecologically and through their ability to climb trees, are capable of reaching fruit clusters high above the ground and out of reach of present day browsing mammals. As we have shown, five squirrels (Sciuridae) are present within the geographical range of the Joshua tree. At least four of them are tree climbers and three of them are known to be yucca seed predators.

The white-tailed antelope squirrel and the Mojave squirrel both harvest seed from fruits on the trees and in doing so accidentally release some seeds that fall to the ground. In the absence of wind-dispersing seed modifications, the Joshua tree seed descent would be a straight glide. However, the Joshua tree world is subject to a great deal of wind, at times of gale force intensity, and as a result the yucca seed shadow would be dependent upon the height of the fruit from the ground and the velocity of the wind. Without seed traps it is impossible to determine how far rodent-released seeds might travel.

Other.—Within the Joshua tree region this includes carnivores such as bears, coyotes and foxes. When available, all carnivores consume at least some juicy or fleshy fruits (Janzen and Wilson 1983) and Stiles (2000) considers them one of the major groups of fruit and seed-eating species of mammals (after primates and bats). There seems, however, to be no account of these animals eating the fruits of the Joshua tree, one reason being that at the time the fruits are ripe they are for the most part out of reach of the animals. The dry post-mature fruits would seem to have little to offer the animals.

Anemochory

The role of rodents in liberating individual seeds from intact fruits has already been discussed (anemochory). At the time when the Joshua tree fruits are ripe, they can be removed from the infrutescence only with considerable effort. On the other hand, the dry post-mature fruits are more easily detached and wind is a factor in the removal of some of the fruits (synaptospermy). Blown about on the ground they eventually come to rest against some barrier. With autumn rains the dry body of the fruit disintegrates, however the enclosed seeds remain together in a single mass. Mature fruits may contain 30–50 seeds and if more than a single seed germinates at a single site this can lead to sibling competition. Evidence that this occurs is revealed by the fact that what often appears to be a young plant with one to three basal branches, will on examination, be found to be two or more individual plants closely appressed. This suggests that they originated from seeds within a single fruit. The plants may or may not be of the same age suggestive of asynchronous germination (Fig. 4). The fact that wind re-

Fig. 4. Two young plants of *Yucca brevifolia*. Originally what appeared to be a single plant with a basal offset when dug was found to be two plants of different ages closely appressed, presumably derived from a single fruit. Antelope Valley. Los Angeles Co., California. Photograph by author.

moves only some of the ripened fruits was noted by Wolf (1945) who suggested that the abundance of dried fruits remaining on the trees might constitute a commercially important source of food for animals and the seeds a source of an edible oil.

Summary

Existing evidence suggests that seeds of the Joshua tree are at present wind disseminated either singly, after release from dried fruits by rodents, or in dried intact fruits. If the above scenario is accepted, we are left with an unanswered question. Why does *Y. brevifolia* allocate so many of its resources to produce large clusters of succulent and nutritious fruits for which there is no market? According to Drury (1998), plants do not invest more energy in their dispersers than they have to. Or, as Barlow (2000) wrote, "Perhaps the fruit is overbuilt for the current mode of dispersal." Is it possible that in the past *Y. brevifolia* had a dispersing agent, or agents, that are no longer present? These questions will be examined in the next section.

SEED DISPERSAL—PAST

In 1990, Tidwell and Parker described a fossil collected in Humboldt Co., northwestern Nevada as *Protoyucca shadishii*. Material consisted of columnar portions of stems as much as 60 cm in diameter and as much as 125 cm long, small branches, leaves, and stem bases with roots attached. After careful anatomical studies and comparisons made with other groups, the authors concluded that overall, the new genus and species had greatest similarities with *Y. brevifolia*. Fruits of *Protoyucca shadishii* are unknown. All living arborescent yuccas have fleshy, nondehiscent fruits and it may be reasonable to assume that *P. shadishii* possessed similar fruits. The fossil specimens were collected in what the authors called the Great Basin Desert and many types of petrified wood have been found associated with *Protoyucca* (Call and Tidwell unpubl.; Tidwell pers. comm.). The sequence of rocks in which the remains were found were dated radiometrically at 14 mya (Bonham 1969), that is, mid-Miocene. There are no Pliocene fossil plant records for Nevada (Sauer 1988).

The following discussion is based on the assumption that arborescent yuccas have had a presence in the Great Basin since at least middle Miocene (15.1–11.2 mya). There is no evidence that ripe fruits of *Y. brevifolia* (not dry post-ripened fruits) naturally fall to the ground. Therefore, a biotic disperser would have had to be one physically capable of reaching the fruits borne in clusters at the ends of branches usually some distance above the ground. There were many large herbivorous mammals in western North America during the Miocene and continuing to the end of the Pleistocene. The Colorado Plateau during the Pleistocene has been referred to as the American Serengeti (Elias 1997); the same may be said of the adjoining Great Basin. Included among the large herbivores were, bison, camels, deer, horses, llamas, proboscideans, pronghorns and ground sloths. We will consider only those that are acknowledged to have been browsers and of a size sufficient for the animals to reach the fruits of arborescent yuccas, these are the camelids, proboscideans and ground sloths.

Camelids.—Conspicuous among the large herbivores roaming western North America during the Miocene were camels that first appeared in North America in middle Eocene (52–43.6 mya) and became the prevalent even-toed ungulates in the Miocene (Webb et al. 1995). From early Miocene (~23.7 mya) to as recent as about nine thousand years ago large herds roamed the western United States.

In America camels experienced autochthonous radiation in the Miocene, reached their peak in the middle Miocene, declined in the Pliocene and became extinct in North America at the end of the Pleistocene (Webb et al. 1995). Of the thirteen recognized genera

of Camelinae (Honey et al. 1998) six were present in the southwest, five of them within the present geographical range of *Y. brevifolia* (Fig. 5). The oldest known camel in the Great Basin was the monotypic *Hesperocamelus,* described from Elko County, Nevada, and later from Kern County, California, and is dated ~18 mya (unless otherwise indicated dates of fossils are from Alroy 2001). Following *Hesperocamelus* was *Aepycamelus,* some of which were huge beasts with extremely elongated stilt-like limbs and long necks clearly adapted for browsing tall trees (Colbert 1955). Lofty as giraffes, they are often referred to as giraffe-camels. The genus *Camelops* is the best known and most widely distributed. *Camelops hesternus,* known as yesterday's camel (Kurtén and Anderson 1980) appeared ~2 mya and was widely distributed throughout the western United States and south into Mexico. A cutoff date for its disappearance has been calculated to be ~8240 ± 960 ya (Mead and Melzer 1989). With their great height, giraffe-camels could easily have reached the fruiting clusters displayed at the tip of branches of an arborescent yucca. The only other camelid that might have been tall enough to pick the fruits was the large-headed llama (*Hemiauchenia macrocephala*) (Dompierre 1995). Somewhat smaller than yesterday's camel, it was larger than the modern llama. However, it is considered a plains-dweller and fed on grass (Kurtén and Anderson 1980).

Present day camels have thin split prehensile upper lips that are capable of selecting individual leaves (Wilson 1989; Dompierre 1995). According to the latter author all were intermediate feeders, i.e., grazers and browsers utilizing all kinds of plant material. As noted earlier, at the time when the fruits of *Y. brevifolia* have their greatest sugar content and contain mature seeds, they are difficult to detach. However, lateral branches are easily removed. A camel could grasp a single fruit and by jerking its head down, easily remove a branch with a number of fruits attached.

A stack of bones does not afford evidence of the behavior of living animals. On the other hand, observations of the behavior of existing relatives may provide a clue to the behavior of their ancestors (Haynes 1991). There is however, a possibility that behavioral patterns may have changed. For observations on the dromedary, hereafter simply, camel, we are indebted to Gauthier-Pilters (1969) who observed the animals in the western Sahara over a period of years. According to the author, the animals are both grazers and browsers. Furthermore, they are efficient feeders that do not overgraze the vegetation and do not degrade desert plant life. While feeding they keep moving and may cover 5 km in 2.5 hours taking only a few bites from any one plant before moving on. In foraging, they grasp vegetation between their long, prehensile lips and either pull off leaves from a branch or clip
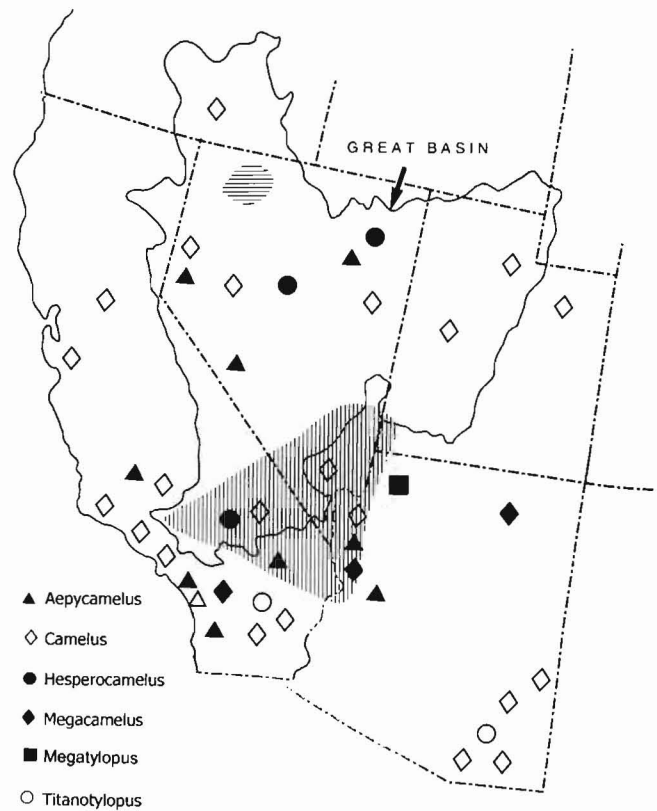

Fig. 5. Representative distribution of fossil sites by counties of western North American genera of camels. Sources: Graham and Lundelius, Jr. 1994; Janis et al. 1998. Vertical shading, present distribution of *Yucca brevifolia,* horizontal shading, distribution of *Protoyucca shadishii.*

off an entire twig, individual fruit or flower, and the animals are able to browse plants to a height of 3.5 m. The extinct *Camelus hesternus,* one of the smallest of the giant camels, was 20% larger than the present dromedary (Kurtén and Anderson 1980) and could in all probability browse to over 4 m.

Mammals have developed a wide range of nutritional and ecophysiological adaptations to diverse habitats and types of nourishment (Wilson 1989). Herbivorous mammals have two major sites of digestion and fermentation of ingested food. They are the forestomach (or foregut) and hindgut (Wilson 1989; Stevens and Hume 1995). Although a foregut fermenter, camelids possess a complex three-compartment stomach. There is a relatively large opening between the first and second compartments and a very small opening between the second and third (Wilson 1989; Stevens and Hume 1995). The modern camel cannot pass an object from the second to the third compartment that is wider than 5 mm (Barlow 2000), however giant camels may have been able to pass larger material. In the process of chewing its cud (remasticating) many seeds would be destroyed. If, however, some of the oil-rich yucca seeds remained intact they could pass into the third compartment and unless destroyed there,

● Gomphotherium
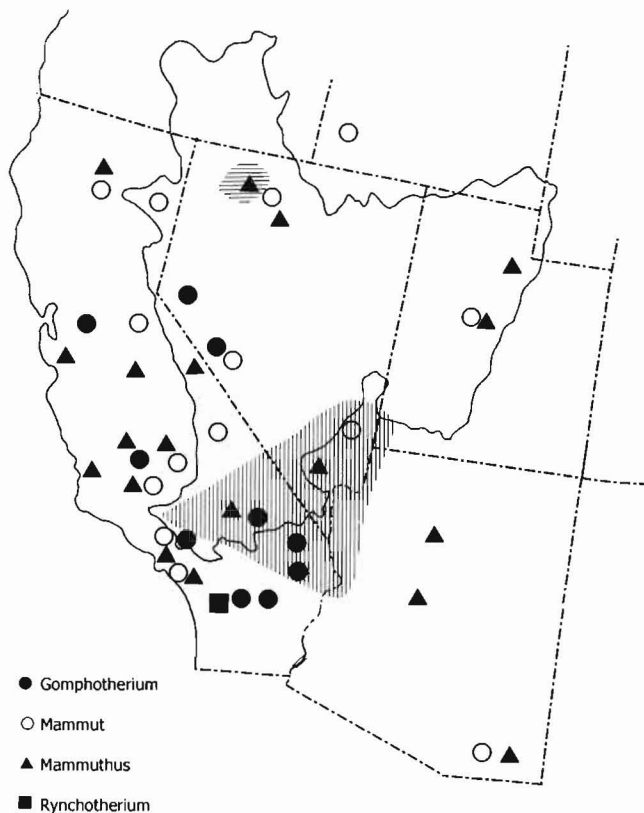
○ Mammut

▲ Mammuthus

■ Rynchotherium

Fig. 6. Representative distribution of fossil sites by counties of western North American genera of proboscideans. Sources: as for Fig. 5. Vertical shading, present distribution of *Yucca brevifolia*, horizontal shading, distribution of *Protoyucca shadishii*.

would eventually be eliminated. Camel dung consists of distinctly shaped pellets, tacky when first produced but quickly drying (Barlow 2000). Any viable seed would be imprisoned in the hard mass until it was released by the forceful breaking of the pellet or its natural disintegration. Mead et al. (1986) found that the dung of the extinct *Camelops* contained only finely chewed material. This in itself does not rule out the camels since yucca fruits are seasonal and Mead's material may not have been fully representative of the animal's diet throughout its range. As foregut fermenters, desert ruminants are adapted to poor quality food in open biomes (Wilson 1989) and as potential seed dispersers, are as a class, inferior to hindgut fermenters (Barlow 2000).

Information on the role of camels as seed dispersers is remarkably limited. Ridley (1930) covers their activities in two short paragraphs devoted mostly to camel poisoning from eating fruits of *Lycium barbarum* [Solanaceae]. Janzen (1986) using as an example *Y. filifera*, (identified as *Y. decipiens*) suggested that *Yucca* [sect. *Yucca*?] might have been favored by fruit harvest from the tall inflorescences [infructescenses] by camelids. In her exhaustive study, Gauthier-Pilters (1969) did not address seed dispersal and her bibliography has no entries regarding seeds or dispersal.

Proboscideans.—Proboscideans were the largest land mammals in North America during the late Cenozoic and America was a major center of evolution of the group (Madden 1987). Lambert and Shoshani (1998) recognize three families in the North American fossil record; the Gomphotheriidae, known as gomphotheres, the Mammutidae, mastodons, and the Elephantidae, mammoths. The Gomphotheriidae was the most successful of the proboscideans, surviving from middle Miocene to the end of the Pleistocene and reaching all continents except Antarctica and Australia. North America was a major center of autochthonous evolution of the group (Lambert and Shoshani 1998). The genus *Gomphotherium* consists of 15 species and was the most widely distributed (Fig. 6) (Lambert and Shoshani 1998). Members of the genus first entered North America from Asia by way of the Bering Straits during the middle Miocene (16.3–10.4 mya) and rapidly became widespread and abundant throughout the continent, and as far south as Honduras. By the end of the Miocene they had become rare and in the early Pliocene (5.2–3.4 mya) are known in the United States only from a single site in Florida (Lambert and Shoshani 1998). Gomphotheres were medium-sized, short-legged animals with teeth that suggest that they were browsers that consumed significant quantities of coarse, woody vegetation much as African elephants do today (Lambert 1992). Although nothing is known about the gomphothere's gastrointestinal tract, that of its extant relative, the elephant, has a simple, relatively narrow stomach (Stevens and Hume 1995) and is a hindgut fermenter (Barlow 2000). In feeding, the African elephant uses the prehensile tip of the trunk as a hand with which single blades of grass may be selected and small berries may be individually chosen and plucked from trees (Sikes 1971; Haynes 1991).

The gomphotheres were followed by mammuts (Mammutidae) with two genera, *Zygolophodon* and *Mammut*. The latter consists of two groups, *M. americanum*, and *M.* sp. (Lambert and Shoshani 1998). The distribution of *Mammut* in the West is shown in Fig. 6. Members of the genus appeared in the Great Basin ~7–6 mya and persisted until ~2.4–1.8 mya (Janis et al. 1998). In the western United States they continued throughout the Pleistocene to about 13,000 years ago (P. S. Martin pers. comm.). Large animals with long tusks they are estimated to have had body masses of from ~2400–3300 kg (Alroy 2001).

The genus *Mammuthus* consists of three species (Graham and Lundelius 1994) the best-known being *Mammuthus columbi*, the Columbian mammoth, with an estimated body mass of 8730 kg (Alroy 2001). Mastodons and mammoths coexisted to around 13,000 ybp (P. S. Martin pers. comm.). Widely distributed throughout much of North America the Columbian mammoth extended south at least to Honduras. Due to

their great size Colombian mammoths could easily have reached the fruiting clusters at the tips of branches of an arborescent yucca. The Columbian mammoth first appeared ~1 mya (Alroy 2001) and persisted to the end of the Pleistocene or early Holocene (<10 kya) (Madden 1987). It is assumed that the behavior of the mastodons was similar to that of their living relatives (Oliver 1982).

Surviving African elephants have an exceptionally broad habitat tolerance and are encountered in near deserts, savannas, woodlands, and tropical forests (Haynes 1991). Carbon isotopic analyses of dentinal hydroxyapatite of the teeth of both mastodonts [*Mammut* + gomphotheres] and mammoths confirm that both groups had generalized feeding habits that included leaves, grasses, twigs, fruits, and nuts (Koch 1988). There is, according to Haynes (1991), no good reason to think that mastodonts and mammoths had different food processing systems. Both the African and Asian elephants today survive on a wide variety of foods that is eaten in enormous quantities due to the fact that the animal's digestive tract is relatively inefficient in converting plants into energy (Mitchell 1916; Benedict 1936). As nonruminants, they are hindgut fermenters (van Hoven and Boomker 1985) where nutrients are quickly extracted, with the digestive time being short, ~24–54 hours (Bax and Sheldrick 1963). This would have been an advantage to the Joshua tree (or *Protoyucca*?) where it has been shown that seed from mature fruits may begin germination within 24 hours. Elephant's boluses weigh from 1–2 kg and are 15–20 cm in size. Generally requiring some time to decompose they provide included seeds time to germinate and become established. Lacking underground water storage organs, young *Y. brevifolia* plants rapidly develop a deep root system. Primary roots may be as much as 15 cm long before a seedling leaf appears above ground (Lenz unpubl.) and Simpson (1975) reported that ninety-five day old seedlings had primary roots as much as 23 inches (58 cm) long. Fecal material acts a fertilizer with the result that in many instances seedlings are more vigorous than those emerging from undigested seed (Traveset and Verdú 2002). Might proboscidean boluses have earlier played the role that nurse plants do today? Elephants are known distributors of seeds of a wide range of plants (Ridley 1930; Pijl 1972; Janzen and Martin 1982; Barlow 2000), and Stiles (2000) considers living elephants the fourth important class of fruit and seed-eating mammals (after primates, bats and carnivores).

Ground sloths.—Laudermilk and Munz (1934, 1938) concluded that Shasta ground sloths, the smallest of the North American ground sloths, were preeminently yucca feeders. Since their pioneering work, others have examined sloth dung and present consensus is that the

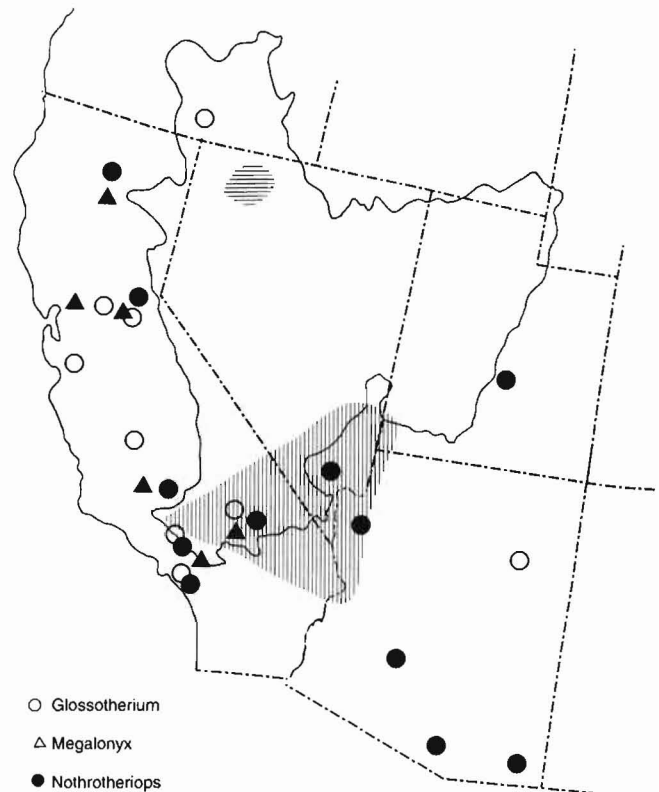O Glossotherium
△ Megalonyx
● Nothrotheriops

Fig. 7. Representative distribution of fossil sites by counties of western North American genera of ground sloths. Sources: as for Fig. 5. Vertical shading, present distribution of *Yucca brevifolia*, horizontal shading, distribution of *Protoyucca shadishii*.

Shasta sloth was an opportunistic feeder that utilized a wide range of plants (Martin et al. 1961; Hansen 1976; Thompson et al. 1980; Poinar et al. 1998). The animals were about the size of a black bear, with relatively small heads, prehensile lips, and a long neck. The forelimbs were long and slender and terminated with extremely long claws (Kurtén and Anderson 1980). Although the sloth may at times have rested upright with the large, heavy tail providing balance, they would not have been able to reach any but the lowest fruits of the Joshua tree. The Shasta sloth most likely fed upon plants near the ground (Elias 1997). If so, it appears reasonable to assume that rather than feeding on the fruits of the arborescent *Y. brevifolia* they may have fed on fruits of the lower growing *Y. baccata* and *Y. schidigera* and may have been a seed-dispersing agent for those species. The Shasta ground sloth was widely distributed from Alberta to central Mexico (Fig. 7) and was originally described from San Diego County, California, and is dated ~3 mya (Kurtén and Anderson 1980). They are believed to have become extinct ~11 kya (Thompson et al. 1980).

Two other ground sloths roamed the southwest during the Pleistocene, Harlan's ground sloth, and Jefferson's ground sloth (Fig. 7). Harlan's sloth, smaller than the mastodons but with the bulk of a rhinoceros, has been described as a massive and powerfully built an-

imal standing as much as 3.5 m tall with a massive chest, short neck and enormous forelimbs, stout hind limbs, powerful claws and a stout tail. Thought to have been clumsy and slow moving, they were widely distributed from Oregon to Florida where they appear to have been very common. Stock (1925) reported that fifty five specimens had been collected from the La Brea tar pits in Los Angeles. Harlan's sloth first appeared ~2 mya (Alroy 2001). In southern California, they are known only from Kern, Los Angeles and Orange counties. They are unknown from Nevada, and in Arizona only from Navajo County (Graham and Lundelius 1994). The fossil record does not show that they were within the present distributional range of the Joshua tree. The abundance of fossils in southern California, and in Florida, suggest that Harlan's sloth may have been a creature more common in coastal than inland areas. It appears to be a poor candidate as a seed disperser for the Joshua tree, but it cannot be ruled out as a potential disperser of seeds of the moderate size *Y. schidigera,* common today in southern California and northern Baja California. A terminal date of ~13.89 kya has been given for the species (Kurtén and Anderson 1980).

Jefferson's ground sloth has been described as about the size of an ox, intermediate between the Shasta and Harlan's sloths. More widely distributed in eastern United States, fossils have been found in numerous locations in southern California, mostly in Kern and Los Angeles counties. (Graham and Lundelius 1994). From fossil records, it appears not to have entered the area occupied by the Joshua tree. The species first appeared ~2 mya and a questionable terminal date of 9400 ± 250 years ago is given for the species (Kurtén and Anderson 1980).

Summary.—Of the three classes of megaherbivores considered, we will eliminate ground sloths from further consideration. Although they may have been active in the distribution of seeds of lower-growing yuccas such as *Y. baccata* and *Y. schidigera,* they arrived only during the Pleistocene long after arborescent yuccas were established in the region.

Both camels and proboscideans were in the Great Basin during the Miocene, and both consisted of species whose heights would have made it possible for them to reach fruiting clusters on tall plants. Both groups possessed specialized mouthparts that permitted the animals to select and remove individual fruits and both were highly adaptable and capable of utilizing a wide range of foods including coarse, woody plant material. Based on living relatives, the gastrointestinal tracts of the two groups were notably different. Camels have a complex three-compartment stomach whereas elephants have a large rather simple stomach. As a ruminant, camels remasticate their food to

the point where it can pass a very narrow opening between the second and third compartments of the stomach. The elephant's digestive tract is inefficient in converting plants to energy and for that reason they consume large quantities of material, much of which is passed undigested within a relatively short period. Camels are foregut fermenters; proboscideans are hindgut fermenters. As a class, the former is considered inferior as potential seeds dispersers. Elephants are known seed dispersers for many species; camels are not. Based on present knowledge, the nod must go to the proboscideans as possibly the most important class of seed dispersing agents for the early arborescent yuccas of the Great Basin. Due to their early arrival in North America the gomphotheres may have been the most important.

DISCUSSION AND CONCLUSIONS

Existing evidence suggests that over the period of time arborescent yuccas have been a presence in the Great Basin they have had two modes of seed dispersal: biotic (megaherbivores) and abiotic (wind). With the termination of the megaherbivores at the end of the Pleistocene, *Y. brevifolia* lost its market for sugar (as well as water and other nutrients). Today the fleshy stage of the fruit can be considered baggage for which the plants have no use; in fact, it is a liability in the sense that in a semiarid land it ties up large quantities of water.

From the viewpoint of *Y. brevifolia,* how effective is wind as an agency of seed dissemination? Seeds of the Joshua tree lack a marginal wing, are thicker and heavier than those of wind disseminated species (sect. *Chaenocarpa*) and are not adapted for long distance dispersal by air currents. The distance that diaspores of *Y. brevifolia* may be carried by wind is unknown but present evidence from field observations suggests that it is limited. In the western portion of the Antelope Valley (Los Angeles County) virgin yucca savanna occurs in a mosaic-like pattern with areas cleared for agriculture as much as a century ago and later abandoned, alternating with virgin stands of *Y. brevifolia.* My observations have been that young plants (cluster of leaves, no stem) or juvenile plants (with stem but unflowered) are found in limited numbers as much as 151 m from potential seed donors (Fig. 8). In Lanfair Valley, California (San Bernardino County), also an area previously cleared and abandoned, the greatest distance was 251 m (Fig. 9). In both areas recruits are of mixed ages. No attempt was made to search for seedlings having only a few grass-like leaves concealed within the protection of a nurse plant.

A half-century ago J. M. Webber (1953) wrote that he considered the future of *Y. brevifolia* "very dim," and following 20 years of observation at three sites—
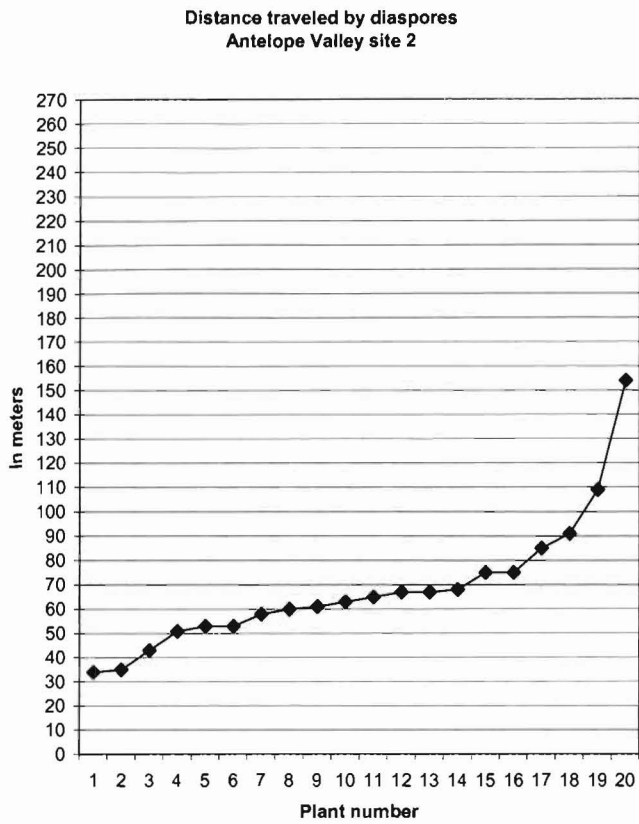
**Distance traveled by diaspores
Antelope Valley site 2**

Fig. 8. Distance traveled by diaspores, Antelope Valley, site 2, Los Angeles Co., California.

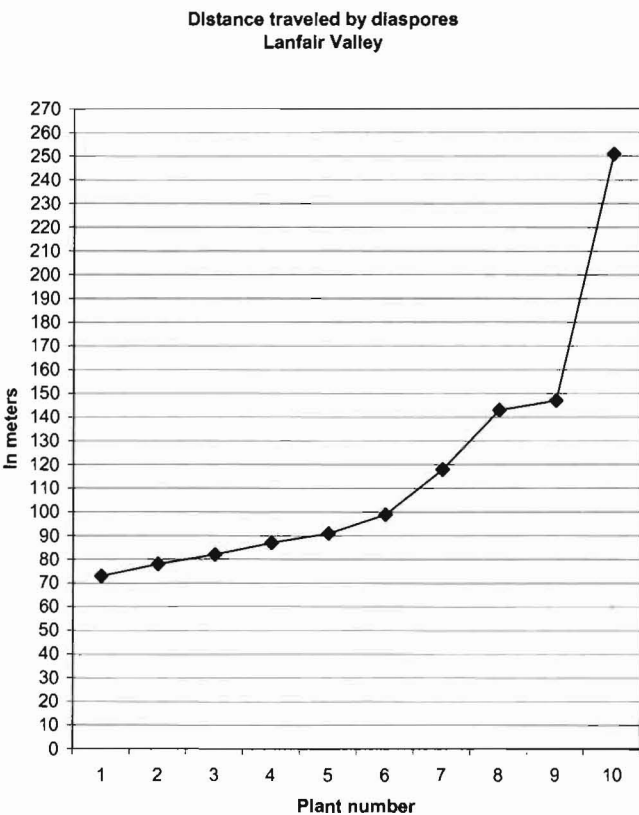**Distance traveled by diaspores
Lanfair Valley**

Fig. 9. Distance traveled by diaspores, Lanfair Valley, San Bernardino Co., California.

Fig. 10. Young plant of *Yucca brevifolia* plant destroyed by black-tailed jackrabbits. Lanfair Valley, San Bernardino County, California. Photograph by author.

two in California and one in Nevada—Comanor and Clark (2000) stated that "no recruitment was evident." This was based on the fact that they had only found two germinated seedlings during their study. In all populations I have observed, including those at the species' geographical limits in Nevada (Goldfield), Arizona (Hualapai Valley) and California (Joshua Tree National Park and Antelope Valley) I have found young and juvenile plants in limited numbers. I did not search for seedlings that would have been concealed within the protection of a nurse plant. In the Lanfair Valley recruitment is low in part due to predation by black-tailed jackrabbits (Patrick Griffith pers. comm.). When young plants reach the stage where they extend beyond the protection of the nurse plant they become vulnerable to predation by rabbits who remove the leaves from the tip of the plant, dropping them on the ground and then proceed to eat the soft young growing tip (Fig. 10).

I regard the current mode of seed dispersal, i.e. wind, as in all probability adequate to sustain the species within, or near, the limits of its present geograph-

ical range under existing environmental conditions, or during incremental changes in climate over time. During major and sudden climatic shifts, *Y. brevifolia* would be unable to 'jump' to distant sites where conditions might be more favorable. Evidence is mounting that during the past few million years there have been many significant climatic shifts and that in some instances these changes took place suddenly rather than incrementally (Adams et al. 1999). Today Joshua trees in many areas appear physically stressed in all probability due to less than optimum growing conditions. An exception is the robust population on the Cima Dome, a much-studied, ancient anomalous geological feature of the Mojave Desert (Norris and Webb 1990) for which no climatic data is available.

Even if the species were able to make sizeable geographical leaps, it would be constrained by the overruling fact that in a single generation it could move only the distance a pollinating moth can fly. The reasoning being that although successfully colonizing a new area and reproducing asexually, the plants without the aid of the pollinating moth would be unable to reproduce sexually and therefore unable to permanently hold new territory. This constraint would also have applied to an earlier period when megaherbivores distributed the seed. Based upon the genetic variation within the populations of the moths that pollinate *Y. baccata* (*Tegeticula baccatella* Pellmyr) Leebens-Mack et al. (1998) suggested that the moths might travel considerable distances. Massey and Hamrick (1999) reported that pollen of *Y. filamentosa* moved from 6 to 293 m (mean 118 m), and Marr et al. (2000) reported that in the same species pollen moved not more than 50.6 m. My limited experience in introducing *Tegeticula mojavella* Pellmyr into a previously moth-free area is that moths may fly as far as 117 m.

With its obligate yucca/yucca-moth mutualism, *Y. brevifolia* appears to have sealed its fate when it conferred exclusive rights for the distribution of its pollen to a single agent. This would be a high price to pay for pollination. All other members of the Agavaceae allocate their pollen to a multiplicity of dispersing agents. As one author wrote, "Perhaps if yuccas could emerge from the cul-de-sac of moth specialization, they would profit from inviting a wider range of pollinators" (Feinsinger 1983). In spite of the two burdens the species bears, *Y. brevifolia,* and/or its predecessor *P. shadishii,* has been a successful part of the western American scene since at least the Miocene. Its resilience has permitted it to successfully endure past environmental revolutions and the loss of its principal seed-dispersing agent, or agents. However, depending upon the intensity and duration of global warming its long-range survival may depend upon the availability of a refugium.

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APPENDIX I

Scientific Names of Animals Mentioned in Text

Alpaca—*Lama pacos*
Bear, black—*Ursus americanus*
Camel—*Camelus bactrianus*
Coyote—*Canis latrans*
Deer, mule—*Odocoileus hemionus*
Dromedary—*Camelus dromedarius*
Fox, grey—*Urocyon cinereoargenteus*
    kit—*Vulpes macrotis*
Guanaco—*Lama guanicoe*
Llama—*Lama glama*
Oriole, Scott—*Icterus parisorum*
    Hooded—*Icterus cucullatus*
Mockingbird—*Mimmus polyglottos*
Rabbit, black-tailed jackrabbit—*Lepus californicus*
Rat
    desert wood—*Neotoma lepida*
    white-throated wood—*Neotoma albigula*
Sheep, bighorn—*Ovis canadensis*
Sloth
    Shasta—*Nothrotheriops shastensis*
    Harlan—*Glossotherium harlani*
    Jefferson—*Megalonyx jeffersonii*
Squirrel
    antelope—*Ammospermophilus leucurus*
    California—*Spermophilus beecheyi*
    Mojave—*Spermophilus mohavensis*
    rock—*Spermophilus variegatus*
    round-tailed—*Spermophilus tereticaudus*
Vicuña—*Vicugna vicugna*
Woodpecker, ladder-backed—*Picoides scalaris*