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An Ecological Model for the Origins of Maize-Based Food Production on the Pacific Coast of Southern Mexico

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Maize-based food production was well-established on the Pacific coast of southwestern Mexico by ~2600 B.P.¹, the beginning of the Late Formative Period. Biogeographical and genetic studies indicate that this cultigen was originally domesticated in Central Mexico by ~9200 B.P., and microbotanical studies suggest that it was widely dispersed to people living in several parts of Mexico and Central America by ~7500 B.P. People living in the Soconusco region during the Archaic Period (~7500–3500 B.P.) were foragers that may have supplemented their diets by cultivating morphologically wild plant species and some cultigens. Microbotanical studies suggest that people in this region added maize to their diets between 6000 and 5000 B.P., but a commitment to maize-based food production did not occur until 2400 years later (2600 B.P.). Based on the paleoecological record for the region and central place foraging theory, we develop a subsistence-settlement model for pre-village, Archaic Period, forager-horticulturalists and evaluate this model with the available archaeological evidence for this interval. We then use an adapted form of the Lotka-Volterra predator-prey model, cultivator-cultigen,

to explore the initial adoption of maize and the development of more intensive forms of maize-based food production in the area. Based on this analysis, we argue that the long-term delay between the introduction of maize and maize-based food production resulted from the relatively low energetic returns of early maize relative to other resources available in the region.

The emergence of food production is inarguably one of the most significant developments in the environmental history of our planet (Redman 1999; Roberts 1998; Dincauze 2000) and a fundamental turning point in human history (Childe 1951; Cohen 1977; Cowan and Watson 1992; Flannery 1973, 1986a; Gebauer and Price 1992a; Gremillion 1996a; Harris 1996b; Hayden 1990; Henry 1989; O'Brien and Wilson 1988; Price 2000a; Price and Gebauer 1995a; Rindos 1980, 1984; Smith 1998, 2001a; Watson 1989, 1995; Zeder 1995; Zohary and Hopf 2000). Originally characterized as a "revolution" (Childe 1951), and more recently as a transition (Price and Gebauer 1995b), true dependence on food production

was often preceded by the low-level use of domesticated plants and animals by people who were essentially foragers (Smith 2001a). Mixed foraging and farming, still practiced today by the Mikea of Madagascar (Tucker, this volume), persisted for millennia in some regions, well after the domestication of key cultigens, and is considered to be a stable and highly successful subsistence strategy within certain ecological contexts. Nevertheless, the persistence of low-level food production often did give way, at different times, to the development of more intensive forms of agriculture involving terracing, irrigation (Doolittle 1990), and other more sophisticated agroecological techniques (e.g., raised fields; Fedick 1996). Once more intensive food production, with its associated surpluses, was established it fueled the development of socially stratified, politically centralized, and technologically innovative state-level societies (Diamond 1997; Nichols and Charlton 1997; Zeder 1991). It also underpins the exponential population growth, urbanization, and environmental destruction evident throughout the world today.

Intense human-plant interaction resulting in changes in the distribution and genetic make-up of plant populations influenced prehistoric foraging and horticultural strategies long before the emergence of intensive agriculture and the reliance upon a few key cultigens (Rindos 1984; Price and Gebauer 1995a; Piperno and Pearsall 1998; Watson 1995). However, the most successful cultigens were often domesticated in primary centers and dispersed into other regions where prehistoric foragers and horticulturalists were living (Diamond and Bellwood 2003; Hastorf 1999; Smith 1998; Wills 1995). It is important to understand how and why prehistoric foragers in various parts of the world incorporated key cultigens into their subsistence regimes (Winterhalder and Goland 1993, 1997), and how these shifts in subsistence altered prehistoric settlement strategies and land use.

In some cases, it is clear from the archaeological record that agriculturalists migrated

into the territories of hunter-gatherers and ultimately replaced or subsumed them into their economies (Ammerman and Cavalli-Sforza 1984; Bogucki and Grygiel 1993; Cavalli-Sforza 1996; Diamond and Bellwood 2003). However, the transmission of domesticates through pre-existing exchange networks also accounts for the rapid spread of domesticated plants and animals into many regions (Gregg 1988; Hastorf 1999; Piperno and Pearsall 1998). Recent studies suggest that the details of this transformation varied greatly throughout the world (Barton et al. 1999; Blumler 1996; Hart 1999; Price and Gebauer 1995a). The principles of Human Behavioral Ecology (HBE; Winterhalder and Smith 2000) predict that the adoption and use of domesticated plants and animals outside the parent region is contingent upon: (1) the availability and productivity of wild resources in the new area, (2) the fecundity and adaptability of the cultigen or domesticated animal species to the new area, and (3) population dependent and independent restrictions, e.g., territoriality, creating localized decreases in wild resources (resource depression; Barlow 2002; Broughton 1999; Cannon 2003).

Food production in Mesoamerica—principally the cultivation of maize, beans and squash—was relatively widespread by the Early Formative Period (~3500 B.P.; Flannery 1973) and by this time the peoples of Mexico and adjacent regions are generally classified by archaeologists as farmers (Flannery 1973; Smith 2001a). Subsistence strategies, however, were diverse and dependent upon differing ecological contexts; substantial reliance on food production occurred earlier in the highlands when compared to the coast, where people combined the cultivation of maize, beans, and/or squash with wild resources from wetland and littoral environments (e.g., fish, shellfish, etc.; Blake et al. 1992a; Clark and Blake 1994; Coe and Flannery 1967; Kennett et al. 2002). The most recent botanical and genetic studies suggest that maize, beans, and squash were domesticated in Central Mexico during

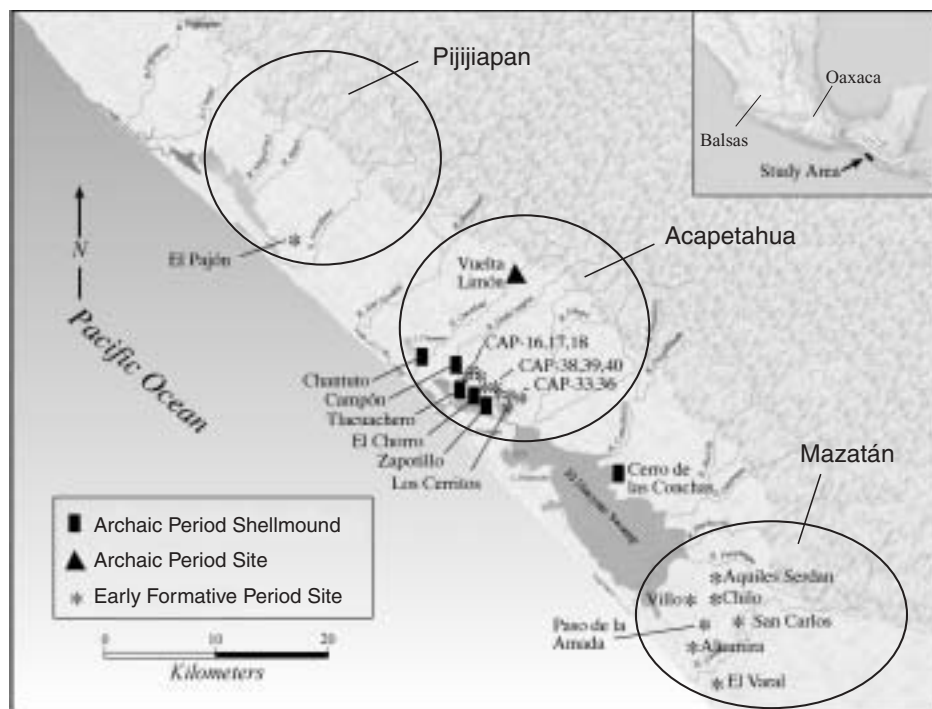


FIGURE 6.1. Study area showing the position of Archaic and Early Formative Period sites.

the Early Holocene (~10000–8000 cal. B.P., Matsuoka et al. 2002; Smith 1997b; Sonnante et al. 1994). Although these three cultigens were grown together after 3500 B.P., each appears to have its own domestication history that ultimately led to the symbiotic effects of growing these plants together in fields (Flannery 1973), a strategy that persists today throughout Mesoamerica. Reliance upon this triumvirate was preceded in many areas, e.g., Tehuacán Valley, Valley of Oaxaca, by a variety of mixed foraging and possibly horticultural strategies, and ultimately low-level food production—the supplementary use of maize, beans and/or squash occurring throughout much of the Early and Middle Holocene (Flannery 1986a; Smith 2001a). In some locations the low-level use of domesticated plants like squash persisted for at least 5500 years prior to a full commitment to food production (Smith 2001a).

In this chapter we analyze how people living in the Soconusco region of southwestern Mexico (Figure 6.1) responded to the arrival of one of these cultigens—maize. Biogeographical and genetic studies point to Central Mexico, the Balsas River region or Oaxacan Highlands, as the most likely area for early maize domestication (Figure 6.1 [inset], Benz 1994, 1999; Doebley 1990; Gonzalez 1994; Matsuoka et al. 2002; Wang et al. 1999). Macrobotanical evidence from dry caves in the mountains of Mexico indicate that domesticated maize had spread through this region by at least 6250 B.P. (Piperno and Flannery 2001); microbotanical studies of pollen and phytoliths from the tropical lowlands of Central Panama and Mexico suggest a far-reaching dispersal of maize as early as 7500 B.P. (Piperno and Pearsall 1998; Pope et al. 2001; Piperno 2001b). We do not assume that maize was the first cultigen to be used by the people of the Soconusco, but this plant is of

particular interest because its use appears to have partially led to the transition to more intensive forms of food production and the emergence of cultural complexity during the Early and Middle Formative Periods (3500 to 2700 B.P.; Blake 1991; Blake and Clark 1999; Blake et al. 1995; Clark 1994; Clark and Blake 1994). Maize is also the most visible domesticate in both the micro- and macro-botanical record in Mesoamerica (Feddema 1993; Jones and Voorhies 2004; Kennett et al. 2002). Maize pollen and phytoliths dating to between 6000 and 5500 B.P. are evident in sediment cores from the Pacific coast of Guatemala, just south of the Soconusco (Neff et al. 2003). Maize phytoliths have also been recovered from Late Archaic Period archaeological deposits in the region dating to ~4600 B.P. (Jones and Voorhies 2004); and small maize cobs have been recovered from Early Formative Period contexts (~3500–3000 B.P.; Blake et al. 1992a; Feddema 1993). During the Late Archaic and Early Formative Periods, maize was used at a relatively low level and in combination with locally available wild resources, particularly from wetland and littoral environments. By the end of the Middle Formative Period (~2600 B.P.) agricultural communities dotted the coastal plain, and food producing economies emphasizing maize were well developed. However, wild foods continued to play an important role in some parts of the Soconusco throughout time (Blake et al. 1992a). The central question here is how a resource like early maize with poor energetic returns became a dominant feature of the subsistence economy in the region.

To model the transition to maize-based food production we first outline the paleoecology of the Soconusco with an emphasis on the biotic zones that parallel the coastline in bands. These biotic zones contained different resource types and densities offering a variety of opportunities for early foraging peoples. Based on these paleoecological data we develop a central place foraging model for pre-village (Archaic Period) forager/horticultural populations in the region and

present the fragmentary archaeological evidence currently available. These data generally support the model, but continued testing will be needed for verification. We then turn to the development of maize-based food production in Mesoamerica, with special attention to the domestication of this plant and the morphological changes that it underwent during the Holocene; from a low productivity plant resembling teosinte, to the more productive forms of modern maize used in the region today. To simulate the dynamic responses of foragers in the Soconusco region to the appearance of maize of different types, we use an adapted form of the Lotka-Volterra predator prey model. Based on this model we predict the responses of foragers in the Soconusco to the introduction of maize at various times, and compare this to the available archaeological record for the Archaic and Formative Periods.

PALEOECOLOGY OF THE SOCONUSCO REGION

Maize was not domesticated in the Soconusco,² but introduced from elsewhere in central Mexico. Therefore, it is important to outline the social and ecological context into which this cultigen was introduced. Detailed environmental and paleoecological overviews for the region are available elsewhere (Clark 1994; Feddema 1993; Voorhies 1976, 2004), and in this section we summarize the pertinent paleoecological details with an emphasis on (1) the distribution and abundance of wild resources available to pre-village foragers/horticulturalists; (2) the early domesticates that may have been available; (3) environmental changes impacting the availability of these resources through the Holocene; and (4) the impact that human exploitation may have had on these resources through time.

The Soconusco is a tropical lowland region at ~15° N. latitude that stretches ~240 km along the Pacific coast from the Mexican-Guatemalan border to Pijijiapan, Mexico (Voorhies 1989a; Figure 6.1). This northwest-southeast trending coastal plain, which is flat and low-lying, is

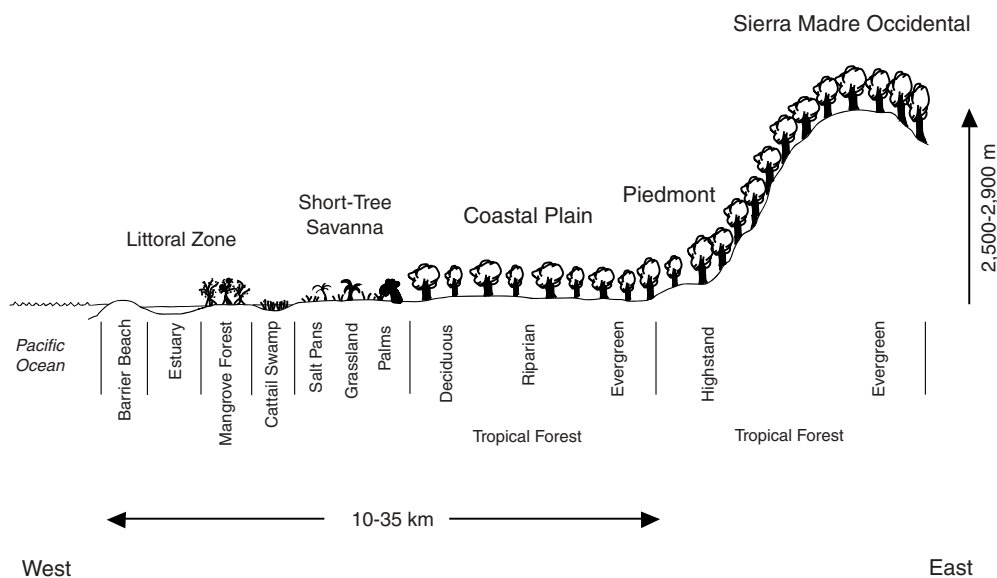


FIGURE 6.2. Cross section of the Soconusco region showing geographical features and primary biotic zones.

flanked by the Pacific Ocean to the west and the Sierra Madre Occidental to the east (Figure 6.2). The width of the plain varies from 10 km near Pijijiapan to 35 km at the border between Mexico and Guatemala. The Sierra Madre rises 2500–2900 m along the eastern edge of the coastal plain, with the highest peak in the region reaching an elevation of 4110 m at the peak of the Tacaná volcano, straddling the Mexican-Guatemalan border. The rivers flowing out of the Sierra Madre form wetlands and lagoons along the seaward margin of the coastal plain; barrier beaches are well-developed along this stretch of coast, natural canals form a sheltered peri-coastal waterway along the entire seaward edge of the region. Archaeological sites, including ones dating from the Archaic to the end of the middle Formative Period (7500–2600 B.P.), are found on the inland side of the lagoon system and inland on the flat coastal plain (see Figure 6.1; Clark 1994; Kennett et al. 2002; Voorhies 1976, 2004; Voorhies et al. 2002).

Ambient air temperature in southwestern Mexico is relatively warm and stable through

much of the year (Annual Mean: 26°C; Range: 20–36°C), but the region is influenced by highly seasonal tropical monsoonal rains (Annual mean: ~1500 mm; Vivó Escoto 1964). Rainfall is heaviest between April and October (~1200 mm, wet season) and much more limited between November and March (~200 mm; dry season). There is also a spatial gradient in the amount of rain that falls within the region; the highest precipitation falling in the mountains and the least falling near the coast. Rivers swell during the wet season transporting sediment out of the highlands onto the coastal plain, replenishing the rich alluvial soils that today support commercial agriculture of bananas and oil palms. Pericoastal environments are also flooded during wet season months, significantly reducing the amount of habitable dry land near the estuarine zone. Resource availability in the littoral zone peaks during the dry season (Kennett and Voorhies 1996). There may also be a general reduction in terrestrial biomass on the coastal plain during the dry season, particularly if arid conditions persist for extended periods. Stable

carbon and oxygen isotopic analysis of mollusk shells from prehistoric sites in the region indicate that this tropical monsoonal rainfall regime persisted during the Archaic and Formative Periods (Kennett and Voorhies 1995, 1996; Kennett et al. 2002; Voorhies et al. 2002) and phytolith and pollen records show the stability of tropical forest growth with the exception of the large anthropogenic effects of burning and forest clearance recorded in these proxy records starting after 5000 B.P. (Jones and Voorhies 2004).

At the time of European contact (~AD 1520), the Soconusco was part of the Aztec Empire and, at the time, was well-known for its forest and agricultural products (Clark 1994; Gasco and Voorhies 1989, 75; Voorhies 1989a). Tribute items from this region paid annually to the Aztec Emperor included a diverse range of tropical bird skins, feathers, spotted animal pelts and cacao beans, by this time a highly prized domesticated tree crop traded widely in Mesoamerica (Gasco and Voorhies 1989).

Monsoonal rainfall patterns and differences in drainage in the region create several environmental zones that parallel the coast (see Figure 6.2). These environmental zones include, from the ocean to interior: (1) the littoral zone (including swampland); (2) tropical short-tree savanna, seasonally inundated and sometimes swampy; (3) forested coastal plain; and (4) piedmont forest. Each of these environmental zones contain several biotic communities (Clark 1994). The compressed nature of these environmental zones provided prehistoric people with a diverse range of economically valuable plants and animals within a relatively small foraging radius of 15–30 km depending upon settlement location within the region. However, the distances were great enough between these zones that prehistoric foragers and farmers had to decide where to establish settlements, determining which resources to exploit residentially and which to collect logistically³ (see central place foraging below).

Resource-rich estuaries and wetlands formed along this section of coast with the sta-

bilization of sea-level between 9000 and 7000 B.P. (Fairbanks 1989; Kennett and Voorhies 1995, 1996). In this region the resources of the open ocean are difficult to access because of very heavy seas, consequently offering few subsistence opportunities for people with simple maritime technology (Clark 1994; Voorhies 1976). Large green sea turtles once laid their eggs on these beaches seasonally, with crabs and shellfish available on beach margins (Table 6.1; Coe and Flannery 1967; see Feddema 1993 for a comprehensive list of resources from different zones). Small animals occupied beach scrub fringing these long stretches of beach. Behind these barrier beaches, still-water aquatic habitats supported a wide range of marine and estuarine fish, mollusks, and crustacea, along with a variety of resident and migratory bird species (Voorhies 1976). It is also likely that shrimp were available during the dry season months in estuarine-lagoon systems open to the ocean (Clark 1994; Voorhies et al. 1991). A series of barrier beach ridges, visible in aerial photographs, show evidence for sequential progradation of the coastline after the stabilization of sea-level that included the infilling of estuarine lagoons. Lagoons are still present today in the Acapetahua portion of the coast (see Figure 6.1), and support several modern fishing and shrimp cooperatives. Large open lagoons also existed to the north (Pijijiapan) and south (Mazatán) of Acapetahua, but many have subsequently filled during the last 7000 years, creating salt pans, tropical savanna, and freshwater marsh systems (e.g., El Hueyate marsh; see Figure 6.1). The interior edge of these estuaries was bordered with a narrow, well-developed strip of mangrove forest and herbaceous swamps that today support a variety of edible plant and animal species. Most notable is the rich array of fauna and migratory waterfowl found in the El Hueyate swamp located toward the southern end of the study region (Alvarez del Toro 1985; Clark 1994).

A tropical short-tree savanna occurs immediately inland of the coastal wetlands. It consists of dispersed palm trees with an understory of

TABLE 6.1
Selection of Plants and Animals from Different Environmental Zones in the Soconusco

LATIN NAME	COMMON NAME	LZ	ST	CP	P	BIOTIC COMMUNITY
<i>Agaronia testacea</i>	mollusk	✓				beach
<i>Anadara reinharti</i>	clam	✓				beach
<i>Chelonia mydas</i>	green sea turtle	✓				beach
<i>Coendou mexicanus</i>	porcupine	✓				mangrove
<i>Crocodylus astutus</i>	river crocodile	✓				estuary/river
<i>Ctenosaura similis</i>	black iguana	✓				beach scrub
<i>Dasypus novecinctus</i>	armadillo	✓				beach scrub
<i>Goniopsis pulchra</i>	small crab	✓				mangrove
<i>Lutjanus colorado</i>	red snapper	✓				estuary/river
<i>Mycteria americana</i>	stork	✓				estuary
<i>Mytella falcata</i>	mussel	✓				estuary
<i>Ocybode occidentalis</i>	beach crab	✓				beach
<i>Ostrea columbiensis</i>	oyster	✓				estuary
<i>Polymesoda radiata</i>	marsh clam	✓				estuary
<i>Sesarma sulcatum</i>	crab	✓				mangrove
<i>Procyon lotor</i>	raccoon	✓				mangrove
<i>Sciades troschelii</i>	marine catfish	✓				estuary/river
<i>Strombus galeatus</i>	snail	✓		✓	✓	beach
<i>Tamandua tetradactyla</i>	collared anteater	✓		✓	✓	mangrove
<i>Peneus spp.</i>	shrimp	✓				estuary
<i>Centropomus sp.</i>	snook	✓				estuary
<i>Caiman crocodilus</i>	cayman	✓				swamp
<i>Cairina moschata</i>	duck	✓				swamp
<i>Cichlasoma timaculatum</i>	bass	✓				swamp
<i>Iguana iguana</i>	water iguana	✓				swamp
<i>Lepisosteus tropicus</i>	gar	✓				swamp
<i>Chrysemys scripta</i>	black turtle	✓				swamp
<i>Staurotypus salvinii</i>	snapping turtle	✓				swamp
<i>Acrocomia mexicana</i>	coyol palm		✓			palm forest
<i>Crescentia cujete</i>	calabash		✓			palm forest
<i>Quercus oleoides</i>	oak		✓			palm forest
<i>Sabal mexicana</i>	fan palm		✓			palm forest
<i>Scheelea liebmannii</i>	corozo palm		✓			palm forest
<i>Dasyprocta punctata</i>	agouti		✓			grassland
<i>Lepus flavigularis</i>	hare		✓	✓		grassland
<i>Nasua narica</i>	coati		✓			grassland
<i>Sylvilagus floridanus</i>	cottontail		✓			grassland
<i>Urocyon cinereoargenteus</i>	grey fox		✓	✓	✓	grassland
<i>Brosimum alicastrum</i>	breadnut			✓	✓	tropical forest
<i>Carica papaya</i>	papaya			✓		tropical forest
<i>Ficus glaucescens</i>	black fig			✓	✓	tropical forest
<i>Persea americana</i>	avocado			✓	✓	tropical forest
<i>Psidium guayaba</i>	guava			✓	✓	tropical forest
<i>Spondias mombin</i>	hog plum			✓	✓	tropical forest
<i>Persea americana</i>	avocado			✓	✓	tropical forest

(continued)

TABLE 6.1 (Continued)
Selection of Plants and Animals from Different Environmental Zones in the Soconusco

LATIN NAME	COMMON NAME	LZ	ST	CP	P	BIOTIC
						COMMUNITY
<i>Sterculia mexicana</i>	chestnut				✓ ✓	tropical forest
<i>Theobroma cacao</i>	cacao				✓ ✓	tropical forest
<i>Agriocharis ocellata</i>	wild turkey				✓ ✓	tropical forest
<i>Alouatta villosa</i>	howler monkey				✓ ✓	tropical forest
<i>Ateles geoffroyi</i>	spider monkey				✓ ✓	tropical forest
<i>Coendou mexicanus</i>	porcupine				✓ ✓	tropical forest
<i>Dasybus novemcinctus</i>	armadillo				✓ ✓	tropical forest
<i>Felis pardalis</i>	ocelot				✓ ✓	tropical forest
<i>Felis yagouaroundi</i>	jaguarundi				✓	tropical forest
<i>Lutra annectens</i>	river otter				✓ ✓	tropical forest
<i>Nasua narica</i>	coati				✓ ✓	tropical forest
<i>Odocoileus virginianus</i>	white-tail deer				✓ ✓	tropical forest
<i>Panthera onca</i>	jaguar				✓ ✓	tropical forest
<i>Procyon lotor</i>	raccoon				✓ ✓	tropical forest
<i>Tapirus bairdii</i>	tapir				✓ ✓	tropical forest
<i>Tayassu tajacu</i>	collared peccary				✓ ✓	tropical forest
<i>Ctenosaura pectinata</i>	iguana				✓ ✓	tropical forest
<i>Quercus oleoides</i>	oak				✓	tropical forest
<i>Sylvilagus brasiliensis</i>	forest rabbit				✓	tropical forest

Note: See Feddema 1993 for complete list. LZ = littoral zone; ST = short tree savanna; CP = coastal plain; P = piedmont.

grass and other herbaceous plants. This zone floods annually during the rainy season due in part to poorly draining soils. Parts of this zone positioned close to the brackish water estuary can be saline, and saltpans sometimes appear during the dry season. The soils in some other low lying sections of this zone are not salty and remain humid well into the dry season. The pith of *Palma real* is edible, as is the nut of the coyol palm (Clark 1994, 67), and it is likely that palms were an important dietary component for preagricultural populations in this region, as elsewhere in Central America (Hoopes 1995; Piperno and Pearsall 1998). As palm sap can be fermented this may have served as an alcoholic beverage prior to the production of maize beer (Blake et al. 1992a; Piperno, this volume). Medium and small sized game, including deer, peccary, armadillos, and tigrillos, are attracted seasonally to this zone (Clark 1994; Helbig 1964; Table 6.1), where important building ma-

terials are also found in abundance (e.g., palm thatch and wild bamboo; Clark 1994). Today the area is primarily used for grazing cattle (Clark 1994).

The coastal plain proper was once covered with a mix of tropical deciduous forest, riparian formations, and evergreen tropical forest (Clark 1994). A gradient of forest types, from evergreen forest near the mountains, to tropical deciduous forest closer to the coast, results from variations in rainfall and drainage on the coastal plain. Rivers and seasonal streams divide the coastal plain into a mosaic of riparian and forested habitats. This mosaic was home to at least 20 different mammal species, 126 bird species, 51 different reptile species, and 21 species of fish (see Clark 1994, 73 and Appendix 1). A selection of these is presented in Table 6.1. This list includes several species such as tapirs and peccaries that are no longer found in the region today (Voorhies 1976) due to their extirpation

by humans. Many kinds of fruit-bearing trees also are available in this forested environment, including sapodilla, cacao, papaya, avocado, guanabana, and guayaba (Clark 1994). The best agricultural lands also occur within this well-drained zone, and horticulture, principally the exploitation and ultimate cultivation of root crops, likely started relatively early in this and other tropical forests (Piperno and Pearsall 1998). Forest clearance would have created small microhabitats in the forest, and paleoenvironmental records for the region suggest that burning and forest clearing started with the earliest visible occupation of the coast and intensified during the Formative Period (after 3500 B.P.) as maize-based food production became more established in the region (Jones and Voorhies 2004). Burning promotes the growth of herbaceous plants and tubers, so would have provided the needed space for fields, but this practice would also have reduced the habitat preferred by larger game animals such as deer and peccary. Today, large pastures are maintained over vast parts of this zone while extensive oil palm and banana plantations and cattle ranches cover much of the region.

The piedmont zone that borders the coastal plain is covered with lower montane rain forest due to higher annual rainfall (Miranda 1975). The rain forest has a high canopy (25–40 m) with dense undergrowth. Once the density of game animals was relatively high in this zone. It is likely that people living in communities on the coastal plain during the Archaic and Formative Periods hunted game in the piedmont region. The lower piedmont is particularly productive because it is well drained, receives plentiful rain, and has highly fertile soil (Table 6.1). Seasonal temperature variations are greater at higher elevations, reducing the growing season for maize, and either limiting the productivity of certain tropical lowland plant species or excluding them altogether (e.g., cacao; Clark 1994).

Determining the frequency and distribution of plant and animal species within each of these environmental zones during the Archaic and Formative Periods is difficult due to natural and

substantial human-induced changes to the environment. The archaeological record for the region is fragmentary, leaving gaps in our current knowledge regarding environmental fluctuations during the Holocene. Radical changes in coastal habitats occurred until sea-level stabilized between 9000 and 7000 B.P. As sea-level stabilized after 7500 B.P., open and productive estuarine lagoons formed along the coast. Tropical deciduous and evergreen forests also covered the coastal plain by this time (Jones and Voorhies 2004). Marsh habitats were more restricted in the Early Holocene compared to today, but developed more fully during the Middle and Late Holocene as estuarine lagoons filled with sediment. The monsoonal rainfall regime was operating in this region by at least 7500 B.P. (Kennett and Voorhies 1995, 1996; Voorhies et al. 2002), but annual, decadal, centennial, and millennial climatic changes are evident in proxy climate records from elsewhere in Mexico and Central America (Voorhies and Metcalfe n.d.). Forest burning and clearing is also evident in pollen records for the region starting as early as 7000 and intensifying after 3500 B.P. Burning provided space for growing root crops, and possibly maize, but the destruction of forest habitat and hunting surely had decreased encounter rates with medium and small animals.

RETURN RATES FOR TROPICAL LOWLAND RESOURCES

The adoption of maize and the development of maize-based food production in the Soconusco region resulted from a series of individual decisions regarding diet choice made by people over several millennia. These choices were made in specific socioecological settings that resulted from changing environmental conditions, both natural and human induced, and fluctuating social landscapes impinging on the availability of resources, especially territoriality and increases in social complexity. Optimal foraging theory (OFT) predicts that foragers will economize with respect to dietary choice, selecting resources, or patches, that maximize the rate of energy gained

per unit energy expended in locating, catching/collecting, and processing prey. Dietary choice is therefore constrained by the availability of resources and social factors limiting access to them such as food taboos or territoriality. Given these environmental and social constraints, the most efficient food acquisition strategies available, it is argued, would be favored by natural selection because extra resources, or time saved, can be invested in additional offspring or provisioning existing offspring or mates. Nutrition and overall health have also been directly correlated with fertility and child mortality rates in different societies (Butz and Habicht 1976; Hill et al. 1987; Moseley and Chen 1984).

Ranking wild resources from highest to lowest returns helps determine the most likely dietary mix in a region and can be used to predict changes in diet breadth when ecological conditions change (e.g., depressed availability of higher ranked resources; Cannon 2003). Whether or not a new cultigen is incorporated into the dietary regime of a forager should be related to the availability of highly ranked wild resources and overall diet breadth (Winterhalder and Goland 1997). Ethnographic studies support the notion that caloric returns, rather than food preference, are robust predictors of diet choice (Hill et al. 1987; Winterhalder and Smith 2000). These studies also show that the size of a resource alone is not a good predictor of these dietary rankings, because resource value results from the caloric value of the resource minus the costs of acquisition and processing. Estimating return rates in prehistoric settings is challenging because each estimation depends upon encounter rates, procurement/processing techniques, and transportation costs, all of which are not directly knowable from the archaeological record. The costs and benefits of exploiting certain types of resources must be inferred from ethnographic studies within similar ecological contexts where this kind of economic data is collected and quantified, and/or from experimental studies that estimate resource return rates for labor investment in producing various technologies.

We examine two ethnographic studies from other tropical forest settings in the New World to garner the economic data needed to estimate return rates for different resources since first-hand observations of foraging practices in the Soconusco region are not available because traditional systems of agriculture and food extraction have given way to larger-scale ranching and cash-crop agriculture. One of these studies was conducted by James Nations and Robert Nigh (1980) among the Lacandon Maya, a small-scale farming/foraging population that re-colonized a portion of the southern Maya lowlands (Chiapas, Mexico) several centuries ago. Re-colonization of this region followed a long period of tropical forest regeneration that ensued with the collapse and abandonment of this area by the Classic Period Maya (AD 250–900; Webster 2002). We consider the foraging practices of these people to provide an apt analogy to the strategies practiced by early foraging and farming populations in the Soconusco region. Unfortunately, detailed information regarding the return rates of different plants and animals were not recorded in this study. To remedy this situation we turn to a second study conducted among Aché foragers who occupy a section of tropical forest in the Amazon and where a detailed study of return rates on a similar suite of resources has been conducted (Hill et al. 1987). We recognize that these data are not ideal, but we argue that they provide at least an approximation of dietary rankings in the forested coastal plain and piedmont zones within the Soconusco region. Ultimately, we are interested in comparing return rates of locally available wild resources with estimated rates of return for maize agriculture at various points in the past (see Tables 6.4 and 6.5 for estimated rates of return for maize-based food production).

The Lacandon Maya practice a diverse land-use system that capitalizes on different resource types from the primary and secondary forest and a variety of aquatic habitats; marshes, rivers, lakes, and streams (Nations and Nigh 1980, 8). At the heart of the Lacandon system is a form of slash-and-burn, or swidden, agriculture, where

TABLE 6.2
 Selection of Plants and Animals Targeted by the Lacandon Maya of Chiapas, Mexico

SPECIES	COMMON NAME	USE
<i>Crassidix mexicanum</i>	grackle	meat
<i>Cuniculus paca</i>	paca	meat
<i>Dasyprocta mexicana</i>	agouti	meat
<i>Dasyopus novemcinctus</i>	armadillo	meat
<i>Didelphis azarae</i>	opposum	meat
<i>Mazama americana</i>	brocket deer	meat
<i>Procyon lotor</i>	raccoon	meat
<i>Sciurus aureogaster</i>	red squirrel	meat
<i>Sciurus deppei</i>	forest squirrel	meat
<i>Sylvilagus brasiliensis</i>	rabbit	meat
<i>Odocoileus virginianus</i>	white-tailed deer	meat
<i>Tayassu tajacu</i>	collared peccary	meat
<i>Annona scleroderma</i>	wild annona	fruit
<i>Brosium alicastrum</i>	breadnut	fruit, seeds
<i>Chamaedorea sp.</i>	guatapil palm	heart, fruit, roofing
<i>Diospyros digyna</i>	zapote prieto	fruit
<i>Ficus sp.</i>	amate	edible bark; fiber
<i>Inga spuria</i>	chalahuite	fruit
<i>Manilkara zapota</i>	sapodilla	fruit
<i>Pachira acuatica</i>	water spote	fruit
<i>Persea americana</i>	wild avacado	fruit
<i>Pachychilus indoium</i>	river snail	meat
<i>Pomacea flagellata</i>	apple snail	meat
<i>Astyanax faciatus</i>	sardine	meat
<i>Ictiobus mevidionalis</i>	pig fish	meat
<i>Rhamadin guatemalensis</i>	catfish	meat
<i>Hyla baudini</i>	tree frog	meat
<i>Thynophrynys dorsalis</i>	marsh frog	meat
<i>Dermatemys mawi</i>	river turtle	meat
<i>Kinosternon sp.</i>	small mud turtle	meat
<i>Crocodylus acutus</i>	yellow river crocodile	meat
<i>Crocodylus moreletti</i>	swamp crocodile	meat

Note: Data from Nations and Nigh 1980.

portions of the tropical forest are cleared and burned to grow maize and other domesticated plants (discussed below). Fields are used for several years, then abandoned to regenerate into forest. Areas of secondary forest growth, and presumably other naturally cleared areas, provide young shoots and saplings and attract a variety of game animals (Nations and Nigh 1980, 17; Table 6.2). Of these animals, white-tail (*Odocoileus virginianus*) and brocket (*Mazama*

americana) deer are hunted most frequently. Because of this, their populations are monitored closely; there is some evidence to suggest that deer populations are managed to a certain degree. Although deer are the favored game in this area, a range of medium and small game animals, paca (*Cuniculus paca*) and collared peccary (*Tayassu tajacu*), are also targeted. These animals spend much of their lifecycle in primary forest habitats and aquatic-terrestrial ecotones;

TABLE 6.3

Return Rates for Selection of Animals Analogous to Those Present in the Soconusco Region during the Archaic Period

	SCIENTIFIC NAME	CAL/HR/PERSON
Brocket deer	<i>Mazama americana</i>	15,398
Biaju fruit	<i>Philodendron sellam (ripe)</i>	10,078
Coati	<i>Nasua nasua</i>	7,547
Virella fruit	<i>Campomanesia zanthocarpa</i>	6,417
Collared peccary	<i>Tajassu tajacu</i>	6,120
White-tipped peccary	<i>Tajassu pecari</i>	8,755 ¹ ; 5,323
Paca	<i>Cuniculus paca</i>	4,705
Pretylla fruit	<i>Ficus sp.</i>	4,414
Brovilla fruit	<i>Casimiroa sinesis</i>	4,181
Kurilla fruit	<i>Rheedia brasilense</i>	3,245
Pychikyrtalla fruit	<i>Annoa sp.</i>	2,835
Membe fruit	<i>Philodendron sellam (unripe)</i>	2,708
9-banded Armadillo	<i>Dasypus novemcinctus</i>	13,782 ² ; 2,662
Palm fiber and shoot	<i>Arecastrum romanzolfianum</i>	2,436
Palm fiber starch	<i>Arecastrum romanzolfianum</i>	3,219 ³ ; 2,246
Challa fruit	<i>Jacaratia sp.</i>	2,549
Boilla fruit	<i>Chrysophyllum gonocarpum</i>	2,884
Palm nut	<i>Acromia totai</i>	2,243
Large palm larva	<i>Calandra plamarum</i>	2,133
Roots	<i>Dioscorea hispida</i>	1,739
Palm growing shoot	<i>Arecastrum romanzolfianum</i>	2,356 ⁴ ; 1,584
Capuchin monkey	<i>Cebus apella</i>	1,370
Small palm larva	<i>Rhynophorus palmarum</i>	1,331
Bamboo larva	Unknown	936

Note: See Hill et al. 1987 for details. 1) First number does not include tracking time. 2) Second number includes optional processing time. 3) Men's return rate is listed first. 4) First number is for animals encountered in the forest and the second is for animals excavated from underground.

reductions in game animals associated with primary forest destruction are well documented in the Lacandon region. The forest also provides a range of edible fruit, bark, or in the case of several palms species, shoots and edible piths or hearts, and a range of reptiles, amphibians, fishes, and invertebrates (e.g., snails) are taken from rich freshwater habitats.

Similar to the Lacandon Maya, the Aché of Paraguay combine small-scale farming activities with hunted and gathered wild foods from the tropical forests of the Amazon (Table 6.3; Hill et al. 1987, 5). Although there are clear differences between the Amazon and the tropical forests of Mexico, a comparison of the resources used shows that many of the same mammal species

and a comparable range of fruit trees, palms, and other edible plants were targeted by both groups. Further examination of the return rates recorded in the Aché case indicate that larger animal species are among the highest-ranked resources, edging out many of the available plant species in the Amazon forest. Some animal species have return rates that fall below or within the range of most plants, most notably paca and monkey, owing to high pursuit and/or processing time (Hill et al. 1987). Fish, armadillos, rabbits, and grasshoppers, if effectively taken in large numbers, can have return rates that rival the largest and most naïve game animals (see Madsen and Schmitt 1998). Post-encounter processing costs can cause highly varied rates of return for the

same resource (e.g., palms; Hill et al. 1987). We suspect that tubers were one component of the diet in the Soconusco region during the Archaic Period; however, as in other parts of the world (Flannery 1973), we have no direct archaeological evidence for this practice (see below). Modern-day foragers in tropical forests of the Philippines have return rates on wild tubers between 484 and 1739 cal/person/hour (Eder 1978). Piperno and Pearsall (1998) have pointed out that if the larger animal taxa were reduced in the tropical forest, wild and domesticated tubers were likely exploited along with other low-ranking plant species.

Return rates for tropical forest resources should be considered relative to those found in the littoral zone. Of these, the archaeological record suggests that fish and shellfish were the most important in the Soconusco region (Clark 1994; Kennett et al. 2002; Voorhies 1976; Wake et al. 2004).⁴ The most abundant and concentrated shellfish species in the littoral zone are marsh clams (*Polymesoda radiata*). Several studies provide information regarding the return rates on the collection of somewhat comparable species of shellfish. Based on experimental work, Jones and Richman (1995) determined that mussel beds on the central coast of California produced about 500 cal/person/hour. In a classic ethnographic study of shellfishing among the Anbarra of Northern Australia in Arnhem Land, Meehan (1977, 524) determined that skilled women collecting clams (*Tapes hiantina*) had return rates in the range of 1000 cal/person/hour. More recently, Bird and Bliege Bird (2000) have quantified the relative return rates for different shellfish species from the reefs of the Meriam Islands of Australia (Torres Strait). In this study, the profitability for adults collecting shellfish varied greatly (300 to 6200 cal/person/hour), and was dependent upon the species targeted. Sunset clams (*Asaphis violascens*) are the most comparable to the species available in the brackish water lagoons of the Acapetahua Estuary and these provide return rates of approximately 400 cal/person/hour. Based on these data we suspect marsh clams

had return rates of between 500 and 1000 cal/person/hour.

Similar to shellfishing, return rates for fishing are dependent upon the overall productivity and character of the targeted fish species and the technology available at the time of capture or harvest. Many sophisticated fishing techniques and devices are known from ethnographic and ethnohistoric studies around the world (Aswani 1998; Lindström 1996; Winterhalder 1981b). Lindström (1996) has conducted a comprehensive study of return rates for fishing with ethnohistoric and experimental data from the Truckee River Basin on the western edge of the Great Basin (California/Nevada). Although these data were collected from a riverine context, it provides at least a proxy for fishing in the Soconusco littoral zone. Lindström calculated return rates for different types and sizes of fish using various fishing technologies. The key observation is that return rates for fish are highly variable and dependent upon the technology used, the season of capture, spawn or non-spawn, and the size of fish (200 to 40,000 cal/person/hour). The small size of some fish vertebrae found in Archaic Period shellmounds in the Soconusco suggest that nets were being used (Cooke et al. 2004). Based on comparable technology in Truckee River Basin, we estimate that fishing in the Soconusco wetlands would produce return rates in the 2000–5000 cal/person/hour range, somewhat comparable to small-sized game and a range of fruit bearing trees and palms. This estimate does not include the manufacture and maintenance of nets, fishing tackle, and boats, investments that would have reduced return rates significantly.

Once reasonable return rates are established for different food types, the economic rational of HBE and the diet-breadth model can be used to make several predictions about prehistoric foraging behavior that can be tested subsequently with archaeological data. The model predicts that as the abundance of higher-ranked prey species increases, the variety of resource types will decrease. Logically, the reverse also follows: if the abundance of high-ranked resources

decreases, diet-breadth will increase. This means that potential prey types will enter a forager's diet based on the abundance of higher-ranked resources and not simply contingent upon immediate value. The availability of high-ranked resources is often population dependent. In other words, as the density of human foraging population increases, the availability of the highest-ranked prey species, such as deer populations, will usually decrease. Climate change may also decrease the availability of high-ranked prey as this clearly occurred at the end of the Pleistocene Epoch throughout much of the New and Old Worlds (Piperno and Pearsall 1998). In the Soconusco case, the archaeological record suggests that the highest-ranked species in the Holocene included medium and small sized game animals and fruit.

As a result of the spatial compression of biotic communities in the Soconusco region, people living on the coastal plain could exploit a variety of resource zones within a 15–30 km radius of their villages. Diet choice has ramifications for settlement location; foragers in this region decided where to establish base camps, which resources to exploit residentially, and which to exploit logistically. Where settlements were located was related to the natural differences in resource density and seasonal availability. The degree of mobility at any given time would also have been restricted by territoriality and subsistence practice, whether foraging or farming. Once foragers established encampments, additional constraints on resource acquisition were imposed by the transportation costs incurred from central place foraging. We now turn to central place foraging theory and our best estimates of Archaic Period subsistence and settlement prior to the development of more intensive maize-based food production during the Formative Period.

CENTRAL PLACE FORAGING IN THE SOCONUSCO

Central place foraging theory provides a point of departure for modeling pre-village, Archaic Period foraging strategies and the development of

settled village life and food production in the Soconusco region. Based on the compressed nature of habitats along this stretch of coast, foragers could choose among a number of alternative locations. Important factors for selecting residential base locations in this region included the availability of drinking water, firewood, and well-drained land to establish a community. Based on these criteria, potential settlement locations were available on slightly higher locations along the inland periphery and islands of the littoral zone, seasonally within the short tree savanna, on the coastal plain, and in the piedmont zone. But not all these zones are equally attractive. Prior to the historical excavations of drainage canals, seasonal flooding in the short tree savanna would have periodically reduced the availability of suitable settlement locations, but old sandbars and small knolls would have provided dry, habitable locations throughout the year. Social factors, particularly territoriality, which would limit the location of settlements on the coastal plain, increased with population growth, environmental infilling, and controlled access to resource patches by certain individuals and groups in the region during the Formative Period (Blake and Clark 1999). The biotic communities, from the littoral zone to the piedmont, provided a diverse range of resources that had variable rates of return. Resource return rates also fluctuated seasonally. For example, in the littoral zone, shrimp and fish increased during the dry season compared with the wet season. Beyond base-level criteria for water, fuel, etc., central place foraging theory provides a set of principles for estimating the optimal settlement locations in the region. The model predicts that, all other variables being equal, foragers will select residential base locations that maximize net central place foraging returns given the pursuit, handling, and transport costs of different sets of resources in each biotic zone (Cannon 2003).

Based on central place foraging principles we would predict that, in the absence of restrictive territorial behavior of other groups and human induced resource depression, Archaic

Period residential bases would have been positioned on the coastal plain adjacent to rivers. Most of these inland locations did not flood on an annual basis and provided easy access to wood for fuel and building. They also were well-positioned for people to exploit a diverse range of animal and plant resources, including deer and valuable tree crops like avocados. Clearing patches in the forest through burning would have promoted the growth of some plant species (Piperno and Pearsall 1998) and possibly attracted deer to feed on new plant growth. Although seasonal fluctuations in forest resources would have been present, perhaps they were well-balanced on an overall annual basis. Over time, population-dependent increases in burning of tropical forest and more intensified hunting near the residential bases would have led to reduced populations of deer and peccary, the expansion of diet breadth, more distant logistical forays, and ultimately the relocation of residential bases. In this changing context, toward the end of the Archaic Period, the coastal littoral zone may have become a viable zone for residential bases.

The establishment of residential bases on the coastal plain during the Archaic did not preclude the use of resources from other, more distant, biotic communities through logistical foraging and/or sexual division of labor (Zeanah 2000, 2004). All resource zones in the Soconusco region would have been within a 15 km foraging radius of residential bases located in the middle of the coastal plain. Which resources were exploited depended upon people's overall dietary breadth at residential bases, along with the pursuit, handling, and transportation costs of more distant resources. These criteria place limitations on the types of resources pursued (Cannon 2003); how they are processed (Bird and Bliege Bird 1997); and the load size needed to make a trip pay off (Barlow et al. 1993). The maximum transport distance (MTD) is an index, developed by Jones and Madsen (1989) in the Great Basin, that takes these variables into consideration, MTD being the distance that a resource can be car-

ried before the calories in the load are exceeded by the costs of procuring and transporting it. Given load and volume limitations (~30 kg [or 64.3 liters], Jones and Madsen 1989; Zeanah 2000), the model predicts that people foraging at distant locations will limit themselves to resources of high net value.

Central place foraging theory also has direct implications for how resources are processed during logistical foraging expeditions. Large animal taxa will be butchered with greater attention to the best cuts of meat and, in some instances, weight restrictions will require that a portion of the edible meat be consumed at the kill site or left behind (Zeanah 2000). Drying meat, to reduce water weight, may also be practiced to maximize the net resource delivery rate to residential bases. Processing techniques like these should be reflected in the archaeological record. That is, skeletal elements associated with high utility body parts, e.g., femura and humeri, should be more frequently deposited at residential bases and low utility skeletal elements should occur at logistical foraging camps. Resources in the coastal littoral zone also would have been attractive to foragers living on the coastal plain. Many littoral resources can be collected en masse (e.g., mollusks, fish, shrimp) and processed to maximize net delivery rate to people living in the interior. If residential bases were positioned on the coastal plain, then these littoral resources were likely collected en masse and processed to maximize net delivery rate to residential bases: shrimp dried; fish gutted, beheaded, split and dried; and clams steamed open and the meat extracted and dried (Voorhies 2004; Voorhies et al. 1991).

Ethnographic studies in the Meriam Islands suggest that the degree of shellfish processing is contingent upon travel distance, processing costs, and the proportional value of the resource (Bird 1997; Bird and Bliege Bird 1997). The shell-to-meat ratio in most species of shellfish makes processing advantageous if transport distances are long, although there may be some advantages to keeping shellfish in their shell

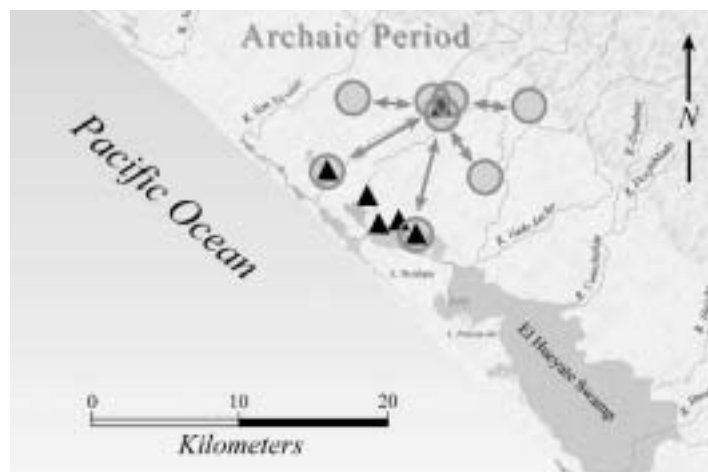


FIGURE 6.3. Central place foraging model for pre-village (Archaic Period) foragers in the Soconusco region (~7500–3,500 cal. yrs. B.P.).

(storage, etc., Kennett 1998). The archaeological implications of processing at special purpose locations in the littoral zone are that shrimp remains, even if preserved, would be rare, cranial elements of fish might be prevalent, and mollusk shells should be common. Shellfish could be collected throughout the year, but people would more frequently visit the littoral zone when shrimp and fish were more available during the dry season. Evidence for permanent occupation of these locations in houses, burials, diverse faunal and tool assemblages should be lacking.

Our Archaic Period central place foraging model for the Soconusco region is displayed in Figure 6.3. In this model, we predict that residential bases were positioned on the coastal plain near rivers. In this period, the forest was cleared from around these central places; wild plants were collected from various forested environments; deer, peccary, and small game were hunted in the vicinity of settlements; and people fished along river courses. Based on the low-level cultivation of some domesticated plants elsewhere in Mesoamerica we suspect that some cultigens were grown close to these settlements. Longer distance logistical trips to the piedmont zone and elsewhere on the coastal plain were employed to hunt larger game animals, and similar forays were used to collect resources in the littoral zone, perhaps more fre-

quently during the dry season months when resources were more abundant.

ARCHAIC PERIOD SUBSISTENCE AND SETTLEMENT DATA

Much of the Archaic Period archaeological record is deeply buried below alluvium and thus fragmentary (Michaels and Voorhies 1999; Voorhies 1996; Voorhies and Kennett 1995), but the data available generally support the central place foraging model proposed here. The archaeologically detectable Archaic Period occupation of the Soconusco coastal plain coincides with the stabilization of sea level between 9000 and 7000 B.P. (Fairbanks 1989). The best evidence for the presence of people during the Archaic Period comes from a series of six large shellmound sites positioned in a line along the coast (Clark 1994; Drucker 1948; Kennett and Voorhies 1996; Lorenzo 1955, Navarrete n.d.; Voorhies 1976, 2000b, 2004). Five of these sites are located in the Acapetahua Estuary, and the other site, Cerro de las Conchas, is situated near the inland margin of the El Hueyate swamp (see Figure 6.1). Shell deposits at Cerro de las Conchas date to between 7500 and 5500 B.P. and currently provide the earliest evidence for human occupation of the Pacific coast of tropical Mexico (Voorhies 2000a; Voorhies et al. 2002). The shellmounds in the Acapetahua Estuary



FIGURE 6.4. Photograph of a Late Archaic Period shellmound (El Chorro) in the littoral zone of the Acapetahua region.

date later, between 5500 and 3500 B.P., but are similar in character to Cerro de las Conchas. Although these shellmounds represent the earliest recognizable human occupation of the coast, earlier sites were probably covered by sediments deposited during the late Pleistocene/early Holocene marine transgression or subsequently by the actively prograding coastline (Voorhies and Kennett 1995). It is likely that small groups of people were living along the coast from the onset of the Holocene. This suspicion is based on clear evidence for human occupation of other parts of Middle America during the terminal Pleistocene and early Holocene (Cooke 1998; Cooke et al. 1996; Cooke and Ranere 1992; Brown 1980; Ranere and Cooke 1991; Piperno and Pearsall 1998; Zeitlan 1984; Zeitlin and Zeitlin 2000).

Work completed at the shellmounds along the Soconusco coast suggests that they were special purpose locations used for exploiting littoral resources, rather than permanently occupied settlements (Kennett and Voorhies 1996; Michaels and Voorhies 1999; Voorhies 1996, 2004; Voorhies et al. 1991). The shellmounds are impressive prehistoric features that form artificial islands within this wetland environment (Figure 6.4). They range in size from 0.20 to 1.17 hectares and are between 3 and 11 meters in

height (Voorhies 2004). Relative to other early sites in the region, they are highly visible in aerial photographs because they are periodically cleared and used in a variety of ways by people living in the littoral zone today. Excavations at these shellmounds indicate that they consist of densely packed layers of marsh clam shell (*Polymesoda radiata*) dating to the aceramic Archaic Period, with an overlying stratum of dark soil containing artifacts, principally ceramics, from later time periods. The Archaic Period deposits are distinctively bedded, with alternating burned and unburned layers of marsh clam shell, that we have interpreted as representing periodic use, rather than continual settlement (Kennett and Voorhies 1996; Michaels and Voorhies 1999; Voorhies 2004). This interpretation is also supported by the general absence of domestic features such as house floors and formal hearths,⁵ a very low diversity of tools, faunal assemblages showing an intensive focus on shallow water lagoonal systems (fish, clams, and possibly shrimp; Kennett and Voorhies 1996; Michaels and Voorhies 1999; Voorhies et al. 1991; Voorhies 1996, 2004). Seasonality data indicate that early in the Middle Archaic Period littoral resources were procured throughout much of the year with an emphasis during the dry season months (Voorhies et al. 2002).

A sediment core placed in the wetlands adjacent to the Chantuto shellmound revealed that the mound extends well beyond its present base. Repeated excavations, and in one case coring, have failed to reach the bottom of any one of these massive accumulations of shell. Terminal dates for these shellmounds fall between 3500 and 3000 B.P. appearing to be coeval with a settlement shift to residential bases positioned just inland of the permanent wetlands, perhaps in the seasonally flooded zone.

Based on the seemingly logistical nature of these shellmounds, we have hypothesized that interior basecamps were positioned on the coastal plain, probably in forest clearings close to surface water and to wild and possibly domesticated food plants (Kennett and Voorhies 1996; Michaels and Voorhies 1999; Voorhies 1996, 2004), as predicted by our central place foraging model. Unfortunately rapid sedimentation rates on this flat coastal plain, associated with seasonal flooding, have obscured much of the record for early interior settlement in the region. A pedestrian survey of the region revealed few sites on the inner slope of the coastal plain that predated the Late Formative Period (Voorhies 1989b). In 1991, we surveyed rivers between Pijijapan and Tapachula in order to discover deeply buried Archaic Period deposits (Voorhies and Kennett 1995). During this survey we discovered one aceramic cultural deposit buried between two and two and a half meters below the surface, but exposed in a natural river cut on the Cacaluta River. Subsequent excavations of this site (Vuelta Limón, see Figure 6.1) unearthed a variety of tools, including groundstone, hammerstones, flakes, and fire cracked rock, suggesting that it was a basecamp (Michaels and Voorhies 1999; Voorhies 1996, 2004). Unfortunately bone and charred seeds were not preserved in these alluvial deposits. However, the absence of ceramics and a single radiocarbon date place the site's terminal occupation at 3800 B.P., near the end of the Archaic Period. Vuelta Limón is located upstream from the Chantuto shellmound in the Acapetahua Estuary, which also dates to the end of the Late Archaic Period, and we suspect

that foragers based at this interior location collected and processed shellfish at Chantuto for transport back to Vuelta Limón. Pollen and phytolith data from the site suggest that palms were in heavy use as building material, and possibly a food source, and that maize pollen was present at very low levels indicating the use of this cultigen by the terminal Archaic Period (see below; Jones and Voorhies 2004). Phytolith data from Vuelta Limón and Tlacuachero, a shellmound site positioned in the coastal littoral, both show evidence for forest disturbance during the Late Archaic Period (after 5000 B.P.).

Although the record is fragmentary, the available data suggest that pre-village foragers in the Soconusco established settlements in forest clearings on the coastal plain and foraged logistically in the littoral zone. It is also likely that these people foraged logistically in the piedmont zone for larger animal taxa, and at other locations on the coastal plain. The material record from the shellmounds strongly supports this hypothesis, as does the more limited evidence for stable interior settlement from Vuelta Limón. Intensive exploitation of highly localized marsh clams from the shallow lagoons in the estuary, combined with large-scale processing through cooking and drying, is also in line with the expectations of central place foraging theory: investment in processing was economically viable given the costs of transporting heavy shells back to interior settlements. Intensive exploitation of shellfish in this way also suggests that diet-breadth was relatively broad starting as early as 7500 B.P., as evidenced at Cerro de las Conchas. This suggests to us that populations of larger animal species were low on the coastal plain due either to predation pressure or because the environment would not support high populations. As a response, human dietary breadth was wide enough to include small marsh clams. The available data also suggest that these settlement and subsistence strategies were remarkably stable for thousands of years (7500 to 3500 B.P.). It was in the context of wide diet breadth and stable subsistence settlement

strategies that maize was first introduced to and experimented with in the region. We now turn to the current state of knowledge regarding the domestication and dispersal of maize as a first step in modeling the incorporation of this cultigen into the Soconusco dietary regime.

DOMESTICATION AND DISPERSAL OF MAIZE

Interest in the domestication of maize has a long, and somewhat controversial, history extending back to the 1930s (Mangelsdorf and Reeves 1939), and a great deal of academic energy has focused upon establishing the progenitor of this important cultigen, argued either to be an extinct wild pod corn (Mangelsdorf 1974, 1986) or the wild grass teosinte (Beadle 1972, 1977, 1980; Galinat 1975, 1988, 1992, 1995). Several species of teosinte (*Zea* spp.) are native to tropical environments in southern Mexico and parts of Guatemala and Nicaragua (Iltis and Benz 2000; Sanchez-Velasquez et al. 2001), with some varieties adapted to semi-arid highland environments above 1800 m (e.g., *Zea mays* subsp. *mexicana*) and others distributed in wetter lowland tropical environments below 1800 m (e.g., *Zea mays* subsp. *parviglumis*). The most recent, and generally accepted, genetic work supports the hypothesis that maize was originally descended from teosinte and was domesticated at ~9200 years ago in southern Mexico; either in the Balsas River Valley (Doebly 1990), or in the highlands of Oaxaca (Matsuoka et al. 2002). These genetic studies suggest that *Zea mays* subsp. *parviglumis* (teosinte), found growing today on well-drained, karstic slopes in the Balsas River Valley (400–1800 m elevation), is the closest wild ancestor to all modern races of maize (Doebly 1990). However, genetic studies also indicate that, of the extant races of maize found today throughout the New World, the most primitive forms occur in the Oaxacan highlands (above 1800 m; Matsuoka et al. 2002). These data suggest that maize was domesticated outside the modern distributional range of the most likely progenitor species (*Z.*

mays subsp. *parviglumis*). Possible explanations for this perplexing pattern are that: (1) wild teosinte (subsp. *parviglumis*) was introduced from the Balsas valley to the highlands where it was subsequently domesticated (Matsuoka et al. 2002, 6084); (2) early Holocene environments favored *parviglumis* at higher elevations (Matsuoka et al. 2002, 6084)⁶ compared with its modern distribution; or (3) the present distribution of extant landraces of maize do not reflect the ancient distribution, and maize was domesticated at low elevations in the Balsas River valley.

Although genetic studies suggest that maize was domesticated early in the Holocene, this has not been corroborated with botanical evidence from well-dated archaeological contexts (e.g., carbonized plant remains, pollen, or phytoliths). Work currently underway in the Balsas River Valley is designed to locate early prehistoric contexts that may contain well-preserved micro- or macro-botanical remains (Piperno, personal communication, 2004). The earliest available evidence for *Zea* comes from microbotanical studies in central Panama and along the Gulf Coast of Mexico (Tabasco). *Zea* starch grains have been recovered from early grinding stones at Aguadulce Rockshelter in central Panama (slightly before 7000 B.P.; Piperno, this volume) and *Zea* phytolith assemblages of the same age have been recovered from prehistoric sediments at Aguadulce and Cueva de los Ladrones, another rock-shelter site in central Panama (Piperno and Pearsall 1998; Piperno et al. 1985). *Zea* pollen grains dating to ~7100 B.P. were also recently recovered from archaeological contexts and wetland sediments in the tropical lowlands of Tabasco (Gulf Coast of Mexico), coeval with the first evidence for forest clearing in the region (Pope et al. 2001). Several microbotanical studies carried out in Northern Belize (Pohl et al. 1996), coastal Guatemala (Neff et al. 2003), coastal Chiapas (Jones and Voorhies 2004), and the Gulf Coast (Rust and Leyden 1994) indicate that maize was one of several cultigens consistently used in the lowland tropics, at least at low levels, by 5000 B.P. These

data help substantiate the early occurrences of *Zea* in Panama and suggest a far-reaching dispersal of maize through the lowland tropics between 7500 and 7000 B.P.

The earliest evidence for *Zea* in the highlands of Mexico comes from fully domesticated maize cobs directly dated to 6250 B.P. at the site of Guilá Naquitz in the Valley of Oaxaca (Benz 2001; Piperno and Flannery 2001). These new dates are slightly earlier than the direct dates on maize cobs from San Marcos and Coxcatlán caves in the Tehuacán Valley (~5500 B.P.; Benz and Iltis 1990; Benz and Long 2000; Fritz 1994a; Long et al. 1989; Smith 1998), originally recovered by MacNeish and studied by Mangelsdorf in the 1950s and 1960s (Mangelsdorf et al. 1967). After decades of work in the highlands, and the clear identification of prehistoric deposits dating prior to 6250 B.P. (Flannery 1986a), micro- and macro-botanical evidence for either teosinte, or a primitive form of domesticated maize, is thus far absent (Piperno and Flannery 2001). Early dispersal of maize through the lowland tropics, and the late arrival of a fully domesticated species of maize in the highlands, supports the hypothesis that maize was domesticated at low elevations in the Balsas River Valley and dispersed widely through the lowland tropics prior to its use in the highlands of Mexico.

There are different varieties of domesticated maize, each with its own agroecological potential and environmental preferences: highlands vs. lowlands, frost resistance, pest resistance, etc. In fact, many landraces of maize are adapted to specific elevations and environments, and are distinct enough that some scholars have argued that maize was domesticated from several different ancestral stocks of teosinte (Galinat 1988). The early *Zea* phytoliths found at Aguadulce Rock shelter in Central Panama dating before 7000 B.P. are morphologically similar to those found in the glumes and rachis of Balsas River teosinte and primitive forms of domesticated maize (Reventador and Maiz Ancho; Piperno, this volume; Piperno and Pearsall 1998, 221). Phytoliths in later de-

posits at the same site are morphologically similar to modern varieties of maize. These data suggest that a primitive variety of domesticated maize was present in Panama just prior to 7000 B.P., well outside the natural range of its progenitor, *Zea mays* subsp. *parviglumus*. Maize macrofossils dating to this early time do not exist, but the primitive form of the phytoliths themselves suggest that this cultigen was morphologically similar to teosinte; with the possible absence of the distinctive cob and its kernels at least partially enclosed by a hard glume (Piperno and Pearsall 1998, 223). These traits made early *Zea* resistant to insect infestation and fungal diseases (Piperno, this volume), but would have contributed to higher post-harvesting processing costs.

The first *Zea* pollen grains (~7100 B.P.) found on the Tabasco coast are small, falling within the range recorded for wild teosinte (48 to 49.8µm; Pope et al. 2001). These data are consistent with the data from Central Panama for an early dispersal of a primitive form of maize through the lowland tropics. Shortly after 7000 B.P., phytolith and pollen assemblages from both Central Panama and Tabasco appear to be morphologically similar to modern maize. However, small *Zea* sp. pollen is relatively abundant at the sites studied in Tabasco until 4500 B.P., and indicates great variability in the morphology of this cultigen through this time (Pope et al. 2001). This suggests early dispersal and continued use at some locations of a primitive form of maize, with subsequent alterations possibly occurring outside of southern Mexico where it was originally domesticated.

Changes in maize did not stop after the clear development of morphologically modern maize, just as distinctive adjustments continue to be made to this plant today (Abbo and Rubin 2000; Martinez-Soriano and Keal-Klevezas 2000). The early maize cobs from Guilá Naquitz (~6250 B.P.) and the Tehuacán valley (5500 B.P.) are remarkably variable in character, but all had rigid rachis that required grain removal by humans if they were to be dispersed and propagated—a clear indication of domestication

(Benz 2001, 2104). Several morphological attributes in these early cobs are intermediate between teosinte and maize, and support the ancestral relationship between these two species (Benz 2001). The earliest maize cobs from Guilá Naqitz were small having fewer rows (two to four) of grain when compared to many modern maize varieties (Benz 2001). Some of the small maize cobs from the Tehuacán valley, thought to be early, have also now been shown to date later in time, but co-occur with cobs of varying sizes until about 4500 B.P. (Benz and Long 2000; Long et al. 1989). This is consistent with the pollen data from Tabasco indicating a mix of small teosinte, and large maize pollen grains starting as early as 7000 B.P., with the persistence of small *Zea* pollen until 4500 B.P. (Pope et al. 2001).

The Oaxacan and Tehuacán specimens suggest that human selection between 6250 and 4500 B.P. sought to maintain or increase the productivity of maize by promoting the naked-grained phenotype and increasing the number of grain-bearing spicklets (Benz 2001). However, the full-sized cobs that we associate with modern maize may not have developed until as late as 3000 B.P. (Benz and Long 2000), when there is clear botanical and stable carbon isotope evidence throughout much of Mesoamerica for more intensive forms of maize agriculture and larger cob sizes (Ambrose and Norr 1992; Benz and Long 2000; Blake et al. 1992a, 1992b; Clark 1994; Feddema 1993; Kirkby 1973; Sheets 2002; Smith 1997a). Evidence from several areas suggests that the varieties of maize available between 4000 and 3000 B.P., although fully domesticated, had relatively small cobs and were not as productive as many varieties of modern maize. A limited number of maize casts in clay from the site of Salinas La Blanca (Middle Formative; Cuadros Phase; ~3000 B.P.; Coe and Flannery 1967), located on the coast of Guatemala, suggest that maize cobs were slightly smaller than many modern varieties. Charred maize cupules and cob fragments ($N = 2280$) recovered from a series of Early Formative Period (3500 to 3000 B.P.) sites

in the Mazatán region of coastal Chiapas, Mexico have 12 row cobs, but are between 20–40% the size of modern maize in the region today (Blake et al. 1992a, 1992b; Feddema 1993).

Not all domesticated varieties of maize have the same agroecological potential, particularly in the lowland tropics, while the types of maize available in Mexico and Central America changed through time. Some of these varieties certainly would have had low return rates relative to other wild alternatives. For instance, one of the hypotheses regarding the late use of teosinte in the highlands, or of an early form of domesticated maize, is that *Setaria* (foxtail grass) cultivation was much more productive (Flannery 1973). This is supported by early evidence for *Setaria* seed exploitation and consumption from Early Holocene coprolite samples collected from dry caves in Tehuacán and Tamaulipas (Callen 1967a). The initial decision to invest time in maize cultivation in the Soconusco region was contingent upon the maize varieties introduced to the region at various times, with the productivity of these varieties correlated to the available alternatives. We now turn to the difficult task of modeling the relative productivity of maize-based food production through time in the Soconusco region.

RETURN RATES FOR MAIZE-BASED FOOD PRODUCTION IN THE SOCONUSCO

In order to compare the economics of foraging vs. farming in the Soconusco, we must estimate the net return rates of maize-based food production during the last 9200 years, the purported date for maize domestication in Central Mexico. Traditionally, farmers in this region annually grew two to three crops of maize, but today in some areas the development of large plantations on the coastal plain has pushed the milpas into more marginal areas of lower piedmont. Maize is grown less often in the lower coastal plain because much of this area has saline soils and/or is flooded during the rainy season (Clark 1994; McBryde 1947), and people living in this zone are also more likely to be engaged in other

economic pursuits such as fishing or saltmaking. Corn and beans were grown together; the first crop planted in May at the beginning of the wet season and harvested in August at the end of the rainy season. The second crop was planted in September and harvested in December and a third crop was sometimes planted in January in humid soils halfway through the dry season then harvested in April (Clark 1994). This third crop was usually planted within old stream channels or on the lower coastal plain close to the water table. Harvested corn was stored in large ceramic vessels or in the rafters of houses (Clark 1994), providing the necessary seed-stock for subsequent crops and food for leaner times of the year. Crops grown on the lower coastal plain were at the greatest risk of failure because of unpredictable changes in rainfall resulting in dry conditions as well as the risk of crop destruction through flooding.

Detailed ethnographic data on the traditional agricultural economy in the Soconusco are not available, but other studies have focused on analogous situations in the lowland tropics of Mesoamerica. We rely upon two ethnographic studies conducted in the Maya lowlands that appear to us to provide the best baseline economic data for establishing estimated return rates for maize agriculture in the Soconusco, the Lacandon Maya of southern Mexico (previously discussed; Nations and Nigh 1980) and the Kekchi Maya that occupy a section of the tropical lowlands in Guatemala (Carter 1969). Both the Lacandon and Kekchi Maya are relatively recent immigrants into these forested habitats and therefore face similar opportunities and challenges to the pioneer populations living in the Soconusco during the Early and Middle Holocene.

We start with the Lacandon Maya of Chiapas, Mexico. These people practice a form of swidden or slash-and-burn agriculture that is widely used by small, relatively dispersed, populations in the lowland tropics of Mexico and Guatemala. In this agrarian system patches of primary and secondary forest are cut, dried, and burned to fertilize the soil and to make way for a suite of domesticated plant species, princi-

pally maize, but including many other plants as well (Nations and Nigh 1980). A range of criteria, including soil and vegetation types, are used to evaluate a potential field location, preferentially locating these fields in well-drained locations. Farmers generally cut primary or secondary forest during the dry months of January, February, and March burning this debris in a highly controlled fashion during the months of May or June. Maize is planted with a digging stick in May or June as the annual rains begin to fall, and a second planting is done 10–15 days later in areas where corn is not sprouting. These fields are planted and harvested for between two and five years and then left to regenerate into forest as other areas are cut and burned to create new fields. Cut fields take approximately 20 years to regenerate into primary forest, so at any given time the land surrounding a Lacandon settlement is a mosaic of primary forest, secondary forest at various stages of regeneration, and fields under cultivation. In the Lacandon case, plots cut from primary forest produce approximately 45 bushels of shelled corn per acre (2.8 metric tons per hectare; Nations and Nigh 1980, 11). This estimated yield is well within the range for other slash-and-burn farmers living in the lowland tropics of Mesoamerica (33 to 50 bu/acre, see Barlow 2002, 71; Stadelman 1940) and for traditional farmers in the Soconusco region (~44 bu/acre for first harvest; Clark 1994). Slightly smaller yields are reported for crops planted in fields cut from secondary forest and for the second crop when two are grown in the same field annually.

To our knowledge the most comprehensive study of labor requirements necessary for slash-and-burn agriculture in a lowland tropical setting were conducted by William Carter among the Kekchi Maya of Guatemala (Carter 1969). In this study, data was collected on the time allocated to a variety of agricultural tasks including: (1) selecting field locations, (2) cutting (slashing) low-story vegetation, (3) felling large trees, (4) creating fire breaks to control fires, (5) firing vegetation, (6) planting corn, (7) fencing sections of gardens to protect crops, (8) tending, watching

TABLE 6.4
Kekchi Maya Labor Costs for Maize-based Food Production

ACTIVITY	PRIMARY	LONG FALLOW	SHORT FALLOW
Site Selection	4	2	2
Slashing	24	40	30
Felling	107	0	0
Firebreaking	4	9	9
Firing	2	1	1
Planting Maize	16	16	16
Fencing	2	2	2
Watching	16	16	16
Weeding	1	20	38
Reeping	35	40	35
Granary Building	8	8	8
Carrying	37	46	37
Storing	19	20	19
Total	275	221	212
Return Rate	1801	1845	1854

Note: Labor costs (person hours per acre) are for maize fields cut into primary forest (8+ years growth), long fallow plots (4–7 years growth), and short fallow plots (1–3 years growth); data from Carter 1969. Final row is the calculated return rate for maize-based food production given yield estimates of 45 bushels of shelled corn per acre and the labor costs associated with the different types of fields (cal/person/hour; see text).

and weeding fields, (9) harvesting (reaping), (10) carrying the harvest to granaries, (11) building granaries, and (12) storing crops. These data are shown in Table 6.4 for fields cut into primary forest (8+ years growth), long fallow plots (4–7 years growth) and short fallow plots (1–3 years growth). These data reveal that the average labor input per acre of land cleared in primary forest is 275 person hours; for land cleared in long fallow plots is 221 person hours, and for land planted in short fallow plots of corn stalks and weeds is 212 person hours. In both the Lacandon and Kekchi Maya cases, there is a slight preference for clearing secondary growth simply because it takes less work to clear these fields. However, the benefits of planting in fields cut from primary forest are that these plots of land can produce slightly higher yields in the first year and weeding is less arduous when compared to low fallow plots. Table 6.4 shows clearly that the gains in labor cost made by not clearing primary forest are largely lost due to the rapid

incursion of weeds into these secondary plots, together with the labor required to remove them.

Given the yield and labor investment data presented above we can now estimate the return rate for maize-based food production on the Soconusco coastal plain. This estimate only applies to farmers using relatively modern varieties of maize with high yields and therefore does not apply to populations living in this region prior to ~3000 years ago (see below for these estimates). We calculate the caloric return rates (cal/person/hour) following the procedure established by Barlow (2002). In this estimate, the return rate (cal/person/hour) for maize farming is equal to:

$$\frac{[x \text{ bu/acre}] [25.2 \text{ kg/bu}] [3550 \text{ kcal/kg}]}{\Sigma y \text{ hr/acre} + [x \text{ bu/acre} * 43.55 \text{ hr/bu}]}$$

Where x bu/acre is equal to the bushels of shelled, dried maize kernels harvested per acre;

TABLE 6.5

Estimated Return Rates for Maize-based Food Production in the Soconusco at Different Intervals during the Holocene

	BU/ACRE	HR/ACRE	PROCESSING (BU/HR)	RETURN RATE CAL/PERSON/HOUR
3000 BP-Present (modern-2 crop)	45.00	212	43.55	1854
4499–3001 BP (60% modern)	27.00	221	45.72	1600
7000–4,500 BP (40% modern)	18.00	275	47.90	1416
7100 BP	10.10	212	50.08	1259
9200 BP	2.43	100	52.26	958

25.2 kg/bu represents the average weight (kg) of shelled, dried maize kernels per bushel; 3550 kcal/kg equals the caloric value for maize; Σ y hr/acre equals the time in all field activities (clearing, planting, weeding, etc., see Table 6.4); 43.55 hr/bu, this equals the time needed to grain, pound, and grind one bushel of harvested, dried maize into meal using stone manos and metates (see Barlow 2002). Estimated return rates for growing maize in different field types, e.g., primary forest, etc., are presented in the final row of Table 6.4. These are based on yield estimates of 45 bushels of shelled corn per acre, which seems reasonable given the similarity between Lacandon maize yields and those recorded historically in the Soconusco region (Clark 1994). Post-harvest processing costs of shelling and grinding dried maize into meal are also accounted for in this estimate and represent between 45 and 90% of all time spent farming (Barlow 2002, 72). Based on this model, we estimate the return rates for maize-based food production in the last 3000 years to be between 1800 and 1860 cal/person/hour, a range dependent upon the type of field planted; whether in primary forest or long/short fallow plots.

Estimating maize productivity in the past is more difficult and must be inferred from harvesting experiments and macrobotanical remains (Flannery 1973, 1986a). Table 6.5 outlines our best estimates for maize productivity during the last 9200 years, since its initial domestication. Pollen and phytolith assemblages

from Tabasco and Central Panama (Piperno and Pearsall 1998; Pope et al. 2001), suggest that a primitive form of maize had dispersed out of Central Mexico sometime between 7500 to 7000 B.P. The early phytolith assemblages in central Panama, dating before 7000 B.P., are similar to those found in the glumes and rachis of teosinte and suggest that early maize had small, hard kernels, closer to the progenitor species than modern maize (Piperno and Pearsall 1998). Our calculations for the earliest collection and cultivation of *Zea* in Central Mexico (~9200 B.P.) is based on teosinte harvesting experiments conducted by Flannery and Ford in the 1970s (*Zea mays*, subsp. *mexicana*; Flannery 1973, 1986a). In these experiments teosinte produced approximately 2.43 bushels of seed per acre. We assume lower in-field labor costs compared with modern maize farmers because wild stands of teosinte were likely managed rather than planted and most of the initial labor costs were limited to time spent harvesting (~100 hrs). However, we have increased the estimate for post-harvest processing by 20% because kernels were harder and more difficult to process.⁷ Therefore we suspect that the return rate for the earliest maize harvests in the central highlands of Mexico prior to the spread of this domesticated was approximately 960 cal/person/hour. This low estimate for early maize is not surprising given that return rates for most wild grasses fall below 1000 cal/person/hour (O'Connell and Hawkes 1981; Simms 1987).

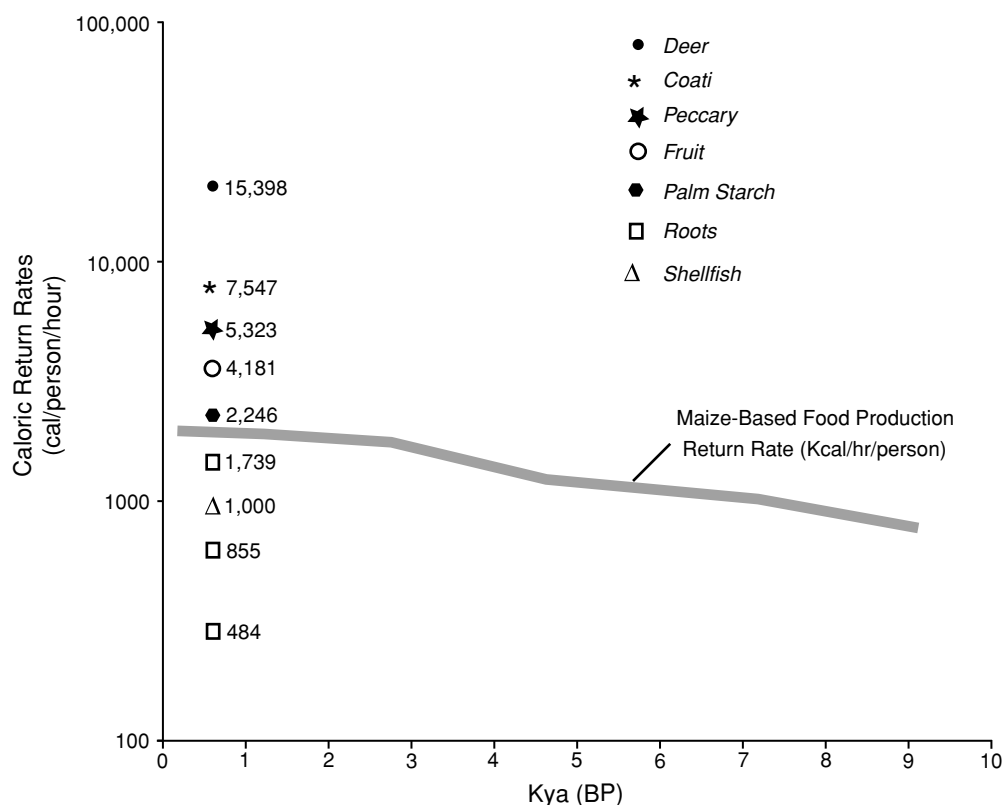


FIGURE 6.5. Energetic returns for foraging and maize-based food production through time.

We estimate the yield of the primitive maize that spread out of Central Mexico (ca. 7100 B.P.) to be comparable to teosinte from Flannery and Ford's highest yield plot located in an abandoned maize field (10.10 bu/acre). Assuming that maize was grown at a low level and that forests were already cleared near Archaic Period settlements we use a labor cost estimate of 212 hr/acre for this early maize, comparable to labor costs in fields where trees have been cleared (see Table 6.4). Field costs are increased after 7000 B.P. based on pollen and phytolith evidence from cores and archaeological sites in the Soconusco region suggesting intensified forest clearance (Jones and Voorhies 2004). Yield estimates after 7000 B.P. are calculated as a percentage of traditional maize productivity in the Soconusco and early macrobotanical evidence

for small, but increasing, cob sizes in Mesoamerica (Benz 2001; Benz and Long 2000; Blake et al. 1992a; Clark 1994; Feddema 1993; Long et al. 1989). Processing costs after 7000 B.P. are decreased incrementally until 3000 B.P. when morphologically modern varieties of maize are thought to be widely available in Mesoamerica.

Figure 6.5 shows the estimated changes in maize productivity through time relative to a selection of wild resources that were available in the region during the Archaic Period. Compared with other alternatives, maize, particularly early varieties of maize, was ranked relatively low, within the range of some small animals and most plant foods. Initially maize probably had lower return rates than locally available tubers and palms, but was higher in protein than these plant foods (Piperno and Pearsall 1998). A possible added

benefit of early maize was also the high sugar content of its stalk and the potential of using this sugar juice for making beer (Smalley and Blake 2003). Therefore, it would appear that the initial incorporation of maize was a response to decreases in the availability of higher ranked prey items and increases in diet breadth or the benefits of this plant for brewing beer; or perhaps a combination of these two factors. The logistical exploitation of small, although highly localized, mollusks by 7500 B.P. is an indication that diet breadth had significantly expanded by this time and that populations of larger game animals had been reduced. The reduction of larger prey after 7000 B.P. was probably exacerbated by deforestation associated with developing agro-economies. We now turn to an adapted form of the Lotka-Volterra predator-prey model to explore the variables involved in the incorporation and intensification of maize-based food production. We develop several variants of this model to explore the adoption and commitment to maize-based food production. These variants are then considered against the available data for the region.

A CULTIVATOR-CULTIGEN MODEL

An adapted form of the Lotka-Volterra predator-prey model is employed here to explore the interactive and symbiotic effects between human foragers and *Zea* in the Soconusco region. This model was originally designed to explore the synergistic population effects between predators and their prey. The basic assumption of the model is that predator population sizes are related to prey population sizes, and vice versa, and that a functional response occurs between the two—the rate of prey capture by a predator is a function of prey abundance (Gotelli 1998).

The Lotka-Volterra model is the simplest model of predator-prey interactions and was developed independently by Lotka and Volterra.⁸ It has two variables, P and V , and several parameters: V is the density of prey, P is the density of predators, r is the intrinsic rate of prey population increase, δ is the capture efficiency coefficient, b

is the reproduction rate of predators per prey eaten, and m is the predator mortality rate. This mathematical model shows how predator populations keep populations of prey species in check. If the predator population is relatively low, the prey population will increase in size, and often results in population cycles that are stochastic in form.

In order to better match reality in terms of human/environmental interactions, we adapted the Lotka-Volterra model to the cultivator (human)-cultigen (maize) relationship that developed in the Soconusco region. Cultivator-cultigen interactions are unlike the relationship between predator and prey because plants, particularly potential cultigens, respond differently to human predation, intensified collection, and consumption. Cultivation and consumption can lead to selective increases in seed size, greater plant densities, and overall increases in cultigen productivity (e.g., Rindos 1984), rather than decreases in density or size. The cutting and burning of forest habitat and the creation of fields also increases the overall density and yield of cultigens due to economies of scale and sometimes creates a functional increase in cultivator population levels. This idea is supported by the close correlation between maize productivity and population densities in the Valley of Oaxaca, Mexico (Kirkby 1973). We argue that this model is appropriate for exploring the interactive processes at work in proto-agricultural biotic communities because net increases in cultigen acquisition, leading to more intensified food producing practices, are a function of changes in the rate of harvesting efficiency and cultigen density rather than intrinsic increases in cultivator population; although the context for adopting these cultigens in the first place may be related to population-dependent reductions in higher ranked prey. Further, the density and rate of cultigen harvest are also dependent on the food-quality being produced due to the demands of the cultivator.

We employ one variant of the Lotka-Volterra model known as the type III functional response. This model allows for changes in feeding be-

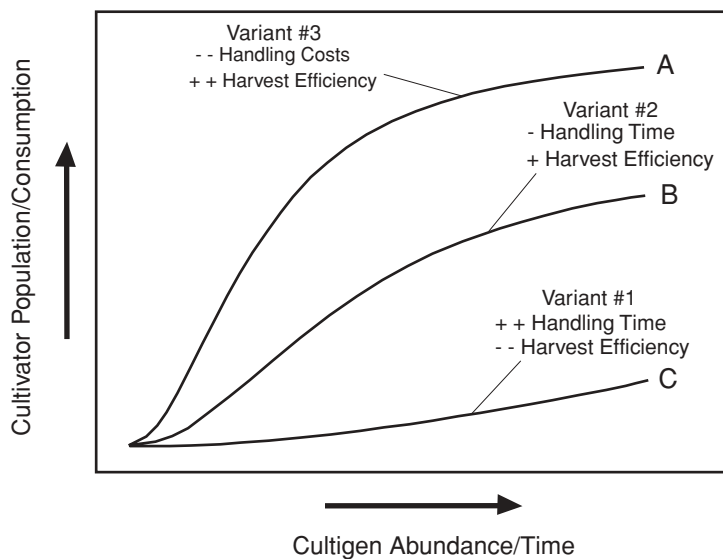


FIGURE 6.6. Graphical representation of three simulations (300 iterations each) of the Lotka-Volterra model with incremental changes in handling costs and harvest efficiency.

havior in response to resource density and availability. The functional response can occur when (1) cultivators switch to cultigens or other resources that become more common; (2) increases in harvest efficiency changes with the abundance of cultigens; and/or (3) costs of food production change, e.g., economies of scale. The quantitative expression of the type III functional response can be expressed (Gotelli 1998):

$$\frac{dN}{dt} = \frac{kV^2}{D^2 + V^2}$$

In this equation: dN/dt = feeding rate, t is the total amount of time a cultivator spends consuming a cultigen, or potential cultigen, and it includes search time plus time spent consuming a cultigen; k is equal to $1/h$, where h is the maximum return rate as influenced by the time necessary to harvest and consume a cultigen; V is equal to cultigen abundance or density; D is equal to $1/\delta h$ where δ represents the abundance of a cultigen given a certain feeding rate that is affected by harvest efficiency and the impact that a cultivator has on the per capita growth rate of the cultigen. As δ becomes larger, the per capita growth rate of the cultigen is depressed more significantly by the addition of a single cultivator.

To operationalize this ecological model we employed ECOSIM, a simulation package that combines object-oriented programming with a modern graphical interface.⁹ Figure 6.6 shows the results of three simulations (300 iterations each) reflecting increases in cultivator consumption rates as a function of cultigen abundance. In these simulations, the feeding behavior of the cultivator is influenced by increases in harvest efficiency and diminishing handling time, the return rate. These variables functionally respond to changes in resource density and yield throughout the course of the simulation. Based on changes in harvest efficiency and handling time, we ran three different variants of the model for comparison against the archaeological record in the Soconusco region (following section). Each variant is shown in Figure 6.6. All three variants assume that harvest efficiency, measured as return rate, was high enough that maize was incorporated into the diet of foragers living in the region. This is related to the abundance of higher ranked prey and overall diet-breadth relative to the return rate for maize-based food production at that time, as discussed previously.

VARIANT #1 (40% OF MODERN MAIZE YIELD). Curve C (lowest) in Figure 6.6 assumes

high handling costs (275 hr/acre [within field] + 47.90 hr/bu [processing]) and low harvest efficiency (18 bu/acre; 1416 cal/person/hour) for maize-based food production. This isocline shows small increases in cultigen abundance through time and equally small increases in cultivator population levels and consumption rates. Initial use of maize may have occurred in forest clearings near settlements on the coastal plain with small increases related to the process of artificially changing early maize density and fecundity through burning and clearing forest habitat. The costs of food production entailed in clearing forests, preparing fields, and husbanding seedlings, along with the high costs of processing, limited rapid increases in cultivator population levels, and consumption rates. We would also expect this type of functional response during the early stages of plant domestication in Central Mexico, and with the initial dispersal of primitive maize before 7100 B.P., if return rates were high enough for maize to be targeted by foraging populations.

ARCHAEOLOGICAL TEST EXPECTATIONS FOR VARIANT #1. If this variant is correct we would expect early evidence, in the form of cobs or kernels, for the use of maize in midden deposits at residential bases on the Soconusco coastal plain. This cultigen would be one of several plant foods collected and consumed after this time and should be reflected in diverse macrobotanical and faunal assemblages of palms, tubers, maize, small and large animals, etc. Low-level use of this plant would be expected with small incremental increases in use through time, until other higher-ranked resources were depressed, or more productive varieties of maize became available. The best evidence for maize consumption should come from residential bases on the coastal plain. Small quantities of maize pollen and phytoliths should also be present in these archaeological deposits and in regional environmental records. Maize pollen may slowly increase through time along with indicators for burning (charcoal), forest clearance (decreases in tree pollen and phytoliths), and disturbance

(increase in grass pollen and phytoliths). Stable carbon isotope data on human bones should indicate a slight increase in the consumption of C₄ plants early on, with gradual increases evident through time.

VARIANT #2 (60% OF MODERN MAIZE YIELD). Curve B in Figure 6.6 assumes intermediate handling costs (221 hr/acre [within field] + 45.72 hr/bu [processing]) and intermediate harvest efficiency (27 bu/acre; 1600 cal/person/hour) for maize-based food production. Once maize was adopted, this isocline shows more rapid increases in cultivator population levels, and hence consumption rates, relative to increases in abundance through time. Similar to Variant #1, the initial use of maize likely occurred in forest clearings near settlements on the coastal plain, but the commitment to maize-based food production occurs more quickly. We would expect this type of functional response if a more productive variety of maize arrived into the region, via exchange, along with agroecological knowledge.

ARCHAEOLOGICAL TEST EXPECTATIONS FOR VARIANT #2. If this variant is correct, we would expect to find a small number of maize cobs and kernels of intermediate size in midden deposits at residential bases in the Soconusco. More rapid increases in the quantity and relative proportion of maize, compared with other plant foods, should be evident in the record. In other words, low-level use of maize would give way to more focused and specialized use through the interval. Similar to Variant #1, the best evidence for maize consumption should come from residential bases on the coastal plain. As maize-based food production became more viable, resources with smaller return rates, particularly resources with low rates of return that were collected logistically (e.g., mollusks), would be dropped from the diet. Compared with Variant #1, the expectation here is that maize pollen and phytoliths would increase more rapidly through time, along with indicators for a developing agroecology. Stable carbon isotope data should indicate a slight increase in the consumption of

C₄ plants initially followed by clear evidence for C₄ plant consumption soon after, rather than the more gradual changes expected in Variant #1.

VARIANT #3 (MODERN MAIZE). Curve A in Figure 6.6 assumes handling costs close to modern maize in the lowland tropics (212 hr/acre [within field] + 43.55 hr/bu [processing]) and the highest harvesting efficiency for maize-based food production (45 bu/acre; 1854 cal/person/hour). This isocline, and the behavior it reflects, would be expected if modern maize were introduced into a new region with an existing agroecology. It shows the most rapid increases in cultivator population levels, and hence consumption rates, relative to increases in cultigen abundance through time. The commitment to maize-based food production would be rapid and the build-up should be instantaneous in the archaeological record. High capture efficiency and minimal handling time in this case are attributable to the prolific nature of modern maize and an existing agricultural economy.

ARCHAEOLOGICAL TEST EXPECTATIONS FOR VARIANT #3. If this variant is correct, we would expect to see a relatively high proportion of large maize cobs and kernels entering the archaeological record. Rapid increases in the quantity and relative proportion of maize compared with other plant foods would be instantaneous archaeologically. Forest burning and clearing would be punctuated, rather than gradual. In other words, there should be no evidence for low-level use of maize, it would be used at a high-level from the beginning. The use of logistical foraging would be abandoned immediately as people invested heavily in forest clearance, field preparation, and other agroecological activities. Storage facilities would become prominent features immediately as subsistence pursuits became more specialized and diet-breadth is reduced. Large quantities of maize pollen and phytoliths should appear abruptly in archaeological deposits and in regional sediment cores. Stable carbon isotope data should indicate a sudden

increase in the consumption of C₄ plants followed by continued use at a high level.

ADOPTION OF MAIZE IN THE SOCONUSCO

The fragmentary paleobotanical and archaeological records from the Soconusco region currently support Variant # 1 of the Lotka-Volterra cultivator-cultigen model, initial low-level use of maize followed by gradual increases in consumption rates through time that ultimately resulted in a reliance on maize-based food production. The earliest evidence for the use of maize in the vicinity of the Soconusco comes from the Pacific coast of Guatemala with maize pollen and phytoliths present in non-archaeological sediments dating to between 6000 and 5500 B.P., along with evidence for burning and forest clearance (Neff et al. 2003). Maize phytoliths were also recovered at Tlacuachero, a Late Archaic Period shellmound in the Acapetahua region (see Figure 6.1), dating to ~4600 B.P. (Jones and Voorhies 2004). The macrobotanical evidence for maize; of carbonized cobs, cupules, and kernels comes from Early Formative Period (3800–3000 B.P.) archaeological assemblages in the Mazatán region (Blake et al. 1992; Feddema 1993). Increases in burning and forest clearance, visible in sediment cores and archaeological sites, also appear to be relatively gradual with some punctuated burning events that could represent periods of more intensive farming, at least in certain locations (Jones and Voorhies 2004; Neff et al. 2003).

The appearance of maize at ~6000 B.P. did not have an immediate effect on Archaic Period subsistence and settlement practices of people living on the Pacific coast of southern Mexico. Evidence from the Middle Archaic Period site of Cerro de las Conchas (7500 to 5500 B.P.) suggests continued logistical exploitation of littoral resources. Although maize was clearly in the region, no evidence for maize cultivation was recovered from Cerro de las Conchas (Voorhies et al. 2002). This is true also of the early part of the record at Tlacuachero, a later shellmound in

the Acapetahua region. At Tlacuachero changes in marsh clam harvesting strategies are evident in an oxygen isotope seasonality study (Kennett and Voorhies 1996). Prior to 5000 B.P. marsh clams were harvested at this location throughout the year with an emphasis during dry season months. A similar shellfish harvesting profile is also evident at Cerro de las Conchas (Voorhies et al. 2002). After 5000 B.P., however, marsh clams were more frequently harvested during wet season months. This culminated at ~4000 B.P. with harvesting solely during wet season months (Kennett and Voorhies 1996). The shift in seasonal harvesting patterns is coincident with the appearance of maize phytoliths at 5000 B.P. We interpret this change as reflecting the greater need during the wet season to obtain resources rich in protein from the littoral zone as a consequence of the seasonal difficulty in obtaining game animals and riverine fish from the coastal plain. Intensive harvesting of marsh clams, as evidenced by these massive shellmounds, ended between 3500 and 3000 B.P.

Our model predicts that the best evidence for early maize cultivation will come from interior settlements on the coastal plain. As previously detailed, complex geomorphological processes have obscured and erased early archaeological sites and ancient land surfaces on the coastal plain. Much of what we know about Archaic Period subsistence and settlement comes from the highly visible shellmound sites along the coast, which we argue only represent part of the overall subsistence and settlement pattern in the region. Therefore, our interpretation of early maize cultivation remains tentative until interior settlements are located and tested. Vuelta Limón, a site on the inner coastal plain that we think was an Archaic Period basecamp, dates to the latest part of the Archaic Period (~3800 B.P.), although the length of its occupation is unknown. The presence of maize phytoliths across portions of the site suggest at least a low-level commitment to maize cultivation by this time.

In the Acapetahua region the earliest visible agricultural villages (Early Formative, 3500 to 2600 cal. yrs. B.P.) were positioned in a line

within or near the seasonally flooded wetlands on the inland side of the Acapetahua Estuary (Figure 6.7; also see Figure 6.1). A similar distribution of Early Formative sites is evident in the Pijijiapan area to the north, particularly the site complex of El Pajón (Paillés 1980), and in the Mazatán region to the south (Blake 1991; Blake et al. 1992a; J. E. Clark 1991, 1994; Lowe 1975), where Early Formative settlements are positioned near the El Hueyate marsh (Figure 6.1). Indeed, Early Formative Period sites are found in or near these distinctive wetland contexts along the coast of Guatemala (Arroyo 1994, 1995; Coe 1961; Coe and Flannery 1967; Estrada Belli 1998; Love 1989, 1993) and into northern El Salvador (Arroyo 1995). Excavations at Los Cerritos, an Early Formative Period site in the Acapetahua region (3400–3100 B.P.; see Figure 6.1 for location; Kennett et al. 2002), suggest a mixed foraging and food-producing economy. Shellfish continued to be collected, but not in such vast quantities as previously. Fish from estuarine habitats dominate the faunal assemblage, but many other reptiles and mammals also were targeted. Phytolith data suggest that maize was grown in the vicinity of the site and that squash (*Cucurbitaceae*) and wild tubers (e.g., *Canna* sp.) also may have been cultivated. The strategic position of this settlement between the highly productive littoral zone and dry land suggests to us that the people living at this location were not fully committed to an agrarian lifestyle.

Excavations at several sites in the Mazatán region also suggest mixed foraging and food production during the Early Formative Period (3500 to 3000 B.P.; Blake et al. 1992). These sites have diverse faunal assemblages that contain a wide range of wild animal species from wetland habitats that were in close proximity to these settlements. Of the seven wild and domesticated identified plants, maize, beans, and avocado were the most abundant (Feddema 1993). Maize was found at the sites of Aguiles Serdán, Chilo, Paso de la Amada, and San Carlos (Figure 6.1). Most of the remains were maize cupules and kernels, but some cob

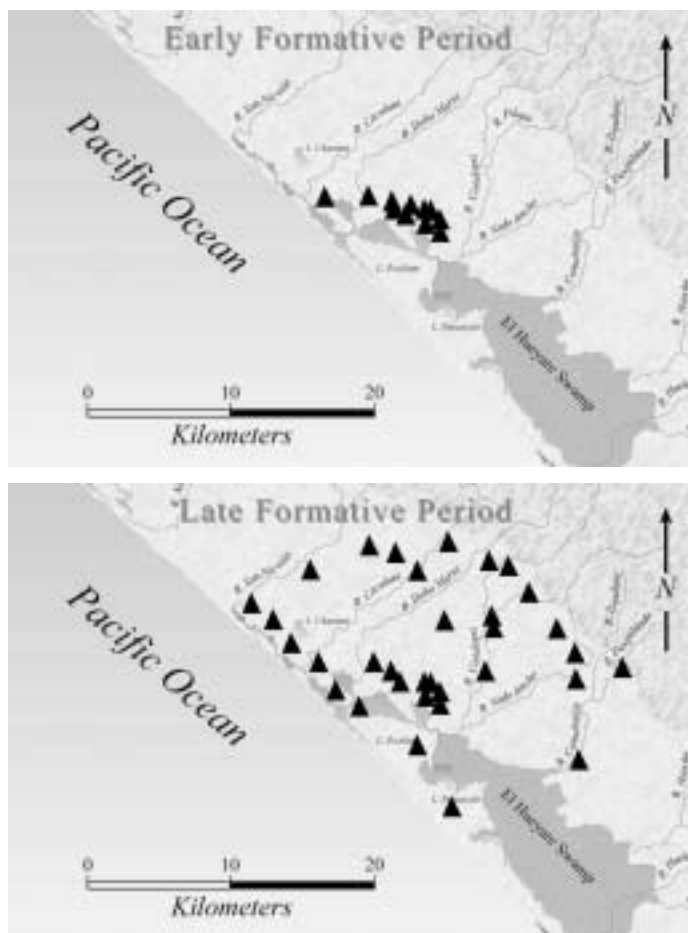


FIGURE 6.7. Early (~3500–2600 B.P.) and Late (~2600–1800 B.P.) Formative Period settlement distribution based on two regional surveys (Voorhies 1989b; Voorhies and Kennett 1995).

fragments were also identified. These data suggest that maize was small (20–40% modern) and that it was not yet a focal resource. Stable nitrogen and carbon isotopic analyses of Early Formative Period human skeletal remains support this hypothesis (Blake et al. 1992b).

A systematic pedestrian survey of the Acapetahua region suggests that settlements were evenly distributed across the landscape by the Late Formative Period (~2600 B.P.; Voorhies 1989b). This suggests to us that maize-based food production was well established in the region by that time. Excavations at the Late Formative Period site of Izapa substantiate this inference (Lowe 1982), as do excavations at La Blanca, a large political and economic center on the northern coast of Guatemala dating to this

period (Love 1993). Nitrogen and carbon isotope data suggest increases in maize dependence by this time (Blake et al. 1992b).

SUMMARY AND DISCUSSION

Visible evidence for maize cultivation appears in the Soconusco region and vicinity between 6000 and 5000 B.P. The first indication of the presence of this cultigen in the form of phytoliths and pollen comes from coastal plain sediments in Guatemala dating to between 6000 and 5500 B.P., and co-occurring with evidence for burning and forest disturbance (Neff et al. 2003). The availability of maize at this time did not stimulate an immediate transformation to maize-based food production, and we suspect

that this cultigen was used at a low level in conjunction with a variety of wild and domesticated plants—perhaps similar to the low-level use of maize by the Mikea of Madagascar (Tucker, this volume).

In the Acapetahua region, evidence from Tlacuachero suggests that the appearance of maize phytoliths at ~5000 B.P. was coeval with the onset of gradual changes in the seasonal collection of littoral resources, particularly marsh clams (Kennett and Voorhies 1996). By 3500 B.P., marsh clams were effectively dropped from the diet, but fish, reptiles, and other littoral resources continued to be procured through the early Formative Period (3500 to 3000 B.P.). By then, the diet included some cultigens, including maize, beans, squash and avocados (Feddemma 1993). In other words, mixed foraging and food production persisted through the early Formative Period.

Additional evidence for mixed foraging and food production through the Early Formative Period comes from an apparent shift in regional settlement during this time. Logistical use of littoral resources from interior base camps dating to the Archaic Period was replaced apparently by a shift to residential bases in intermediate locations between the coastal wetlands and the coastal plain. This settlement pattern is perplexing because the best agricultural lands are on the inner coastal plain, away from the littoral zone. One possible explanation for this pattern is that interior settlements are deeply buried under the alluvium and await future discovery. Another possibility is that population increases and persistent hunting on the coastal plain through the Archaic Period reduced the abundance of medium- and large-sized game animals. In this scenario, overall reductions in central place foraging returns stimulated the establishment of residential bases close to the littoral zone where fish, birds, and reptiles were abundant and their pursuit was more cost effective from settlements close to the wetlands because transportation costs were reduced.

The distribution of late Formative Period settlements (~2600 B.P.) over the entire width of

the Soconusco coastal plain suggests that maize-based food production was well established by this time, if not earlier. Excavations of late Formative Period sites in the Mazatán region of Mexico and in the adjacent Guatemalan coast substantiate this inference. However, hunted and collected wild foods continued to be of great economic importance to people living in the region throughout prehistoric time (Blake et al. 1992a).

The early dispersal (7500 to 7000 B.P.) of maize through the lowland tropics, as seen in Tabasco, Mexico and Central Panama, is not visible in the known archaeological and palaeoenvironmental records from the Soconusco region. Absence of early maize may indicate that this cultigen did not pass through the Soconusco on its way to Central Panama. This seems to us unlikely given the similarity in lowland tropical habitat and the natural route of dispersal out of Central Mexico and down the Pacific coast. There are three other possible explanations for this pattern. The first, and least likely, is that the dates for early maize in central Panama are too early. The second is that maize was grown at such low levels in the Soconusco between 7500 and 6000 B.P. that it has thus far remained undetected in environmental records and archaeological sites, which are both seriously restricted. The third explanation, favored by us, is that return rates for maize cultivation were unfavorable at this early time, relative to the available alternatives in the Soconusco, and foragers chose not to cultivate it. This is most comparable to the situation in the Mexican highlands where it appears that the annual grass *Setaria*, which has higher return rates than teosinte, was preferred to early maize (Flannery 1973, 1986a).

Once maize entered the diets of foragers after 6000 B.P. it was used at low levels until the beginning of the late Formative Period (~2600 B.P.). Why such a delay? In the Soconusco, as elsewhere, there would have been several impediments to successful maize cultivation. As operationalized in the Lotka-Volterra cultivator-cultigen model (Variant #1), the investment of time and energy in planting, weeding,

watering, and harvesting decreased the energy gained from this cultigen compared to other wild alternatives. This would include opportunity costs associated with cultivation, that is, the time invested in clearing forest and other tasks related to food production would have detracted from the time spent hunting deer, fishing, and collecting wild tubers. This, we argue, resulted in the slow growth of cultivator populations and associated slow growth in cultigen abundance. Technological limitations also may have contributed to this delay. Heavy dependence on dried seeds such as maize kernels and beans requires soaking and prolonged cooking. Seeds can easily be soaked in wooden bowls, gourds, or even leaf-lined pits, but protracted cooking requires direct heating that was not available until the development of ceramic technology. This may be one reason for the more rapid commitment to maize-based food production after the advent of ceramic technology in the Soconusco at ~3800 B.P. It is also possible that the net energy return from maize farming was heavily discounted (i.e., devalued, see Chapter 1, this volume), as it is among the Mikea of Madagascar (Tucker 2001, this volume), because of the delayed return to investment and the risks associated with crop failure.

CONCLUSION

Central place foraging theory predicts that foragers in the Soconusco region would have established residential bases in clearings on the forested coastal plain near rivers. The model also predicts that foragers would have hunted and collected the mix of wild animal and plant foods that maximized central place foraging returns within the vicinity of these settlements. This did not negate the use of longer distance logistical forays to hunt and collect resources in the piedmont and littoral zones, but these resources would have been hunted, collected, and processed in ways that maximized net delivery rates to centralized residential bases. The fragmentary archaeological data from the Soconusco support this model, with Vuelta Limón being a

centralized residential base, and the shellmounds representing specialized logistical foraging locations where littoral resources were collected and processed prior to transport back to residential bases elsewhere on the coastal plain. Predation pressure on the largest animal species, leading to resource depression at interior locations, would have increased diet breadth and promoted more frequent logistical forays. Persistent logistical use of littoral resources suggests that this strategy was stable for ~4000 years, between 7500 and 3500 B.P.

The microeconomic principles of the diet breadth model predict that maize would have entered the dietary regime of Soconusco foragers as higher ranked prey items were reduced and diet-breadth expanded to include lower-ranked plant foods such as maize. Gradual increases in the use of maize after 6000 B.P. are supported by the palaeoenvironmental and archaeological records currently available. These data fit the Lotka-Volterra cultivator-cultigen model (Variant #1) showing initial low-level use of maize followed by gradual increases in the commitment to maize-based food production. We argue that the delayed commitment to maize-based food production resulted from the initial response of foragers to a resource of low, but increasing, value. Due to the fragmentary nature of the palaeobotanical and archaeological records we stress that this model requires further testing. More systematic survey work is needed to locate Archaic and Early Formative period settlements deeply buried under alluvium on the coastal plain. Additional sediment cores also are needed in the Mazatán, Acapetahua, and Pijijiapan areas to define sub-regional differences in maize use in the Soconusco through time.

NOTES

1. Ages are expressed as calibrated calendar years before present (B.P.).
2. Soconusco is an adaptation of the Aztec name for this region.
3. Logistical foraging involves the strategic use of distant resources by people living at more centralized residential bases. People often travel

long distances, exploit and process a resource, and return to residential bases with the resource to provision their households.

4. Shrimp were probably an important resource, but are invisible in the archaeological record. Shrimp larvae enter the estuary, which serves as a nursery. During the dry season they grow appreciably and are easily captured with simple technology. These juvenile shrimp are an important aspect of the subsistence and cash economy in the region today.
5. Evidence for structures is present on one clay surface discovered at Tlacuachero, but this floor construction and the structures that were upon it, appear to be unique (Voorhies et al. 1991).
6. This is highly unlikely because drier conditions during the Late Pleistocene would have pushed

Balsas teosinte downslope (Dolores Piperno, personal communication 2004).

7. However, it is possible that early maize was popped rather than ground or that the stalks and seeds were eaten green. This would have significantly reduced post-harvest processing costs.
8. Lotka-Volterra predator-prey model:

$$\frac{dV}{dt} = rV - \alpha VP$$

$$\frac{dP}{dt} = bHp - mP$$

9. The program used is ECOSIM (Beta-Version), Empresarios. Agrupados A. I. E. Mogallones, 3,28015 Madrid, Spain.