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Summary. Frugivory by extinct horses, gomphotheres, ground sloths, and other Pleistocene megafauna offers a key to understanding certain plant reproductive traits in Central American lowland forests. When over 15 genera of Central American large herbivores became extinct roughly 10,000 years ago, seed dispersal and subsequent distributions of many plant species were altered. Introduction of horses and cattle may have in part restored the local ranges of such trees as jicaro (*Crescentia alata*) and guanacaste (*Enterolobium cyclocarpum*) that had large mammals as dispersal agents. Plant distributions in neotropical forest and grassland mixes that are moderately and patchily browsed by free-ranging livestock may be more like those before megafaunal extinction than were those present at the time of Spanish conquest.

New World terrestrial biotas have long contained a rich fauna of large herbivores. During the Pleistocene, until around 10,000 years ago, the North American mammalian megafauna was comparable in its number of genera of large mammals (those exceeding 40 kilograms in adult body weight) to that of Africa in historical time (*1*). Although quantitative estimates of prehistoric biomass cannot be obtained directly from the fossil record, the high carrying capacity for domestic mammals of New World ranges—a capacity similar to that of African game parks—indicates that the Pleistocene biomass of native New World large herbivores was high. Martin (*2*) estimated an average preextinction biomass for unglaciated North America north of Mexico at 21 animal units per square kilometer or 28.2×10^6 metric tons on 7.8×10^6 square kilometers (1 unit = 1 cow plus a calf or 1 horse = 449 kilograms). While patchily distributed, the megafaunal biomass of lowland Central America must have been comparable, exceeding 50 animal units per square kilometer on favorable sites.

The number of species of large Central American Pleistocene herbivores in Neogene deposits of the last 10 million years greatly exceeds the number present in the past 10,000 years. Tapir, deer, peccaries, monkeys, and capybara occur as Pleistocene fossils, but the remains of gomphotheres (mastodon-like proboscidians), ground sloths, glyptodonts, extinct equids, *Mixotoxodon*, *Toxodon*, and other extinct large herbivorous animals (Table 1) are more common. If Neotropical ecologists and evolutionary biologists wish to determine who eats fruit, who carries sticky seeds, and who browses, grazes, tramples, and voids that segment of the habitat that would have been within reach of a variety of megafaunal trunks, tusks, snouts, tongues, and teeth, the missing megafauna must be considered.

There are prominent members of the lowland forest flora of Costa Rica whose fruit and seed traits can best be explained by viewing them as anachronisms. These traits were molded through evolutionary interactions with the Pleistocene megafauna (and earlier animals) but have not yet extensively responded to its absence. We first examine this evolutionary and ecological hypothesis by reconstructing the interaction between an extant palm and its Pleistocene megafauna. Without concerning ourselves with what caused the Pleistocene megafaunal extinctions (*3*), we are considering a portion of what happened when roughly three-quarters of all the species and individuals of large mammals were suddenly removed from a dry tropical region and its adjacent rain forests. The present-day analogy is a tropical, forested African habitat stripped of its elephants, rhinoceroses, zebras, elands, bush pigs, and other large herbivores and left alone for 10,000 years.

We focus on the trees that did not go extinct when their dispersal agents were removed. We do this because (i) tree-disperser interactions are not so tightly coevolved that a reasonable natural history consequence is extinction of one immediately following extinction of the other; (ii) if there is a large extinct Pleistocene megaflora in tropical America, it has so far escaped detection by paleobotanists; (iii) the plants that did go extinct cannot be directly studied; and (iv) we are confronted with a number of puzzling fruit and seed traits whose mystery disappears when interpreted in the light of the extinct Pleistocene megafauna. Although megafaunal extinction resulted in

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major changes in intrahabitat plant species composition and population traits, 10,000 years is too short a time to expect all the surviving trees to have come to a new evolutionary equilibrium with the surviving animals and other plants.

A Reconstruction of the Fruiting of *Scheelea* 12,000 Years Ago

We shall reconstruct an event from the Costa Rican lowlands about the time a portion of the megafauna vanished. Toward the end of the dry season in the Pacific coastal plain, at a time when nutritious forage is scarce, there is the major peak in ripe fruit fall from the large forest palm *Scheelea rostrata*. In the dense riparian palm groves and upland mixed forest, the yellow egg-sized drupes fall by the thousands. The fruit fall attracts a herd of five gomphotheres (*Cuvieronius*), members of the family Gomphotheriidae and more closely related to the extinct North American mastodonts (*Mammut*) than to mammoths (*Mammuthus*) (*4*). They forage here daily and consume about 5000 *Scheelea* fruits per day. The hard nut wall (bony fruit endocarp) protects the large soft seeds from the gomphotheres' massive molars and most of the nuts are defecated intact. Below most palms, the ground is picked clean of the fallen fruit. The palm groves and individual palms are connected by well-traveled trails along which small piles of defecated *Scheelea* nuts are common. Such piles of nuts are also scattered about in other areas where the gomphotheres browse, such as in tree-falls, along river banks, and at forest edges.

Nut-rich dung is frequented by agoutis (*Dasyprocta punctata*) and other small rodents that remove the nuts. They gnaw some open and bury others, which are disinterred when food is scarce. Occasionally, when an agouti finds an intact *Scheelea* fruit, it eats the oily sweet pulp and discards the nut. The palm fruits that escape the gomphotheres and agoutis are eaten by tapirs (*Tapirus bairdii*) and collared peccaries (*Tayasu tajacu*). These animals chew off the pulp and spit out the hard nuts. Some *Scheelea* fruits and nuts are taken by squirrels (*Sciurus variegatoides*) which prey on the seeds.

Insect seed predators (adult bruchid beetles) oviposit on exposed nuts in the gomphothere dung. The larvae destroy virtually all the seeds in the nuts left on the ground surface. By ovipositing on nuts before the rodents get them, these insects even kill many of the seeds in the nuts buried by rodents.

The palm population occurs in riparian vegetation, dry hillsides, and wooded patches in grassland and is largely main-

Fig. 1. Fruits (all to the same scale) in Santa Rosa National Park, Guanacaste Province, Costa Rica, that were probably eaten by Pleistocene megafauna: (A) *Crescentia alata* (Bignoniaceae), (B) *Enterolobium cyclocarpum* (Leguminosae), (C) *Sapranthus palanga* (Annonaceae), (D) *Annona purpurea* (Annonaceae), and (E) *Acrocomia vinifera* (Palmae) (*19*). The white portion of the rule in (B) is 15 centimeters long.

tained by the seed input from the gomphothere dung. A seedling commonly appears many kilometers from its parent yet in the vicinity of conspecific adults. There are even adults in habitats where seedlings have extremely low survival probabilities because the gomphotheres generate repeated palm recruitment attempts in them. Many seeds are killed by seed predators, and most seedlings grow from seeds that were missed by both bruchids and agoutis because they were deeply buried in dung or were carried far from the concentrations of seed predators near the parent trees. Also, the rodents fail to retrieve some of the nuts they bury. The fruit phenology (that is, the timing of fruit fall within the day and season), fruit nutrient content, nut shape and hardness, seed crop size, germination timing, and other reproductive traits are molded and maintained by complex interactions in which the gomphothere, with its huge stomach, massive molars, and peripatetic behavior, plays a central role.

Then the gomphotheres are gone. The palm fruits fall as usual; in a month as many as 5000 accumulate below each fruit-bearing *Scheelea* palm. The first fruits to fall are picked up by agoutis, peccaries, and other animals that are soon satiated. As the pulp rots off fallen fruits beneath the parent palm, the bruchids oviposit on virtually all of the exposed nuts. The bulk of the seeds perish directly below the parent. Even if they escape the predators, the seedlings from the undispersed seeds are overshadowed by an adult conspecific, one of the strongest competitors in the habitat. In the next century the distribution of *Scheelea* begins to shrink. In several thousand years the local distribution of *Scheelea* has reached a new equilibrium

Table 1. Missing large herbivores of Central America.

Scientific name	Common name	Size in animal units (1 = 440 kilograms)	Habitat	Food	Origin of fossil record
Edentata					
Megatheridae					
Eremotherium (including *Megatherium*)	giant ground sloth	8	Lowland tropical forest, savanna	Leafy browse (*39*)	Guatemala (*40*), Panama (*41*)
Mylodontidae	mylodont ground sloth	2 to 4	Savanna	Grass (*42*), browse (*43, 44*)	Guatemala (*40*), Venezuela (*45*)
Megalonychidae	megalonychid ground sloth	1 to 2	Forest	Browse	Nicaragua (*46*)
Dasypodidae					
Pampatherium	giant armadillo	1 to 2	Savanna	Omnivore (terrestrial)	Venezuela (*45*)
Chlamytherium					Guatemala (*40*)
Glyptodontidae					
Glyptodon	glyptodont	1 to 2	Arid lowland tropics, warm temperate	Grass (*23*), fruit, carrion	Venezuela (*45*), Guatemala (*40*)
Rodentia					
Hydrochoeridae					
Neochoerus	giant capybara	0.3	Riparian forest	Riparian and aquatic plants	Venezuela (*45*)
Carnivora					
Ursidae					
Arctodus	extinct bear	1 to 1.5	Forest, savanna	Meat, fruits, foliage	Venezuela (*45*)
Tremarctos					
Notoungulata					
Toxodontidae					
Toxodon	toxodon	3	Savanna	Grass, low browse	El Salvador (*47*), Nicaragua (*46, 48*)
Liptoterna					
Macraucheniidae					
Macrauchenia	macraucheniops	2	Savanna	High browse	Venezuela (*45*)
Proboscideae					
Gomphotheriidae					
Haplomastodon	gomphothere	5 to 8	Tropical forest, savanna	Fruits, browse	El Salvador (*47*), Brazil (*49*)
Cuvieronius					Costa Rica (*50*), Venezuela (*51*)
Elephantidae					
Mammuthus	mammoth	10 to 15	Forest, savanna	Grass, browse	El Salvador (*47*)
Perissodactyla					
Equidae					
Equus (*Amerhippus*)	native horse	1	Savanna, forest edge	Grass, browse, fruits	Central America (*23*), Guatemala (*40*), Nicaragua (*48*), Costa Rica (*19a*), Venezuela (*45*)
Artidactyla					
Tayassuidae					
Platygonus	flat-headed peccary	0.3	Savanna, forest edge	Grass, browse, fruits	Mexico (*52*)
Camelidae					
Paleolama	extinct llama	0.7	Savanna	Grass, low browse	Venezuela (*45*)
Bovidae					
Bison	extinct bison	1	Savanna, forest edge	Grass, low browse	Guatemala (*40*), Nicaragua (*48*)

pattern that involves fewer habitat types and a lower density of adult trees. The palm grows only in those microhabitats so favorable that recruitment occurs with minimal seed disperal and escape from seed predators.

Now enter the biologists, assuming that they are studying a coevolved system that approximates an evolutionary equilibrium. They search the morphological and behavioral features of the existing biota for adaptive meanings. They study *Scheelea* nut wall thickness and hardness (*5*), size of fruits and dispersal agents (*6, 7*), the ratio of one- to two- to three-seeded nuts (*6, 8*), the spatial pattern of seed predation (*9*), fruiting phenology (*5, 9*), seed predator satiation (*5, 6*), and the balance between the fruit pulp reward and the seed content reward to the foraging rodent (*10*). These investigators notice the huge surplus of fallen nuts that remain directly below the parent *Scheelea* and attribute it to contemporary removal of dispersers by hunters or simply poor adjustment of seed crop size to the disperser guild. If they were working in Africa, however, they would notice the *Scheelea*-elephant interaction; in Central America they do not consider the former *Scheelea*-gomphothere interaction. The investigators attend only to the living fauna, although they take care to study native, not introduced, animals in a seemingly natural habitat.

Researchers have regarded nut wall thickness as an evolutionary adaptive response by *Scheelea* to the drilling abilities of bruchid larvae and the gnawing abilities of rodents. The main selective pressure determining nut wall thickness, however, could well have been the crushing force of a gomphothere's molars, and bruchids and rodents might simply have evolved to where they could penetrate this defense. The researchers assumed that the reward of fruit pulp should exceed the work expended by a rodent to get at the edible seed minus the value of that seed; throughout most of the evolutionary history of *Scheelea*, however, terrestrial rodents may have gotten fruit pulp only rarely. Coevolution of rodents and *Scheelea* fruits was assumed; the alternative hypothesis was not considered; the rodent is simply making use of a food source that was suddenly plentiful because of Pleistocene megafaunal extinction. Biologists did not suspect that flowering schedules, plant heights, leaf replacement rates, fruit crop size and phenology, or even the genetic structure of a palm population could now be seriously anachronistic if it was evolved to match the habitats occupied and type of population distribution pattern that is generated by dispersal through an extinct wide-ranging large mammal. If the fruiting traits of *S. rostrata* are now in major part anachronistic, as we suggest, then much of its interaction with present-day animals may hardly be evolved, to say nothing of coevolved (*11*).

Table 2. Native trees and large shrubs of lowland Pacific coastal deciduous forests in or near Santa Rosa National Park, Guanacaste Province, Costa Rica (*19*), whose seeds were probably dispersed by extinct megafauna.

Family	Scientific name	Common name
Anacardiaceae	*Spondias mombin*	jobo
	Spondias purpurea	jobo
	Spondias radlkoferi	jobo
Annonaceae	*Annona purpurea*	soncoya
	Annona holosericea	soncoya
	Annona reticulata	anona
	Sapranthus palanga	palanco
Bignoniaceae	*Crescentia alata*	jicaro
Bromeliaceae	*Bromelia karatas*	piñuela
	Bromelia penguin	piñuela
Ebenaceae	*Diospyros nicaraguensis*	persimmon
Euphorbiaceae	*Hippomane mancinella*	manzanillo
Leguminosae	*Acacia farnesiana*	huisache
	Andira inermis	almendro del monte
	Caesalpinia coriaria	divi divi
	Dioclea megacarpa	ojo de buey
	Enterolobium cyclocarpum	guanacaste
	Hymenaea courbaril	guapinol
	Pithecellobium mangense	
	Pithecellobium saman	cenizero
	Prosopis juliflora	mesquite
Malpighiaceae	*Bunchosia biocellata*	cerezo
	Byrsonima crassifolia	nance
Moraceae	*Brosimum alicastrum*	ramon
	Chlorophora tinctoria	mora
	Ficus spp.	higo, fig
Palmae	*Acrocomia vinifera*	coyol
	Bactris guinensis	biscoyol
	Bactris major	biscoyol
Rhamnaceae	*Zizyphus guatemalensis*	naranjillo
Rubiaceae	*Alibertia edulis*	trompillo
	Genipa americana	guaitil blanco
	Guettarda macrosperma	mosqueta
	Randia echinocarpa	
Sapotaceae	*Manilkara zapota*	nispero
	Mastichodendron capiri	tempisque
Tiliaceae	*Apeiba tibourbou*	peine de mico

The Megafaunal Dispersal Syndrome

In the lowland deciduous forest of Guanacaste Province, Costa Rica, there are at least 39 species of trees or large shrubs (Table 2) that are reasonable candidates for a reconstruction such as that envisioned for *Scheelea* palms and gomphotheres. These trees and shrubs display a set of fruit and seed traits in common—traits that are puzzling if examined only in the context of the potential native dispersal agents. We view these traits as part of the following megafaunal dispersal syndrome.

1) The fruits are large and indehiscent (Fig. 1) and contain sugar-, oil-, or nitrogen-rich pulp. The seeds they contain are obviously not dispersed abiotically as are the seeds in the large explosive schizocarp of *Hura crepitans* (Euphorbiaceae) or the large samara-filled dehiscent fruit of *Swietenia macrophylla* (Meliaceae).

2) The fruits look, feel, and taste like those eaten by large seed-dispersing mammals in Africa and have seeds and nuts of similar size, hardness, and shape to those in African fruits that are eaten by large mammals.

3) The large nuts or seeds (Fig. 2) are usually protected by a thick, tough or hard endocarp or seed coat that usually allows them to pass intact by the molars and through the digestive tract when eaten by introduced large mammals such as horses, cows, and pigs. Seed scarification in the animal digestive tract sometimes occurs during dispersal, and some scarified seeds are digested.

4) If the seeds are soft or weak, they are very small (as in figs) or imbedded in a hard core or nut like those in *Spondias*, *Scheelea*, and *Hippomane*. Fruits with soft seeds may also contain seed-free hard sections in the pulp or core that

block occlusion of the molar mill, as in the sweet and woody fruit of *Guazuma ulmifolia*.

5) Different species bear ripe fruits at different times of the year in a given habitat.

6) Many of the fruits fall off the tree upon ripening or even well before they ripen; this is best described as behavioral presentation of fruits to earth-bound dispersal agents.

7) The fruits usually attract few or no arboreal or winged dispersal agents such as bats, guans, or spider monkeys. If these animals are attracted, as they are to figs or *Spondias* fruits, there is usually a much larger fruit crop than they can eat.

8) In present-day forests, a high proportion of a tree's fruit crop rots in the tree or on the ground beneath it without being tasted by any potential dispersal agent. This is true even in those national parks where sizable wild vertebrate populations may equal or exceed their pre-Columbian densities.

9) Peccaries, tapirs, agoutis, and small rodents usually act as seed predators and dispersers of these trees; these animals do not act purely as dispersal agents, but at present they are often the only ones.

10) The fallen fruits are avidly eaten by introduced horses, pigs, or cattle (or by more than one). Free-ranging populations of these animals at carrying capacity normally consume all of the fallen fruit in most trees' crops. At least some of the seeds pass through the digestive tract of these animals and eventually germinate. The introduced large herbivores may reenact many portions of the interaction the trees had with the extinct megafauna.

11) The natural habitats (such as alluvial bottoms or gentle slopes) of these trees are on the edges of grassland and in adjacent forest that are likely to be attractive to herbivorous megafauna and usually not on steep rocky outcrops and precipitous slopes.

As we come to know more of the natural history of the Costa Rican trees, more species will undoubtedly be added to the list in Table 2. For example, in southwestern Costa Rica in the lowland evergreen rain forest of Corcovado National Park, at least the following have most or all of the traits listed above: *Achmaea magdalenae, Astrocaryum standleyanum, Calophyllum macrophyllum, Dusia macrophylata, Enallagma latifolia, Elais melanococa, Hymenaea courbaril, Parkia pendula, Pouteria* spp., *Raphia taedigera, Scheelea rostrata, Simaba cedron, Terminalia catappa, Theobroma* sp., *Zamia* spp. *Coumarouna panamensis* nuts come from a tree common in many Panamanian and Costa Rican rain forests; the nuts are dispersed by contemporary mammals (*12*) and were probably dispersed by gomphotheres as well.

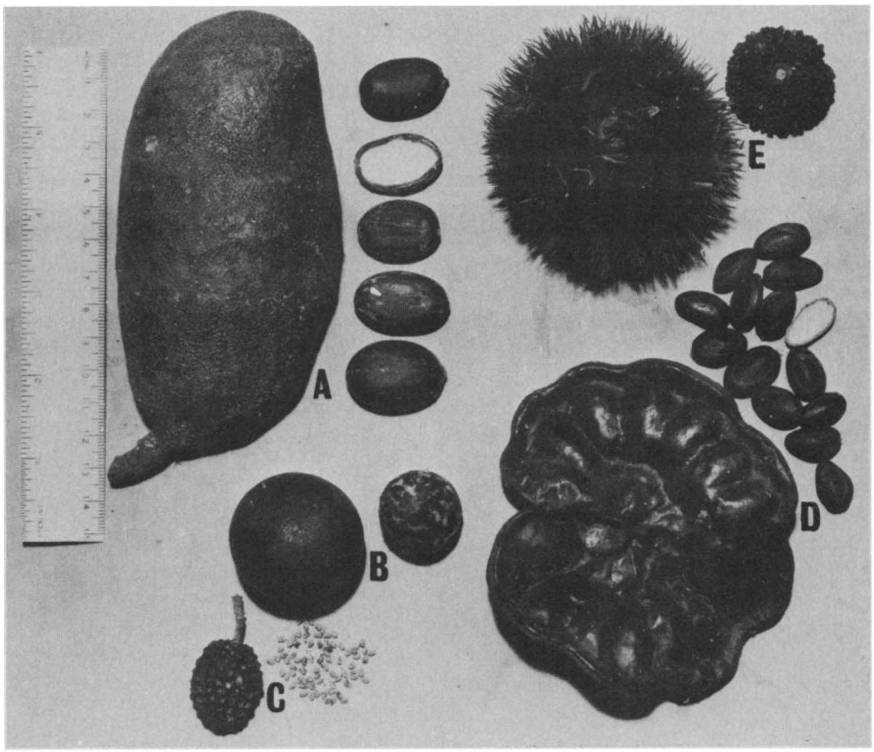

Fig. 2. Fruits and their seeds from Santa Rosa National Park that were probably dispersed by Pleistocene megafauna. The seeds to the right of each fruit represent a normal quantity of seeds found in each fruit. (A) *Hymenaea courbaril* (Leguminosae). (B) *Acrocomia vinifera* (Palmae). (C) *Guazuma ulmifolia* (Sterculiaceae). (D) *Enterolobium cyclocarpum* (Leguminosae). (E) *Apeiba tibourbou* (Tiliaceae) (*19*).

Certain species listed in Table 2 have instructive exceptions to the traits listed above. Although *Acacia farnesiana* has no sweet flavor or other attractant easily perceptible to humans in the mesocarp of its dry, pulpy, and indehiscent fruit, cattle and horses seek out and eat the fruits (*13*), just as do African big game animals with African *Acacia* (*14*). *Prosopis juliflora* (mesquite) is especially interesting in this context. In the arid southwestern United States, horses and cattle are known to have aided in the dispersal of mesquite seeds and the ripe pods of various *Prosopis* species are often sweet and pleasant tasting to people. In Guanacaste, the ripe pods of *P. juliflora* are only slightly sweet and somewhat astringent. Horses and cattle in Guanacaste eat the pods but not as eagerly as do these animals in northern Mexico, Texas, and southern Arizona. Because of the very local and patchy distribution of *P. juliflora* in Guanacaste (landward margins of mangrove swamps and high beach dunes), it has had minimal contact with livestock.

The relation between habitat and palatable fruit production is important. In Guanacaste, the species in Table 2 occur on relatively flat ground on terrain suitable for large mammal movement. On steep rocky slopes in the dry tropical forest (short-tree forest) of southern Sonora, terrain unsuitable for foraging of large mammals, Gentry (*15*) listed 32 prominent woody species, none of which have fruits or seeds adapted for large mammal transport. These include *Ceiba acuminata, Bursera simaruba, Willardia mexicana, Conzattia sericea, Caesalpinia platyloba, C. standleyi, Cassia emarginata, Lysiloma divaricata, L. watsoni, Tabebuia palmeri, T. chrysantha, Haematoxylon brasiletto, Jatropha platanifolia, J. cordata*, and *Ipomoea arborescens*. On the adjacent floodplains and arroyo bottoms there are species that have fruits adapted for megafaunal dispersal: *Sassafridium macrophyllum, Vitex mollis, Guazuma ulmifolia, Pithecellobium dulce, P. mexicanum, P. undulatum, Prosopis chilensis*, and *Randia echinocarpa*. Thus, in southern Sonora, where deciduous tropical forest reaches its northern limit, at about 28°N, the trees with hard seeds and

sweet fruits that are palatable to large mammals, including humans, are found in canyon bottom habitats that would have been the natural corridor for movement of the extinct megafauna, just as they are for introduced livestock.

The diets of the extinct neotropical herbivorous megafauna. Many large mammals (Table 1), including edentates, gomphotheres, notoungulates, and at least some equids, were in contact with neotropical and subtropical floras for tens of millions of years, an ample period for the evolution of a plant-megafauna dispersal syndrome. On the basis of field studies (*13, 14, 16, 17*), we assume that, just as contemporary large grazing and browsing mammals and some large carnivores readily consume wild fruits and defecate the seeds alive, the extinct ones did as well.

Hypotheses and Tests

Our evolutionary hypothesis can be tested by comparing the array of fruits eaten and seeds dispersed by large mammals in Africa and Asia with the fruits of tropical America on the one hand and with the fruits of New Guinea or tropical Australia on the other; the latter two tropical land masses have never had a mammalian fauna that would select for a well-developed megafaunal dispersal syndrome. We can also test our hypothesis by reintroducing Pleistocene mammals such as horses (*18*) to the neotropics and observing their response to the fruits and the response of the plant populations to the mammals. Since the experiment has been running for 400 years, a number of the relevant tree populations may have already regained population structures that are more similar to those of the Pleistocene than they are to those of recent pre-Columbian times. Nevertheless, on a very local scale the opportunity exists for experimentation with tree population structures by the introduction of horses, as does the opportunity to study horse responses to detailed fruit and seed traits.

The interaction between Costa Rican range horses and jicaro trees (*Crescentia alata*) is an example. In Santa Rosa National Park (*19*), a horse population that is usually on an unsupplemented diet ranges freely through a portion of the mixed deciduous forest and grassland where there are Pleistocene fossil horse remains (*19a*). The contemporary horses in Santa Rosa eat substantial amounts of fallen fruit of jicaro as well as fruits of many other trees listed in Table 2.

In this park, as elsewhere in Mexico and northern Central America (*20*), jicaro grows above small patches of grass in diffuse, nearly monospecific stands. Scattered individuals also occur in the adjacent forest. Reaching a height of 3 to 4 meters, jicaro has the spreading and shrubby shape of a savanna tree (Fig. 3). It would not look out of place in Nairobi National Park in Kenya.

The spherical fruits of jicaro (6 to 15 centimeters in diameter) contain 200 to 800 seeds that are similar in size and shape to broadened cantaloupe seeds and are embedded in a slippery, fibrous pulp. Although the seeds are stiff and solid, they are more rubbery than hard. Toward the end of the dry season (March to May), and again in mid-rainy season (August to September), the still-green hard fruits fall from the tree. After a month or more the fruit turns brown and is ripe. There is a very thin layer of sugar on its outer surface at this time. During ripening, the inner light-colored pulp changes from one with a flat and slightly astringent flavor to a slimy black mass that is quite sweet. Despite a penetrating fetid odor, the pulp is quite palatable to humans (*21*). In horse-free habitats the indehiscent fruits lie on the ground and rot in the rainy season, and fermentation of the fruit pulp kills the seeds. A falling fruit occasionally cracks open on impact, but one of us (D.H.J.) has not found seedlings to be produced as a result. When the jicaro tree is in or near forest, an occasional fruit is chewed open by squirrels. These rodents remove the seeds from the fruit pulp and chew them up. This seed predation results in occasional seed dispersal, since the animal may carry the fruit to a site better protected from predators and drop some seeds along the way or leave some inside the fruit. The vast majority of jicaro fruits are not subject to this treatment.

When range horses are free to forage below the trees, they quickly consume the crop of jicaro fruits. The hard fruits are broken between the incisors (Fig. 4), an act that requires a pressure of about 200 kilograms (*22*). The gooey pulp is scooped out with the tongue and incisors and swallowed with little chewing. For more than ten consecutive days, three captive and well-fed range horses ate the fruit pulp of 10 to 15 fruits in each of two meals a day, one in the morning and one in the evening (*22*). A herd of 17 range horses broke and consumed 666 jicaro fruits in one 24-hour period (*22*). The percentage of seeds that survive passage

Fig. 3. Adult *Crescentia alata* with full-sized immature fruit during the dry season. Naturally fallen ripening fruits are visible on the ground to the left of the tree (*19*).

through the gut of a horse is not known, but the dung becomes filled with viable jicaro seeds on the second day after the horse starts to eat the fruits. About 97 percent of these filled seeds germinate after they are washed out of the horse dung and placed on moist soil or paper. Seeds washed out of the pulp and placed on moist paper also show 97 percent germination. Sapling jicaro trees are commonplace in horse pasturing areas inside and outside of Santa Rosa National Park, provided that the habitats are not burned annually. Seedling and sapling jicaro trees are extremely rare in those areas of the park where horses do not have access, even in grass and forest habitats that have dense stands of adults and are rarely burned.

These observations indicate that Pleistocene horses were an important part of the disperser coterie of *Crescentia alata*. Since the Pleistocene horse evolved in the New World (*23*), there might even be elements of coevolution in the interaction of horses and jicaro fruits.

Today, jicaro and its congener (*Crescentia cujete*) are widespread in the drier parts of Central America (*20*). This distribution is probably the result of both the immediate pre-Columbian distribution and the post-Columbian spread of *Crescentia* by introduced horses. In addition, the hard fruits are used by humans as household tools such as bowls, ladles, and rattles, and the trees are therefore dispersed in this way too (*21*). At the time that the domestic horse was introduced, *C. alata* was very likely a relatively rare tree, occurring in small patches in relatively open vegetation such as marsh edges, along topographic breaks, and on floodplains, just as it is now in lowland Costa Rican habitats free of horses. With essentially no seed dispersal, the trees were limited to those sites where populations could survive with minimal seedling recruitment. The return of horses after 10,000 years resulted in intensified seed dispersal and has undoubtedly resulted in the appearance of more adult jicaro trees in many more kinds of habitats.

The postulated constriction of the range of *C. alata* after the extinction of the Pleistocene horse may affect other animals in the habitat. For example, nectarivorous bats would be affected by a reduction in jicaro density. The flowers of *C. alata* are nocturnal, abundant, and heavily visited by four species of nectarivorous bats in Guanacaste deciduous forests (*24*), and are the only common nectar source available to bats in the park forests during several months of the rainy season. The decline of the jicaro

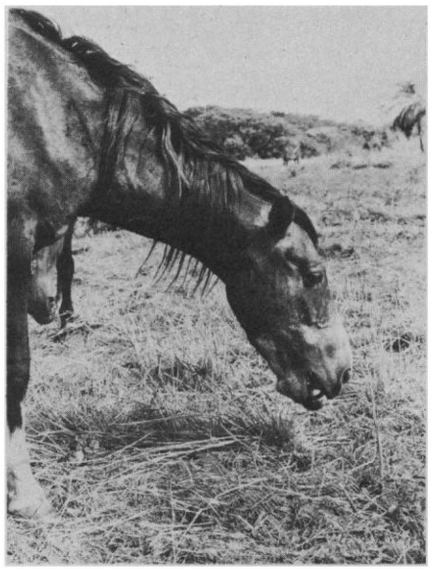

Fig. 4. Range horse breaking a ripe fruit of *Crescentia alata* between its incisors (*19*).

population would have strongly affected the population dynamics and structure of the many other plant species that are pollinated or dispersed by bats in the Central American deciduous forest lowlands.

Jicaro fruits are not the only fruits readily eaten by introduced horses. A similar interaction takes place between the fruits of *Enterolobium cyclocarpum* (guanacaste) (*25*), *Guazuma ulmifolia* (guacimo), and *Pithecellobium saman* (cenizero) and horses and cattle.

Additional Considerations

Partial loss of dispersal agents. Although some frugivores may be little more than fruit thieves (*26*) or deposit the seeds in lethal sites, a tropical tree usually has a complex seed shadow produced by several quite different types of animals (*12, 27*). Extinction of the Pleistocene megafauna would eliminate some of a tree's disperser coterie and thereby excise part of the tree's seed shadow. For example, two bat-generated seed shadows (*28*) of *Andira inermis* (Table 2) contained many fruits that fell below the parent tree and were passed over by pigs, cattle, and horses, perhaps because of antibiotic compounds in the fruit pulp. The seeds in such fallen fruits are killed by the larvae of weevils (*28*), and the fallen and wasted seeds were viewed by biologists as a cost of having a sloppy seed disperser and perhaps as due to the tree's being in an area where the human-disturbed bat populations are lower than those to which the fruiting behavior of the tree is genetically adjusted. However, we suspect that during the Pleistocene the fallen fruits would have been picked up by foraging gomphotheres, toxodons, and other animals that dispersed the nut-encased, soft seeds more effectively, and perhaps to quite different places.

Bats and other aerial or arboreal vertebrates would generally have taken their share of a fruit crop before it was available to the terrestrial megafauna, and therefore megafaunal extinction should have had little direct effect on them or the seed shadows that they generate. However, monkeys, squirrels, guans, and curassows, animals that forage for fruit both on the ground and in the tree crown, would have had more opportunity to harvest fruits after the megafauna extinction. Some increased seed dispersal by these groups could be expected and this might have compensated in part for the loss of the larger dispersers.

Response by seed predators. Vertebrate seed predators such as agoutis, peccaries, and small rodents experienced a substantial increase in their food supply after the megafaunal extinction. As food availability increased, so should their populations, habitat coverage, and species density.

Arthropod fruit eaters and seed predators were also affected by megafaunal extinction. Three species of *Cleogonus* weevils feed on the ripening fruit of *Andira inermis*, and their larvae develop in the fruit pulp and seeds of fallen fruits (*28*). If fruits were removed from below *Andira* trees by large vertebrates, there would not be the sizable weevil populations that there are at present. The density of *Zabrotes interstitialis* bruchids, and thus their intensity of seed predation on seeds of *Cassia grandis*, is greatly increased when the fruits are left on the trees until they rot (*29*). When a *Pithecellobium saman* fruit crop falls, its primary insect seed predator, *Merobruchus columbinus*, has just left the fruits (*30*); we suspect that the risk of being eaten by a large mammal (now extinct) accounts for the insects' rapid exits. Ripe fruits are rotted by their occupant microbes as a way of defending this resource against large herbivores (*31*); a major selective pressure for such microbial behavior disappeared when the Pleistocene Neotropical megafauna disappeared. Likewise, other associates of large mammals, such as dung beatles (Scarabaeidae), ticks, horse flies (Tabanidae), cowbirds, and vampire bats, must have been depleted by the loss of the Pleistocene megafauna.

Vegetative defenses against an extinct megafauna. The extinct tropical Pleistocene herbivores consumed substantial

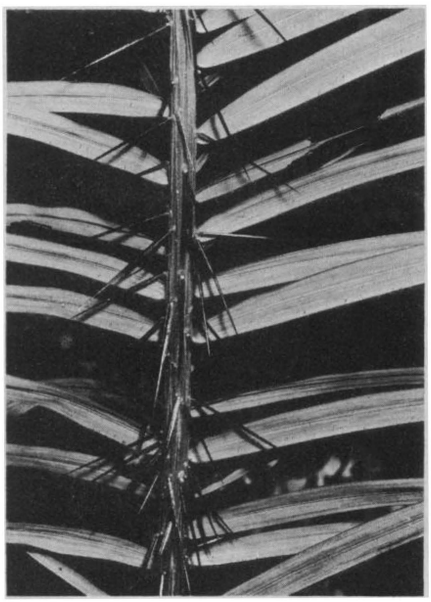

Fig. 5 (left). Spines, 7 to 11 centimeters long, on the underside of the petiole of the leaf of sapling *Acrocomia vinifera* (*19*). Fig. 6 (right). *Desmodium* (Leguminosae) beggar's-ticks stuck to the forelegs of a free-ranging horse on the edge of the Costa Rican rain forest (*38*).

amounts of browse as well as fruits and seeds. We expect that some "functionless" but potentially defensive vegetative traits exhibited by trees in modern habitats are Pleistocene anachronisms. Spininess of African plants developed as a defense against large herbivores (*32*). There are numerous New World spiny plants in habitats where causal herbivores are missing. Spines on palm trunks are probably important in keeping climbing rodents from getting at developing fruits (for example of *Bactris* spp. and *Astrocaryum* spp.), but the long spines on leaves of *Bactris* and *Acrocomia* (Fig. 5) cannot be explained this way. An attempt to explain the spines without visualizing large browsing mammals as part of the interaction has led to construction of a model in search of a realistic selective pressure (*33*). In Santa Rosa National Park and elsewhere in Central America, prominent spines on the trunks and sometimes leaves of *Hura crepitans*, *Ceiba pentandra* (saplings only), *Ceiba aesculifolia*, *Acrocomia vinifera*, *Bombacopsis quinatum*, *Xanthoxylum setulosum*, and *Chlorophora tinctoria* (saplings only) are defenses of trees, especially young trees, against a browsing megafauna. Although such mechanical defenses may be diminishing because of the relaxation of selection for them, they have not yet disappeared. The recurved thorns on the twigs and leaves of *Mimosa guanacastensis*, *Pithecellobium platylobum*, *Acacia riparia*, *A. tenuifolia*, and *Mimosa eurycarpa* could easily have deterred ground sloths or gomphotheres. The same applies to the needle-sharp tips of the leaves of the understory shrub *Jacquinia pungens*, which is leafy in Costa Rica only during the dry season (*34*). On well-armed deciduous forest trees, the spines are commonly best developed within 4 to 6 meters of the ground in the neotropics just as they are on African trees. In open vegetation in southern Sonora, we observed that the shrubby cymbal-spine acacia, *Acacia cochliacantha*, is extremely thorny. Nearby taller conspecific trees growing in regenerated low forest are almost entirely unarmed.

External seed dispersal. Contemporary beggar's-ticks (*Desmodium* spp.) stick tightly to the hair of domestic horses (Fig. 6). Although they failed to adhere to the sleek coat of an adult captive tapir, or to that of a paca, collared peccary, and white-lipped peccary, experiments and observations by D.H.J. in Santa Rosa National Park show that the bur fruits of *Pisonia macranthocarpa*, *Desmodium* spp., *Krameria cuspidata*, *Triumfetta lappula*, *Aeschynomene* sp., *Petiveria alliacea*, and *Bidens riparia* stick tightly to the denser coats of horses and cattle. Except for *Pisonia* and *Krameria*, these plants are herbaceous; they depend on early colonization of open or nearly open ground for survival. With the loss of a megafauna we suspect that many of these plants declined severely in density and some even suffered local extirpation, as the once open and well-trampled habitats were reforested and as seeds were no longer dispersed by large shaggy beasts such as gomphotheres, toxodons, and ground sloths.

Discussion

In this addition to current evolutionary thought about the equilibrium state of contemporary neotropical habitats, we propose an answer to the riddle of why certain trees produce far more edible fruits than their current dispersal agents will remove, produce fruits that are not eaten by contemporary dispersal agents, bear fruits that resemble those eaten by African megafauna, and bear fruits avidly eaten by introduced livestock. These are traits of a megafaunal dispersal syndrome that has not been evolutionarily eradicated after the extinction of the dispersal agents 10,000 years ago. An alternative hypothesis is that these trees are not closely coevolved with particular frugivores and that the system is just very inefficient, as has been suggested for a Panamanian rain forest tree (*35*).

The fate of fruit crops in African game preserves is instructive in considering these two hypotheses. Observations by D.H.J. in Uganda and Cameroon forests suggest that it is indeed a rare event when the intact animal fauna does not consume all of the fallen fruit crop. For example, in a portion of Kibale Forest near Fort Portal, Uganda, where all the elephants had been killed, the fruits of *Balanites wilsoniana* (100 to 150 grams and 10 to 15 centimeters long) were abundant and rotting on the ground below parent trees. The fruits of *B. wilsoniana* contain a 40-gram nut and are about the same size and flavor as sapotaceous fruits of the Costa Rican rain forest which often lie rotting in large numbers below parent trees. *Balanites* fruits are swallowed by elephants (*36*, *37*) and in the portions of Kibale Forest where elephants were numerous, all the fallen *Balanites* had been immediately and thoroughly removed by them. In this portion of Kibale, there are germinating *B. wilsoniana* seeds in elephant dung along forest trails.

Even if our hypothesis were to be rejected because it could be shown that in certain truly pristine neotropical habitats the extant animals can fully process the annual fruit fall, the intriguing matter of the fate of those seed species that were dispersed by Pleistocene mammals is not explained. Even if most population structures are now adjusted to the loss of the dispersal megafauna, we do not think that this is likely to be the case with evolutionary or coevolutionary equilibria. We doubt that those trees with lifespans of 100 to 500 years have experienced sufficient generations since the Pleistocene to replace the syndrome that is no longer highly functional. Let us

assume that the agouti was once a trivial dispersal agent and figured primarily as a seed predator. With the removal of the Pleistocene megafauna, the agouti suddenly has the opportunity for a variety of evolved and coevolved interactions. However, it may well not have yet exploited the opportunity (*11*). It may shift its day-to-day activities in ways that serendipitously serve the dispersal needs of certain species of tree moderately well, even though no evolution has taken place in plant or animal.

Our discussion has focused on neotropical plants and animals, but it can be generalized to the sweet-fleshed large fruits of the Kentucky coffee bean *Gymnocladus dioica* and honey locust *Gleditsia triacanthos* (Leguminosae), osage orange *Maclura* (Moraceae), pawpaw *Asimina* (Annonaceae), and persimmon *Diospyros* (Ebenaceae). When there was a megafauna available to disperse their seeds, such genera may have been denser and had much wider ranges. The extreme spininess of various New World extra-tropical shrubs that are found in moist as well as arid regions has not been well explained. The vesicatory ripe fruits and weak-walled nuts of *Gingko biloba* might even have been evolved in association with a tough-mouthed herbivorous dinosaur that did not chew its food well.

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19. Santa Rosa National Park, on the Pacific coastal plain in extreme northwestern Costa Rica, in Guanacaste Province, has a mix of deciduous forest, old abandoned cattle pastures, and evergreen riparian forest (0 to 350 m in elevation). The photographs in Figs. 1 to 5 were taken there.

19a. L. D. Gomez (personal communication) reports that Pleistocene horse remains are common in the Costa Rican lowlands, particularly in Guanacaste Province.

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Reporting of Faculty Time: An Accounting Perspective

Arthur L. Thomas

The Office of Management and Budget's requirements for 100 percent reporting of faculty time on federally sponsored research, set out in circular A-21 (*1*), are provoking controversy (*2, 3*). A much broader reporting dilemma, of which 100 percent reporting is a special case, is rooted in a theoretical difficulty so radical that there is nothing comparable to it in our ordinary experience. Yet, accountants in the business world must prepare similar reports under like difficulties and have learned to live with such requirements. Their experience, and comprehension of the real nature of the theoretical difficulty, may assist government agencies, universities, and investigators. First, I will briefly describe the federal reporting requirements, their context, the uses made of the figures, and reasons advanced for objecting to such reports.

Terminology, Requirements, and Controversies

For many years, our federal government has supported basic research in the sciences through grants and contracts. To simplify a bit, these have reimbursed universities for two things: "direct costs" and, symmetrically, "indirect costs." The distinction between the two may be explained by an example. Let us suppose that the government is sponsor-

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