LARGE MAMMALS AND THE COMMUNITY DYNAMICS OF AN AMAZONIAN RAIN FOREST

BY

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Maximiliana maripa is a large seeded palm that occurs in monodominant patches within the rain forest of Maraca Island, Roraima, Brazil. Rodents, collared peccaries (*Tayassu tajacu*), deer (*Odocoileus virginianus* and *Mazama* spp.) and primates ate the pulp of palm fruits, but dropped from 97 to 100 % of the seeds within 5 m of parent plants. Tapirs (*Tapirus terrestris*) swallowed entire fruits and defecated thousands of viable seeds at latrines located up to 2 km from the nearest palm clump. Bruchid beetle larvae killed 77 % of the seeds remaining near parent trees, but only 0.7 % of the seeds dispersed by tapirs.

Densities of zero year to fifth year seedlings were significantly higher around tapir latrines than around nonpalm control trees, and both were significantly higher than around parent trees. Seeds secondarily dispersed from tapir latrines by rodents gave rise to the seedlings around control trees.

Adult palms and seedlings of five age classes occurred at discrete densities (lumps) rather than in a continuous range of densities. The highest density lumps for first through fourth year seedling classes occurred at tapir latrines, with the next highest density lumps located at controls and parent trees, respectively. High density lumps are the result of dispersal by tapirs, while lower density lumps are created by dispersal by rodents.

Seed predators interact to affect seed traits. White-lipped peccaries (Tayassu pecari) cannot crack the thickest endocarps, and thus select for increased endocarp thickness. Rodents and beetles can penetrate even the thickest seeds, but seldom kill all of multiple endosperms, thus selecting for multiple endosperm seeds. Most seeds in the study palm population were thick single-endosperm seeds, suggesting that white-lip peccaries have been important historical consumers.

By radio-collaring 5 of 39 and 2 of 130 individuals in two white-lip herds, respectively, I determined that the larger herd had a home range of 109 km^2 and the smaller herd one of 22 km^2. The smaller herd's range was completely enclosed within the larger herd's range during the study period. Two collared peccary herds had smaller home ranges.

CHAPTER 1
INTRODUCTION

Large terrestrial fruit- and seed-eating mammals such as tapirs (Tapiridae) and peccaries (Tayassuidae) in the Neotropics (Smythe 1989), and elephants (Elephantidae), rhinoceruses (Rhinocerotidae), wild pigs (Suidae) and tapirs in the Paleotropics are likely key elements in seed dynamics and forest regeneration. Because of their size, these large mammals can ingest or destroy vast numbers of fruits and/or seeds at one time, or move them large distances away from the parent plant. Temporally, large mammal populations can be very variable in size due to catastrophic mortality and population fluctuations (Young 1994). Such temporal variability in fruit and seed consumers, when combined with the variability in fruit production by the tree itself, can lead to punctuated mass episodes of seedling establishment by plants rather than continued low-level establishment.

In the Neotropics, large mammals include both seed dispersers and seed predators. White-lipped peccaries (_Tayassu pecari_) and collared peccaries (_Tayassu tajacu_) are frequently described as omnivorous, although their diet can consist of as much as 60 % fruit (Bodmer 1989a). However, since they commonly consume the seeds attached to fruit, dispersed seeds and seedlings they are generally considered frugivore/granivore (Bodmer 1989a, 1989b, Kiltie 1981a, 1982). They travel in herds of varying size, so that plants are affected by the combined biomass of herd members. Tapirs (*Tapirus terrestris* in South America and *T. bairdii* in Central America), in contrast, are frugivores in that they swallow fruits but usually defecate entire seeds (Bodmer 1990, 1991a). Although they are solitary, their large body size implies the ability of a single individual to ingest large amounts of fruit. Despite their usual classification as browsers, about 30 % of their diet may consist of fruit (Bodmer 1989a). The pattern of movements and social interactions of these consumers should affect seed shadows by determining where seeds are dispersed and in what amount, and the intensity of predation to which they are subjected.

Large, terrestrial frugivores also provide a link with past ecological interactions, because they continue into the present the dynamics of the extinct megafauna of past millennia. Understanding the current role of large ungulates in seed dynamics may help us understand the dynamics that created some aspects of forest structure and of those seed/fruit traits we see today. These large mammals, however, are among the first to disappear from human inhabited sites (Emmons 1984). Studies of forest dynamics in sites where large mammal extirpations have occurred may not be providing an accurate picture of forest dynamics in sites with an intact fauna. If we study ecological interactions only in fragmented and disturbed forests that are lacking components present in other regions, we limit our understanding of these processes or at best derive incomplete or distorted conclusions.

Despite an awareness of the limitations of studies in disturbed or fragmented sites, there have been few studies of the interactions of large terrestrial frugivores with their seed and fruit foods in intact Neotropical sites. The sites where most studies have been conducted (La Selva, Costa Rica and Barro Colorado Island, Panama) lack these species or have them only at low densities. In sites where they do occur they have proven to be difficult to observe, monitor, capture and track (R. Kiltie pers. comm., L. Emmons pers. comm., J. Berger pers. comm.). Since they are not seen, big mammals are often not considered (see, e.g., Bradford and Smith 1977 in Costa Rica, Clark and Clark 1984 in La Selva). Manu National Park in Peru is the only relatively undisturbed site thus far studied in all of the Neotropical rain forests. However, only recently have seed dynamic studies been initiated there (Terborgh et al. 1993). Results from one site can hardly be considered representative of the Neotropics or even Amazonia, especially a site with such a unique habitat mosaic as occurs in Manu (Gentry 1990).

Large fruits and seeds are considered to be evolutionary responses to selection by large vertebrate frugivores (e.g., Janzen and Martin 1982, van der Pjil 1982). Palms are especially noted for their production of large fruits. With respect to seed dynamics, palms are good study species because they produce copious amounts of large, visible seeds and the adults themselves are abundant and are therefore a good model system for a study of interactions among seeds, seed-predators and dispersers. They also present a model system in which to compare the results of, and conclusions drawn from, studies in disturbed versus undisturbed sites.

If palms are to be used as model systems, a more complete understanding of their evolutionary and ecological dynamics would be obtained at sites still inhabited by populations of the megafaunal species that may have coevolved, or at least co-occurred, with them for long periods of time. For the Neotropics, however, the literature is dominated by studies conducted at Barro Colorado Island, Panama, and La Selva, Costa Rica. Given that large mammals such as white-lipped peccaries and tapirs, and species that normally prey on them (*Felis concolor*, *Panthera onca*) are extirpated, rare, reintroduced or semi-domesticated at these sites (Clark 1994, J. Eisenberg pers. comm., Leigh et al. 1982), the conclusions drawn about palm seed dynamics in particular and dynamics of large seeds in general based on these studies may be incomplete or not representative of dynamics at intact sites.

This study describes the natural history and ecology of white-lipped peccaries and collared peccaries, and how they interact with tapirs, rodents and beetles to affect the seed dynamics and regeneration of *Maximiliana maripa*, a common arborescent palm. The study took place in one of the least disturbed rain forest areas in Amazonian Brazil, the Maraca

Island Ecological Reserve in northern Roraima state. The area has never had non-Amerindian populations, has not been inhabited by Indians in the recent past. Only isolated families with few heads of cattle and small rozas ever used the land. It currently experiences minimal levels of hunting.

CHAPTER 2

REGENERATION DYNAMICS OF AN AMAZONIAN PALM. PART I: SEED DISPERSAL AND MORTALITY

Introduction

Seed-dispersing frugivores can influence several related aspects of seed dynamics, including seed survivorship, seed distribution, and the inter-specific dynamics of plants (e.g., Clark and Clark 1984, Connell 1971, Forget 1992a, Howe and Smallwood 1982, Hubbell 1980, Janzen 1970, Portnoy and Wilson 1993). Few studies address all or even several aspects of disperser-seed dynamics, due to the difficulty of obtaining a large enough sample size and a long enough study period to track many individual plants from surviving seeds through maturity (Howe 1993b). Most studies describe either seed mortality patterns, effectiveness of different dispersers in terms of quantity of seeds removed, or patterns of adult distribution independent of the recruitment biology of a species. Recently, Howe (1993b) has stressed the importance of linking these different types of studies for single species. In a system where few individuals survive to adulthood, patterns of seed mortality and dispersion may be the ultimate determinant of tree species diversity and forest structure. Such comprehensive studies are of particular interest in the tropics, where the maintenance of high tree species diversity has long been a topic of contention (Clark and Clark 1984, Howe 1993a, Terborgh et al. 1993).

This chapter describes the dispersal of seeds of the arborescent palm, *Maximiliana maripa*, by mammalian frugivores in an undisturbed Amazonian forest and patterns of seed mortality at the dispersal site. I test the hypothesis that rodents (primarily *Dasyprocta* and a smaller, unidentified *Sigmodon*-sized animal), peccaries (*Tayassu tajacu*, *T. pecari*), primates (*Ateles belzebuth*, *Cebus* spp., *Saimiri sciureus*) and deer (*Mazama americana*, *M.gouazoubira*, *Odocoileus virginianus*) are poor dispersers of *Maximiliana* seeds compared to lowland or Brazilian tapirs (*Tapirus terrestris*) because they drop most seeds near parent trees and within conspecific adult aggregations. Since the area around the parent tree is the area of highest seed mortality (Chapter 3, Kiltie 1981a, Janzen 1971), I tested the hypothesis of poor dispersal quality by describing the distances seed where dispersed by different frugivore species and comparing the mortality of dispersed seeds and seeds remaining near parents and within conspecific aggregations to that of seeds dispersed far from parent trees and conspecific aggregations. The largest source of mortality for palm seeds in my study site, as well as elsewhere in the Neotropics, is infestation by bruchid beetle larvae (different beetle species at different sites; Bradford and Smith 1977, Janzen 1971, Terborgh 1983, Kiltie 1981a, Smythe 1989). I therefore examined the role of the different vertebrate consumers in allowing escape from beetle larvae. Subsequent chapters describe the pattern of seedling survivorship and the mechanism by which seed and seedling survivorship translate into adult dispersion patterns.

Neotropical arborescent palms are ideal study plants for questions of seed dynamics and adult diversity in that they produce large numbers of large, easily located seeds that are highly attractive to a variety of consumers, including vertebrate predators and dispersers and invertebrate predators (Bodmer 1990a, 1991a, van der Pjil 1982, van Roosmalen 1985). Mature palms are often numerical dominants in neotropical forests (Kahn and de Granville 1992, Peres in press). Terrestrial (rather than arboreal) frugivores and granivores are the most important seed predators and dispersers for large-seeded arborescent palms, consuming the pulp or seeds after they have fallen to the ground. Few mammals, except for some primates and occasionally squirrels, harvest the fruit or seeds from the tree itself, and both these animals frequently descend to the ground to feed on palm seeds or fruits (Bodmer pers. comm., Terborgh 1983). This predominance of terrestrial consumers may be due to the habit of individuals of many palm species of ripening and dropping an entire fruit crop over a short time period (pers. obs.). Even the most specialized avian palm consumer known, the Hyacinth macaw (Anodorhynchus hyacynthinus) of the open

Pantanal habitat, feeds on palm seeds from the ground rather than the canopy (Munn et al. 1990).

Despite this diversity of palm consumers, research on terrestrial mammalian palm consumers and their role in seed dispersal/predation has thus far been biased toward rodents (de Steven et al. 1987, Forget 1990, 1991, 1992a, 1992b, Smythe 1989), largely because their numerical abundance and habit of scatter-hoarding seeds makes them conspicuous potential seed dispersers. The same is true for other large-seeded tropical plants (Hallwachs 1986, Janzen 1982a, 1982e, Schupp 1992). Less attention has been paid to large terrestrial frugivores such as ungulates because they are less abundant in general and in some cases have disappeared from the study sites due to human disturbance. In the absence of data on these larger frugivores, rodents are often assumed to be the most important extant seed dispersing agents for large-seeded tropical plants such as palms (see, e.g., Bradford and Smith 1977, Janzen 1971). Animals such as tapirs, however, are large enough to ingest hundreds of fruits in one day and may have an important and as yet undescribed impact on the dynamics of large seeded plants. Tapirs have existed continuously in tropical forests, both Asian and American, since the Pleistocene (Simpson 1980) and probably continue ecological interactions described as unique to extinct mega-fauna and large seed-bearing plants by Janzen and Martin (1982). An understanding of the tapir seed dispersal patterns and the seed and seedling shadows they generate may provide an explanation for tree species dispersion/diversity patterns established in the past by now extinct Pleistocene megafauna. If tapir defecation of clumps of seeds leads to clumped dispersion of Maximiliana trees, then perhaps the clumped tree distributions noted in several neotropical forests today could have been set in motion by the similar defecation behavior of extinct megafauna.

Methods, Study Species and Study Site

Study Site

The study took place from October to December 1991 as part of a two-year project (December 1990 to December 1992), on Maraca Island Ecological Reserve. Maraca Island lies at 3°25'N and 61°40'W, at the northern edge of the Amazon River basin in Roraima state, Brazil (Fig 2-1), near the boundary between savanna habitat and the Amazon rainforest. It is formed by the branching of the Uraricoera river, a tributary of the Rio Branco (Amazon drainage). All 110,000 ha of tropical rainforest, wetlands, and isolated savannas forming the reserve are protected by I.B.A.M.A. (the Brazilian Secretariat for Wildlife, Ecological Reserves and Parks) as a site for research and forest protection. The dominant vegetation of the region is primary, tropical evergreen lowland rainforest (Moskovits 1985), contiguous with the great Amazon rainforest (Milliken and Ratter 1989). Maraca supports substantial and unhunted populations of mammalian frugivores, including two peccary species (*Tayassu tajacu* and *T. pecari*), three deer species (brocket deer, *Mazama americana*, *M. gouazoubira*; and white-tailed deer, *Odocoileus virginianus*), brazilian tapirs (*Tapirus terrestris*), eight primate species (*Cebus apella*, *C. nigrivitatus*, *Alouatta seniculus*, *Ateles belzebuth*, *Saimiri sciureus*, *Aotus trivirgatus*), and caviomorph rodents (*Dasyprocta agouti*, *Agouti paca*, *Myoprocta* sp.) (Nunes 1993, Nunes et al. 1988). The island has not been populated by humans (although approximately eight families inhabited the margins of the eastern tip of the island at different times up until 1977) or logged within historical time. Only the eastern half of the island currently has a trail system allowing access to a variety of habitat types; this constituted the primary study area.

The study site is generally representative of the climate and habitat of the central Amazonian habitats with an intermediate level of precipitation, but not of the drier or moister extremes to the north and south (Nunes 1993). Rainfall varies between 1750 and 2250 mm per year. The dry season, with less than 100 mm monthly on average, occurs between October and April, and the wet season, with greater than 350 mm monthly, occurs between May and September. There are two forest-wide fruiting peaks, a marked one during the middle of the rainy season and a weaker one at the end of the dry season (Moskovits 1985).

Study Species

Maximiliana maripa is a large subcanopy to canopy palm common throughout the Amazon basin, Maranhao, Mato Grosso, Ceará, and the Guianas (Kahn and de Granville 1992, Pesce 1985). The large size of Maximiliana fruits (and seeds), together with their yellowish color, allows them to be easily located on the forest floor. Adult trees reach heights of 35 m (Kahn and de Granville 1992, Pesce 1985) and produce from one to four infructescences, each bearing from hundreds to over two thousand fruits. Counts of two mature fruit bunches revealed 2405 fruits in one and 1108 in the other (Silvius, unpublished data). The fresh fruits (pericarp and seed) weigh from 14 to 26 g and measure 5 to 6.5 cm in length (n=30), while fresh seeds weigh from 7 to 17 g. The hard woody endocarp ranges from 1.5 to 6.5 mm in thickness (n=1034) and contains one, two or three endosperms (n=305). On Maraca, Maximiliana frequently occurs in large patches, commonly adjacent to Mauritia swamps. It also occurs as solitaires in the upland forest and in high density patches beneath the forest canopy (pers. obs.; Milliken and Ratter 1989). Patches were identified from the air as well as from the ground. During both study years, the Maximiliana population flowered synchronously at the end of the dry season (March to April) and then produced fruit synchronously during the middle of the wet season (May through August).

Although most of the population flowered, only a few trees developed fruit. Even at these low levels of availability, *Maximiliana* fruit was one of the most frequently recorded items in feeding observations during the study period. Fruits were used by white-tailed deer, agoutis, pacas, *Cebus* monkeys, brocket deer, howler monkeys, spider monkeys, squirrel monkeys, both peccary species, tapirs, parrots (*Amazona* sp.) and trumpeters (*Psophia crepitans*) (pers. obs.). *Maximiliana maripa* pulp constituted 10.1 % of the spider monkey's (*Ateles belzebuth*) diet on Maraca during one of the months of fruit scarcity, but only 1.23 % of the yearly diet (Nunes 1993). Seeds of *Maximiliana* in the feces of lowland tapirs on Maraca ranged in frequency of occurrence from 0 to 100 % in 355 samples taken during an entire year (1991-1992) and were present in feces in five out of 11 months sampled (Huffman and Fragoso in prep.).

Elsewhere in the Neotropics, *Maximiliana* seeds and fruits are reported as consumed by primates (*Cebus albifrons*, Defler 1979, savanna-forest boundary in eastern Colombia); marsupials (*Philander opossum*, *Didelphis marsupialis*, Charles-Dominique et al. 1981, French Guiana); squirrels (*Sciureus spadiceus*, Peres in press, western Brazilian Amazon; *Sciureus aestuans*, Charles-Dominique et al. 1981, French Guiana); and other rodents (*Dasyprocta agouti*, *Echimys armatus*, *Agouti paca*, Charles-Dominique et al. 1981, French Guiana).

Methods

Seed Dispersal by Vertebrates other than Tapirs

I selected six fruiting Maximiliana palms, located in two forest patches dominated by Maximiliana, but including other tree species. Palm patches were identified visually both from the air and on the ground and were defined as aggregations with a density of 13 or more trees per 1/4 hectare. All the study plants had ripe fruit beneath them, but only one had completed fruitfall. Seeds in intact fruits were considered undispersed, as were those in rotted fruit; however, seeds whose pulp had been consumed by frugivores were considered dispersed even if they remained beneath or near the parent crown. Opportunistic but intensive searches (carried out daily from July 1991 to January 1992 during daily forest census transects for large vertebrates) for the seeds at each location revealed that only tapirs were dispersing seeds beyond 30 m of parents at the time of peak fruit fall (July). Even if some seeds were carried by other frugivores beyond 30 m but remained within the parent clump, a) the numbers were so low that I could not detect them, and b) they would likely have been deposited within 30 m of another Maximiliana within the clump. To determine the dispersal distance of nontapir dispersed seeds, I demarcated a circular area of 30 m radius around each tree, then subdivided this area with rope into four equal-size wedge shaped quadrats. These units were further subdivided by concentric rings spaced at 5 m intervals from the tree out to the 30 m line. A 30 m radius was chosen based on research indicating that up to 90 % of rodent-dispersed seeds remain within 10 m of parents (Hallwachs 1986 for *Hymenea courbaril*, Forget 1990, 1991, 1992a for *Gustavia superba* and *Euperua grandiflora*). On July 31, two people walking abreast of one another searched each ring for seeds and fruits. All *Maximiliana* fruit and seeds observed were counted and categorized as 1) intact fresh ripe fruit, 2) intact rotted fruit, 3) bare seeds with no exocarp or mesocarp attached, 4) rodent-attacked fruit (seeds with small teeth marks gnawed in a circular pattern around bits of remaining mesocarp), and 5) fruits attacked by other vertebrates. The number and percent of seeds in each category were calculated.

I was able to distinguish among fruits handled by different vertebrates by examining seeds handled by captive animals (peccaries) or seeds handled by animals observed feeding in the wild (peccaries and all other consumers). Rodents left a characteristically small amount of pulp and fibre attached to the seeds relative to the other frugivores discussed here. Collared peccaries left more pulp than rodents, and their larger, more pointed teeth left deeper and v-shaped gashes in the remaining pulp. White-lipped peccaries were not foraging in the *Maximiliana* patches at this time. Monkeys left finer and flatter gashes in the fruit pulp than did the peccaries. Tapirs (*Tapirus terrestris*) and deer used their molars to scrape off the fruit pulp. Deer spat out much of the fruit and left a pattern of pulp chunks seemingly removed by plier-like tools (the molars). Because of the difficulty separating deer and tapir-spat seeds, both were grouped together in the analysis. In cases where we could not identify the frugivore responsible for fruit consumption, the seeds and fruits were placed in the "unknown" category.

Seed Dispersal by Tapirs

Although tapirs are most frequently reported as defecating in wet areas such as rivers and ponds (Fragoso 1987, Janzen 1981b, 1982b), on Maraca tapirs also defecated in terra firme "latrines." These were sites, usually next to an emergent tree, where at least one animal defecated repeatedly throughout the study period. Piles of tapir feces were easily recognized; they consisted of aggregations of poorly digested plant matter, similar in appearance to horse dung. One feces consists of all boluses defecated at one time. I searched for Maximiliana seeds in all fresh tapir feces encountered from October to December 1991 (the last months of the Maximiliana fruit-fall period) within the study area, over 60 km of trails. Assuming that distance is the most important variable affecting survival, I lumped nontapir dispersed and undispersed seeds together since most remained within 10 m of parent trees. Clearly this does not consider the impact of seed handling by frugivores on survivorship. I compare the survivorship of these seeds to those dispersed by tapirs 100 to 1000 m distance from *Maximiliana* aggregations. I randomly selected 10 seeds (N=440 seeds) from 44 feces (those with at least 30 seeds) distributed over eight tapir latrines. I randomly selected (by choosing the seed nearest the marked end of a stick thrown under the tree) 10 seeds from underneath each of 20 randomly selected (coordinates and distances from the trail chosen from a random number table) parent trees (N=200 seeds), from six conspecific patches. Each seed was categorized as 1) whole, 2) killed by bruchid beetles, either with larvae or with an exit hole, 3) killed by rodents, 4) killed by white-lipped peccaries, 5) killed by fungus, 6) aborted with an undeveloped endosperm, and 7) germinated. Seeds opened by rodents and white-lipped peccaries (at tapir latrines) could be easily identified by the characteristic gnawing and crushing pattern left by these animals. Seeds that appeared whole were opened to confirm their viability. Tapir-dispersed seeds were sampled while feces were fresh. The seeds around parent plants were obtained from freshly fallen ripe fruit or shortly after the pulp had rotted or was consumed by frugivores, over a period of 4 days (October 31 to November 3).

Results

Vertebrate Dispersers other than Tapirs

Considering all the fruits from all six trees, the pulp of 47 % of the fruits found on the ground had been at least partially consumed by frugivores, but an almost equal amount, 37 %, rotted (Table 2-1). Rodents were the primary fruit pulp consumers, accounting for 32 % of the attacked fruits found within 30 m of parent trees (Table 2-1). Collared peccaries ate 3 % of the fruit, primates 4 %, and deer and tapirs only 0.6 %. The unknown category contained 8 % of the seeds. There was no evidence that rodents or other vertebrates ate the seeds themselves at this point in the fruiting period, when the seeds were sampled.

The number of fruits under each tree ranged from 181 to 1788 (mean 778.17, s.d. 537.54). There was high variation among individual trees in the number of fruits in each category (Table 2-2).

Despite their intensity of feeding, rodents left 1381 intact seeds (representing 97% of the fruits they handled) within 5 m of the parent tree's trunk (Table 2-1). Only 2 % were moved from 5 to 10 m (n=33) and only 1 % from 10 to 20 m (n=5). No rodent-dispersed seeds were found between 20-30 m beyond the parent tree (Tbl. 2-1). Ninety-eight percent of all seeds found within 30 m remained within 5 m (the approximate diameter of parent tree crowns) of the tree trunk (Table 2-1). Only 3 seeds were carried more than 15 m from palm trunks. While I sampled distances beyond 30 meters from the parent tree more informally than those within 30 m, I am confident that there were few seeds in that area for two reasons: 1) In my study site seeds dispersed or buried by large rodents (e.g. agoutis) were easily found even if buried due to conspicuous sign of digging left on the soil surface. This sign became obvious to me after I watched agoutis burying objects throughout the forest; and 2) it would be highly unusual for, rodents or other dispersers, to have skipped a 20-meter section around the parent tree (see Forget 1990, 1991, 1992a, Halwachs 1986). These results are similar to those of Hallwachs (1986) for *Hymenea courbaril*, and Forget (1990, 1991, 1992a) for *Gustavia superba* and *Euperua grandiflora*), who found that 90% of seeds were dispersed no further than 10 m from parent trees.

Dispersal by Tapirs

Throughout the study, I discovered tapir latrines in eight seasonally flooded wetlands, one dry stream bed and 25 terra firme forest sites. I saw three adult tapirs and one juvenile in the study area, individually recognizable by scars and other markings. Only six seasonally flooded latrines (dry during the study period) found from October to December 1991 were used in this analysis. At these latrines, tapirs passed 6140 seeds in 78 feces, and 2 additional feces contained no *Maximiliana* seeds (mean of 78.71 seeds per feces containing *Maximiliana* seeds, range 11-210) (Table 2-3). Ninety-eight percent of the randomly sampled, dispersed seeds were viable, compared to only 17 % of the randomly sampled seeds beneath parent trees (Table 2-4). Beetle larvae infested 63 % of the latter seeds, and adult beetles had killed an additional 14 %. A few seeds were killed by fungus, and a few had never developed endosperm and presumably had been aborted. In total 81% of the seeds were already dead or would soon die (Table 2-4). I did not find any *Maximiliana* seed fragments in piles.

Discussion

Ecological Relationships

Plants are hypothesized to produce fruit pulp to attract frugivores. These frugivores then disperse seeds away from the area of high mortality and competition around the parent plant, and towards germination sites of varying quality (Snow 1971, Janzen 1970, Connell 1971). In this study, however, almost all *Maximiliana* seeds spat out by medium to small-bodied terrestrial frugivores remained below the crowns of parent trees. Rodents (pers. obs.), collared peccaries (pers. obs.), deer (pers. obs.) and monkeys (pers. obs., Nunes 1993) ate the pulp from large numbers of fruit, but left the seeds beneath the crowns of parent trees. Here they were subject to high mortality from beetle larvae infestation, and would later be susceptible to density-responsive predators such as white-lipped peccaries (Chapter 3). This pattern of eating fruit pulp and dropping seeds under the parent tree has been documented many times for many frugivore species (e.g., primates, Corlett and Lucas 1990; bats, Fleming 1986, birds, Levey 1987). Seeds dispersed outside of conspecific "parent" clumps experience greater survivorship.

The first part of the study described here took place over one day, at the peak of fruit availability. As fruit availability declines, rodents begin to both feed on and scatterhoard the seeds of *Maximiliana maripa* (see below, and Chapters 3 and 5). However, they do not immediately do so, and seeds remaining beneath the parent plant for any length of time are subject to infestation by beetles and destruction by peccaries. Tapirs, on the other hand, although they do spit out the larger seeds of other palm species (Bodmer 1989a), removed large numbers of *Maximiliana* seeds away from the parent plant and clump soon after fruit-fall. To the extent that mortality by beetles affects *Maximiliana* regeneration, these results indicate that on Maraca, the relationship between nontapir frugivores and *Maximiliana* is less important to the plant than the one with tapirs in terms of numbers of seeds moved away from high mortality sites. This conclusion is further supported by the higher density of *M. maripa* seedling and sapling densities found at tapir latrines relative to a) parent trees and b) randomly selected plots of land (presumabbly representing seedlings gemininating from seeds dispersed by non-tapir seed dispersers) (Chapter 3).

Even rodents, generally considered good seed dispersers, discarded most seeds that were found within 5 m of parent trees. These results are similar to those of Forget (1992a), who experimentally determined that 51.3 % of Gustavia superba seeds presented to rodents with the pulp already removed were left by rodents within 5 to 10 m. Although he tracked seed fate quantitatively for only 28 days, Forget considered this seed displacement sufficient for survival. Later in the year, however, he observed disproportionately high seed and seedling mortality of these weakly dispersed seeds, evidence that contradicts his initial conclusion that rodents play an essential role in dispersing G. superba. Hallwachs (1986) also experimentally determined that most Hymenea courbaril seeds dispersed by agoutis (Dasyprocta punctata) stay within 10 m of their origin, although a large number were also moved between 10 and 100 m of their origin. Hallwachs considered agoutis to be adequate dispersers of H. courbaril, but notes that if white-lipped peccaries were still extant in the area they would have consumed these seeds, due to their habit of foraging near trees or other areas where high densities of seeds or seedling are likely to occur (Kiltie 1981a). A possible confounding effect in Hallwachs' study was that her fruit clumps contained fewer fruits than would naturally occur beneath adult trees following fruitfall. There is some evidence that rodents are more likely to remove seeds at low seed densities (Forget 1992a, Hallwachs 1986, Moegenburg 1994).

In both Forget's (1992a) and Hallwach's (1986) studies, rodents ate some seeds. Note, however, that for my study of fruit consumption beneath parent plants, neither rodents nor any of the other vertebrates fed on the *Maximiliana* seeds themselves. At times when they do feed on the seeds, rodents may contribute to seed dispersal through scatter hoarding, and the other vertebrates through seed ingestion and defecation. Rodents are important secondary dispersers for *Maximiliana* and other seeds first dispersed by tapirs (Chapter 3 and 4) and domestic horses (*Equs caballus*; Janzen 1982b).

Predispersal seed destruction by beetle larvae is also high for other palm species. Kiltie (1981a) found that 98% of undispersed *Astrocaryum macrocalyx* fruits beneath parent trees were attacked by bruchid beetles. Smythe (1989) recorded a similar pattern for *Astrocaryum standleyanum* on Barro Colorado Island, Panama, with 100% mortality of seeds. Janzen (1971) examined bruchid beetle destruction of predispersal seeds of *Scheelea rostrata* palms that appeared whole and found that mortality, while initially low in newly dropped fruit, in time reached 90 to 98 %. Mortality in that study would have been higher had Janzen included seeds already killed by beetles (with adult exit holes) or other agents.

There is a potential difference between palm and large-seeded, nonpalm trees in the distance-mortality relationship. Terborgh et al. (1993) found a distance effect for their one palm species in Manu National Park (*Astrocaryum macrocalyx*), but not for four nonpalm species, and attributed this difference to the greater intensity of bruchid beetle predation on the palm species. Forget and Milleron (1991) found that only 2.25% of freshly fallen, pre-dispersal Virola nobilis fruit-seeds were infested by bruchid beetles. However, predispersal Spondias mombin fruits/seeds suffered more than a 95% mortality rate due to bruchid beetle destruction (Janzen 1985c). Clearly, the sources of mortality will vary among species and study sites, limiting the applicability of conclusions on the value of dispersal away from the parent plant unless the sources of species-specific mortality near the parent plant are documented.

Some studies have not found evidence for escape from larvae by dispersal for palm fruits. Wilson and Janzen (1972), in an experimental study, found that S. rostrata seeds whose pulp had been scraped in imitation of rodent pulp-feeding and placed 8 m from parent tree canopies were as frequently infested by bruchid beetle larvae as seeds placed near parent trees. They concluded that seed dispersal did not reduce predation by bruchid beetles. However, as with the previously discussed studies, this conclusion should be restricted to dispersal by rodents, since tapirs were not examined as possible dispersers.

Since rodents have much smaller home ranges than tapirs (Eisenberg 1989), seeds dispersed by rodents (or by simulated rodent dispersal) are more likely to remain within conspecific palms patches and within the bruchid infestation zone. In contrast, tapirs have very large home ranges (Williams 1984) and may move seeds tens of kilometers beyond the parent palm patch and established bruchid infestation zones. This hypothesis of the benefits of tapir dispersal is supported by Janzen's (1972) observation that *Sterculia apetala* seeds moved 500 m or more beyond the nearest fruit-bearing tree escaped predation by the bug *Dysdercus fasciatus*.

In this study, most tapir-dispersed seeds escaped destruction by beetles, while seeds remaining beneath parent plants contained live beetle larvae or had their endosperms destroyed by larvae. Because tapirs do not destroy seeds, and appear to be killing the bruchid beetle larvae and eggs already on fruits by passing seeds through their guts, frugivory by tapirs is probably more effective at preventing seed mortality by beetles than frugivory by rodents. While fruit-eating rodents also may remove larvae and eggs from fruits when they scrape pulp from seeds with their teeth, the mechanical nature of rodent pulp removal leaves much of it (and perhaps larvae) on the seed. *Maximiliana* pulp is fibrous and well attached to the seed, and much of it remains attached when peeled by the teeth of rodents, peccaries (*Tayassu* sp.), deer, and monkeys. Tapirs, in contrast, remove the pulp by chemical means and defecate seeds with no attached pulp. Thus any larvae on the fruit would be chemically removed along with the pulp. The digestive fluids in a tapir's stomach or perhaps its body temperature could possibly kill larvae already in the endosperm.

A close examination of the larvae in undispersed seeds revealed that they were small, approximately 1/5 of premetamorphosis size. Fruit swallowed by tapirs would thus have been infested with beetle eggs or larvae prior to ingestion. The larvae must then have been killed in the digestive tract before they penetrated the seed wall and perhaps while they were still on the fruit peel or pulp. This is supported by the observation that Maximiliana fruits are infected by beetle larvae while they are still attached to the tree (Audulto Ribiero, pers. comm.). It is unlikely that tapirs selectively ingested uninfested seeds, because a comparison of seeds in tapir latrines with those under parent plants indicated that there were no differences between them in any other seed characteristic (Chapter 4).

Similar patterns of infestation and larvae removal have been documented for other palm species. Fruits of Chamaedora tepejilote in Mexico were infested by larvae on the tree but not on the ground (Oyama 1991). Forget (1991) observed that Astrocaryum paramaca palm fruits were infected by bruchids during fruit maturation on the tree and that the grub penetrated the endocarp before the fruit fell. Similarly, for sabal palms (Sabal palmetto) in Florida, bruchid beetles initially attacked fresh green seeds in fruits on the trees (Moegenburg 1994). Janzen (1982d) also found that bruchid beetles laid eggs on ripe Guazuma ulmifolia fruit before they fell to the ground. Howe (1989) found that passage of fruit through the digestive tract of domestic cattle and horses killed beetle larvae already in *G. ulmifolia* fruit and suggested that plant reproduction benefits twice from the mutualism with the domestic animals: first by seed dispersal, and second by the reduction in seed predation resulting from the reduction in numbers of seed-predators.

In contrast to the results of my study, Janzen (1981b, 1982b), working with the feces of one tame tapir and 11 collected from wild tapirs, reported that the animal was a digestive seed-predator of the large seeds of the legumes *Enterlobium cyclocarpum* and *Cassia grandis*. These results could have occurred because 1) Janzen worked with a different tapir species, *Tapirus bairdii*, 2) *Maximiliana* seeds are larger and harder than the legumes he used, 3) there was some artifact peculiar to the use of a domestic tapir in Janzen's study or 4) the sample size of feces was too small and represented too short a time period to produce a representative description of the system. The South American tapirs in my study defecated viable seeds of many species in large numbers, including thousands of *Enterolobium cyclocarpum* in single feces (Huffman and Fragoso, in prep., seed viability tested by opening seeds and by germinating them). I suspect wild Central American tapirs will be found to do the same once a greater number of feces is sampled.

Coevolutionary Relationships

The relationship between tapirs and *Maximiliana* appears to be a coevolved mutualistic system as defined by Howe and

Eastabrook (1977) and Janzen (1980, 1985b); "an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population" (from Janzen 1980): the lack of seed fragments in the feces suggests that no seeds were destroyed in the tapir's stomach, and swallowed seeds had a significantly greater survivorship rate than seeds remaining beneath parent trees. *Maximiliana* fruits and seeds exhibit all the traits posited by Janzen and Martin (1982) as indicative of "megafaunal anachronisms," seeds that originally may have been dispersed by extinct Pleistocene megafauna and currently utilized by less effective dispersers. A test of the megafaunal anachronisms hypothesis would involve showing that current dispersers are not successful at maintaining plant regeneration, and that past dispersers did a better job. Clearly, the second part of this test is impossible when the megafaunal species is already extinct. A species dispersed by tapirs, however, has an extant megafaunal disperser, and the quality of its dispersal can be compared to that of other, smaller dispersers. *Maximiliana maripa* and other palm trees utilized by both tapirs and rodents provides an ideal test species for the hypothesis.

Thus, individual *Maximiliana* trees produce very large fruits and seeds, much of the crop rots beneath parent trees, and the pulp attracts a variety of frugivores that, apart from tapirs, do not appear to be ideally suited to dispersing its seeds. The large sizes of the fruits and seeds make them difficult for small organisms to swallow, except perhaps deer and spider monkeys. The white-tailed deer I observed feeding on *Maximiliana* fruit removed the pulp and spat out the seeds beneath parent trees and therefore did not contribute to seed dispersal away from the bruchid infestation zone. Spider monkeys ingested the entire fruit, as indicated by seeds found in their feces, but their small stomach size and the bulkiness of *Maximiliana* seeds suggest that they should avoid swallowing seeds or avoid eating the pulp if it involves swallowing the seed. Spider monkeys fed heavily on *Maximiliana* fruit only during one month, August, when other fruits were scarce (Nunes 1993), suggesting that it is not a preferred food. Dispersal by rodents has already been described. Tapirs seem to be the most effective disperser for *Maximiliana* on Maraca. Whether this dispersal leads to recuritment is examined in later papers (Chapters 3 and 4).

Tapirs have been in the New World tropics for approximately 2 million years (Rancy 1991, Simpson 1980), certainly long enough to have influenced the evolution of plant fruit traits. In several well-studied neotropical sites, tapirs already are becoming the latest representatives of the extinct Pleistocene megafauna, and large seeded palm trees may thus be anachronisms in the making.

Table 2-1: The number of *Maximiliana* fruit and seeds eaten by different frugivores beneath 6 fruiting trees. Samples from one day at the peak of the fruting season. Within-category percentages given in parentheses. Percentages in total column represent percent of total seeds.

	Distance from Parent (m)						
Fruit category	0-5	5-10	10-15	15-20	20-25	25-30	TOTAL
Ripe	694	15	0	0	0	0	709
	(97.9)	(2.1)					(15.9)
Rotted	1659	14	0	0	0	0	1670
	(99.2)	(0.84)					(37.4)
Seeds Only No Pulp	0	1	0	0	0	0	1
		(100)					(0.02)
Rodent Left	1381	33	4	1	0	0	1419
	(97.3)	(2.3)	(0.28)	(0.07)			(31.8)
Collared Peccary. Left	121	1	0	0	0	0	122
	(99.2)	(0.82)					(2.7)
Primate Left	160	0	1	0	0	0	161
	(99.4)		(0.62)				(3.6)
Deer/Tapir Left	25	0	0	0	0	0	25
	(100)						(0.56)
Unknown	336	21	1	0	0	3	361
	(93.7)	(5.82)	(0.28)			(0.86)	(8.1)
TOTAL	4373	85	6	1	0	3	4468
	(97.9)	(1.9)	(0.13)	(0.02)		(0.07)	

Table 2-2: Mean and standard deviations of fruits in each category under six *Maximiliana* palm trees sampled once at the peak fruiting period.

Fruit category	Mean	S.D.	Min-Max
Ripe	118.17	65.80	30 - 188
Rotted	278.33	491.62	0 - 1249
Seeds Only No Pulp	0.17	0.41	0 - 1
Rodents	236.50	109.82	39 - 344
Collared Peccaries	20.33	27.51	0 - 61
Primates	26.83	38.14	0 - 98
Deer/Tapir	4.17	10.21	0 - 25
Unknown	60.17	70.79	0 - 191
Total	778.17	537.54	181 - 1788

Table 2-3: The sum of *Maximiliana* seeds for all feces at eight wetland tapir latrines sampled from October to December 1991. Only data from the first six sites were used in the analysis.

Area	No. feces with seeds	Total no. of seeds	Mean no.seeds / feces	SD
Forest Lake	24	1790	74.58	8.80
Savanna Lake	16	1197	74.81	12.31
Bactris Swamp	14	1024	73.41	17.68
Trail 4 Buritizal	3	182	60.67	29.21
Tapir Pool	1	51	51.00	0.00
New Buritizal	18	1724	95.78	27.86
Western End of Island	1	80	80.00	0.00
Station Savanna	1	92	92.00	0.00
Total	78	6140	70.82	8.03

Table 2-4: Condition of *Maximiliana* seeds beneath parent trees, and at tapir latrines. Sampling dates as in previous tables.

Seed Category	Tapir Feces N (%)	Parent Tree N (%)
Viable	433 (98.4)	34 (17)
With Beetle Larvae	1 (0.1)	126 (63)
With Beetle Exit Hole	2 (0.45)	28 (14)
With Fungus	2 (0.45)	7 (3.5)
Undeveloped	2 (0.45)	5 (2.5)
TOTAL	440	200

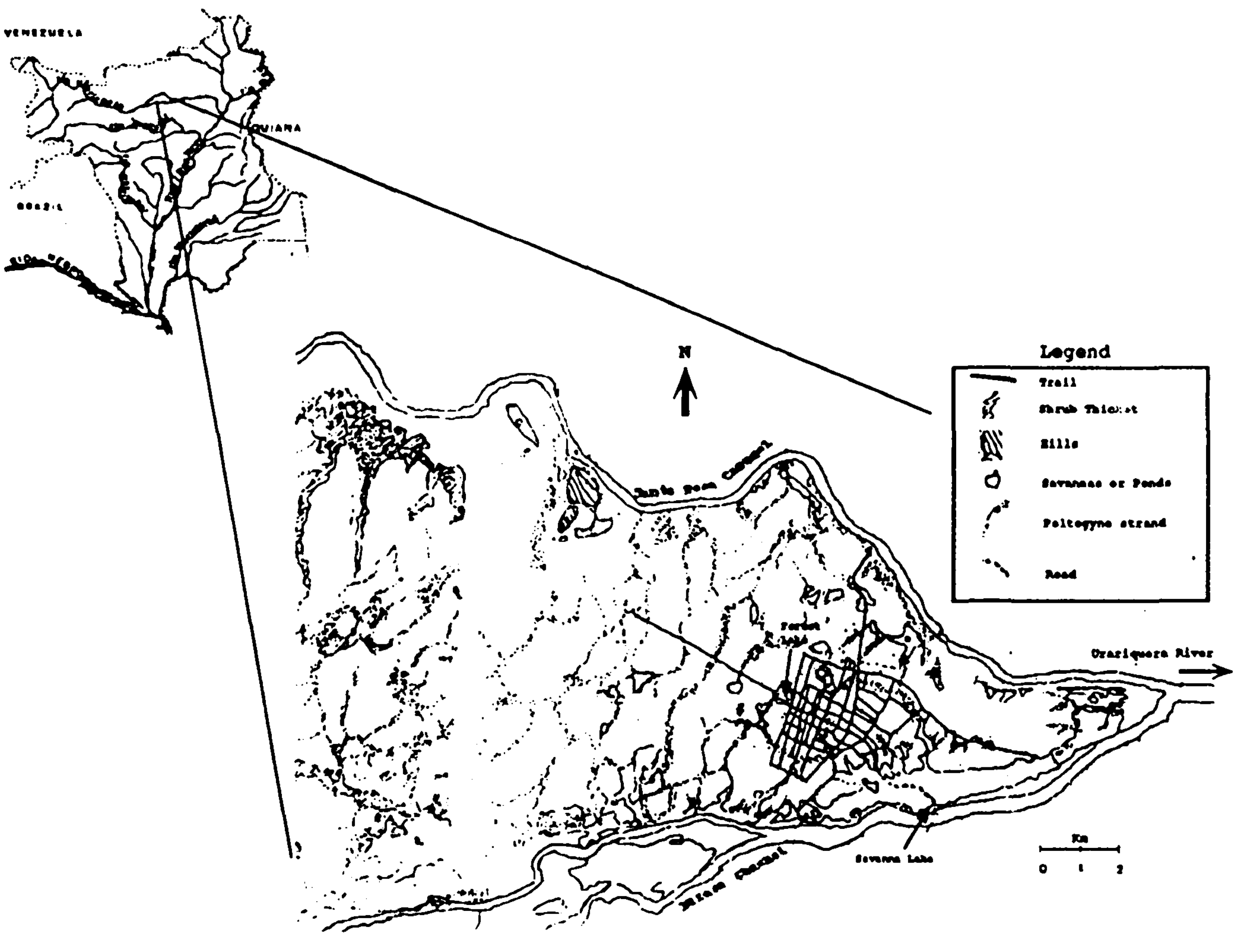

Figure 2-1: Maraca Island Ecological Reserve lies at 3°25'N and 61°40'W, at the northern edge of the Amazon River basin in Roraima State, Brazil.

CHAPTER 3
REGENERATION DYNAMICS OF AN AMAZONIAN PALM. PART II: SEEDLING SURVIVAL

Introduction

Tropical rain forests are among the most diverse plant communities known. The question of what maintains this diversity continues to be debated. Janzen (1970) and Connell (1971) posited that tree species diversity is high due to almost complete seed and seedling mortality near parents, which limits recruitment to areas distant from adult conspecifics. As a result, adults are more evenly spaced than expected from the pattern of seed fall. The open space near parents becomes available for colonization by other species, competitive exclusion is less likely, and more species can coexist in the community (Clark and Clark 1984, Hubbell 1979, Schupp 1992). There have been continuing field tests of the hypothesis, with varying outcomes (e.g., Clark and Clark 1984, Condit, et al. 1992, Howe 1993b, Hubbell and Foster 1987, Leigh et al. 1993, Schupp 1992, Thorington et al. 1982, Hubbell 1980).

The Janzen-Connell hypothesis and its subsequent tests, however, are based on the assumption of an even distribution of adult individuals in tropical forests. This assumption has repeatedly been proved wrong, with many species in

Central American rain forests showing a clumped or random rather than an over dispersed distribution (Hubbell 1980, Leigh 1982, Thorington et al. 1982). A better question to address is therefore what is the spatial pattern of distribution of species, and what processes create these patterns. The same processes invoked as resulting in the Janzen-Connell pattern--seed dispersal, seed predation, and seedling predation--need to be considered, but with more attention to the interaction among these different stages. It is the dispersion pattern, interacting with the scale of sampling, which will then determine the diversity of a forest plot (Thorington et al. 1982).

In Amazonian forests, palm trees in particular tend to occur in monospecific or single species dominant patches (de Granville and Kahn 1992, Kiltie 1981a, Peres in press, Sist 1989). A partial explanation for this pattern lies in the edaphic factors such as soil type and water regimes (Castro and Kahn 1985, Kahn and de Granville 1992), but biotic factors such as seed dispersal and predation patterns need to be examined as well, either on their own or in interaction with the edaphic factors. I have already shown that seed dispersal by tapirs can lead to clumps of seeds away from the parent plant. I now examine patterns of seedling density to determine if seed clumps give rise to seedling clumps, and to infer alternative mechanisms, other than tapir dispersal, for the formation of seedling clumps.

Studies of ecological interactions affecting the structure and diversity in tropical forests are often carried out in areas where large mammals have been extirpated, adding to the difficulty of deciphering the already complex interactions. The project described here, in contrast, took place in the undisturbed and unfragmented rain forest of the Maraca Island Ecological Reserve in the Brazilian amazon. This area supports populations of white-lipped peccaries (Tayassu pecari), tapirs (Tapirus terrestris), harpy eagles (Harpia harpyia), jaguars (Panthera onca), and cougars (Puma concolor), large vertebrates that have disappeared from many Neotropical regions, and in particular are rare or absent at Barro Colorado Island (BCI), Panama and La Selva, Costa Rica, two sites where most studies of Neotropical seed-vertebrate interactions have taken place. In a situation where large seed-eating mammals and their activities are very conspicuous, one is more likely to look for alternatives to the assumptions that birds, bats, primates and rodents are the most important vertebrates in shaping forest structure. Tapirs defecate large numbers of viable seeds of the arborescent palm Maximiliana maripa and other species of seeds at their latrines (Chapter 2, Huffman and Fragoso in prep.), and these seeds have higher survival probabilities than seeds left beneath parent trees (Chapter 2). Tapirs may thus play a critical role in the ecology of the plants whose fruits they eat, with dispersal leading to more seedling establishment, and ultimately higher recruitment into older age classes. In this study I compared M. maripa seedling abundance in six age classes at nonpalm trees used as latrines by tapirs, at randomly selected nonpalm-nonlatrine trees ("controls"), and at Maximiliana trees that produced fruit the previous year. This allowed me to assess the importance of dispersal by tapirs and rodents, and of predation by white-lipped peccaries, on the survival of Maximiliana seedlings.

Methods, Study Species and Study Site

Study Site and Study Period

The field study took place from December 1990 to December 1992. Data on seed predation and dispersal were collected during the entire period. The seedling and sapling data were collected from October to November 1992. Maraca Island Ecological Reserve is a 110,000 ha area, composed of a 60 by 25 km island, and other smaller islands in the Uraricoera River, in Roraima, Brazil (Fig. 2-1). The research station is located at 3°22'N 61°26'W. A complete description of the study site is given in Chapter 2.

Study Species

Tapirs

Tapirs have a solitary social structure and in the Amazon are generally frugivores that do not ingest seeds (large seeds) or else pass intact seeds through the gut (small seeds) rather than seed predators (Bodmer 1989a,1989b, 1990, 1991b; Fragoso, pers. obs.). Although a short experiment by Janzen (1981b) with one captive animal suggested that the Central American tapir (_Tapirus bairdii_) destroys seeds by digestion, his results are contrary to the evidence from the field and may have resulted from the artificial conditions of the experiment. When feeding on fruits, wild tapirs do so for extended periods of time, filling their digestive tract. Janzen fed his experimental animal only a few seeds at a time, which may have altered the normal treatment of seeds in the gut. On Maraca, tapirs dispersed both small and large seeds (Huffman and Fragoso in prep.).

Maximiliana

Maximiliana is a large subcanopy-to-canopy palm common throughout Amazonia (Kahn and de Granville 1992, Pesce 1985). _Maximiliana_ fruit-fall in my study area occurred from May to October 1991 and was synchronized within and among patches (Chapter 2). Adult _Maximiliana_ exhibit a clumped distribution, although they do sometimes occur singly (Chapter 2, Kahn and de Granville 1992, Pesce 1985).

I classified juvenile palms into six size classes, the first four of which correspond to yearly age classes, as estimated from individual seedlings that were tracked over time. Class zero _Maximiliana_ seedlings were those that had recently germinated and had a cotyledon still attached to the hypocotyl. The hypocotyl and cotyledon remained below ground, and the seedling consisted of one or two unsplit leaves without obvious petioles, all under 20 cm in height. Class one seedlings had two to three unsplit (no pinnae) leaves, which attained 20 to 35 cm lengths. The number of leaves on class two saplings ranged from two to four, some of which may be in the process of splitting, and some of which may have short petioles. Class three saplings had well-formed petioles, three to four split and splitting leaves and attained heights of about 130 cm. Class four saplings were similar in appearance to class three, but their stems were thicker, they ranged from 140 10 160 cm heights, and all leaves had well developed pinnae. Class five saplings had four or more exceptionally thick petioles. The leaves had well-developed pinnae, and the plant attained 170 to 210 cm heights but had yet to develop a trunk.

Methods

Tapir Latrines

I initially searched for tapir latrines at all large emergent trees (in terra firme forest) along 60 km of trails within the study area, and in the forest between trails. Since in terra firme forests, latrines occurred most commonly adjacent to large buttressed emergent trees, and especially tauri (*Couratari multiflora*) trees, these became the focus of the searches.

Seedling Patterns

I compared seedling abundance in the six age classes among three tree categories: 25 randomly selected Maximiliana adults that produced fruit in 1991 (chosen from random coordinates and distances along a trail, within conspecific clumps randomly chosen from all known clumps in the study area); 25 tauri latrines, most located more than 500 m from Maximiliana clumps; and 25 randomly selected nonlatrine, nonpalm trees (henceforth "controls"), emergent trees located more than 60 m from tauri-latrines and more than 500 m from Maximiliana clumps. The second and third types had few to no adult Maximiliana in the vicinity. All seedlings in the six age classes were counted within concentric circles to a distance of 20 m from the tree trunk (four 5 m radial increments). To ensure accuracy in counting, I roped off the 20 m diameter area into 12 equal parts. Each part was then searched by two or three people walking abreast. These data were gathered from October to December 1992, with three to five trees sampled per day.

I used a two-factor ANOVA to compare seedling densities between the three tree types and the six age classes. Post-hoc t-tests with Bonferroni adjustment for P values were used for pair-wise comparisons of sites, using data transformed to seedling density per meter square.

Results

Tapirs and Latrines

Four tapirs were known to use the study area, three adults and one infant (the animals were individually recogniable from scars and other markings, making a complete census possible during mammal density transects). They defecated large numbers of viable seeds of many species, including Maximiliana (Chapter 2, and Huffman and Fragoso in prep). Tapirs defecated thousands of seeds into both seasonally flooded wetlands and terra firme forest. In the latter habitat they defecated almost exclusively around the base of tauri trees (96 % of tapir latrines; n=24). One latrine was located by an emergent Ficus sp. tree, and two other emergent trees, a Peltogyne gracilipes and a Ficus sp. had one defecation each. These were not considered latrines because there was no accumulation of older feces indicating long-term repeated use.

Seedling Patterns

Latrine and nonlatrine trees had few Maximiliana adults within 500 m (Table 3-1), indicating that most seeds had been carried in by animals from distant parent trees. The number of seedlings and saplings ranged from 240 to 686 per 20 m radius area (1256.64 m^2) at latrine sites, from 46 to 533 at parent sites, and from 52 to 545 at nonlatrine trees, respectively. Statistically significant differences in seedling densities per site (df=2, F=30.23, P=.0001) and for all size classes (df=5,F=64.38, P=.0001) were observed. Densities of all size classes were highest at tauri tapir latrines than at the other tree types (Fig. 3-1, Table 3-2). The randomly selected controls had higher seedling and sapling densities than parent trees, except for size class one, but these differences were significant only for size classes two through four (Table 3-2).

The direction of density differences among the three site types was the same for all size classes except class two. In general, densities were highest at latrine sites, and lowest at parent trees. Class zero seedling densities were significantly higher at latrine than at control sites, or parent trees, but were similar between control and parent trees (Table 3-2). The densities of class one seedlings were significantly higher at latrine than control or parent trees, but were similar between control and parent trees. For the class two saplings, density was significantly higher at latrine than control trees, latrine than parent trees, and control than parent trees. For class three saplings, there were significantly higher densities at the latrine than the control or parent trees, and control than parent trees. As for class four saplings, densities were significantly higher at latrine than random, or parent trees, and control than parent trees. For class five saplings, densities were also greater at latrine than random or parent trees. However, sapling densities were similar between control and parent trees.

Discussion

Long-distance seed dispersal by tapirs significantly influenced the recruitment patterns of seedlings, with higher densities of seedlings of all age classes occurring in the latrines than under parent trees or under randomly selected trees.

White-lipped and collared peccaries uproot and eat recently germinated Maximiliana seedlings (Chapter 6). White-lipped peccaries also incidentally uproot and kill older seedlings when searching for buried seeds around the parent plant. These seedling predators were probably responsible for the higher seedling mortality close to parent plants than elsewhere: seedling densities for all size classes were highest at tapir latrines, located outside of Maximiliana clumps and usually beyond 500 m from parent trees. In addition, randomly selected and parent trees had similar densities of class zero and class one seedlings.

Predators that focus on high density seed or seedling patches should concentrate their activities near conspecific adults. Both Maximiliana seeds (Chapter 2) and seedlings that germinate within 20 m of parent trees were subject to high predation rates. For the latter, the density of zero class seedlings starts out high within a meter of parent trees, but by the end of the year seedling predators have lowered densities to levels lower then sites > 5 m from adults (Fragoso unpublished data). The fact that there was lower mortality at latrine sites, in spite of their high density of class zero and class one seedlings, indicates that density-responsive predators are focusing on the more common parent trees rather than on the rarer latrine trees: It is adult density rather than seed or seedling density that predators use as an indicator of food availability.

Seed dispersal by tapirs, and predator foraging patterns resulted in lowered recruitment near adults. The Maximiliana age data show that for all age classes densities were much higher at latrines than at parent trees. They also show that for three age classes densities were higher at random sites than by parent trees. Seeds under parent trees are undispersed seeds, or seeds moved short distances by rodents or spat out by ungulates. Seeds under control trees presumably were moved there by rodents, especially scatter-hoarding agoutis. In many cases tapir latrines were the closest seed source, so that rodent dispersal represents secondary dispersal of seeds already moved by tapirs.

Although these results support the Janzen-Connell model in the sense that seedling mortality is highest near parent trees due to the activities of density and seedling specific predators, they also show that recruitment patterns are more complex than those described by the model. Seedling recruitment was lowest near parent trees, but neither seeds nor seedling mortality was complete. This is the same pattern found by Hubbell (1979, 1980) in Costa Rica. In addition, high survivorship at nonpalm sites conflicts with the prediction of the Janzen-Connell hypothesis that the pattern of mortality near parent trees increases tree diversity. Seed dispersal by tapirs created new high-density clumps of seedlings and saplings and reduced space for other species. These aggregations could eventually become high density clumps of adults (range of 13 to 32 adults in five quarter hectare plots sampled). Seed predators did reduce seed survivorship (Chapter 2) and seedling density around parent trees, potentially opening space for other tree species, but on a forest-wide scale, diversity is probably reduced because tapir seed dispersal creates new clumps of *Maximiliana*. Thus, the scale at which one measures diversity plays a critical role in understanding the dynamics that affect diversity (as suggested by Thorington et al. 1982, and Schupp 1992). For plants whose seeds are dispersed or destroyed by terrestrial frugivores such as tapirs and white-lipped peccaries, scale-dependent phenomena may be more apparent in forests sustaining large vertebrate frugivores and seed predators.

Zero class seedling densities were highest at latrine trees because tapirs dispersed thousands of viable *Maximiliana* seeds into latrines. They were low at parent trees because most seeds that remained there were killed by bruchid beetles (Chapter 2) and white-lipped peccaries

(Chapters 5 and 6). Thus, while mortality of *Maximiliana* seeds and seedlings beneath parents is not complete, it is greater than at tapir latrines, and even higher than at randomly selected large trees throughout the forest. Thus the prediction that tapirs dispersed seeds into "safe sites" that are also good sites for germination and recruitment into older population levels was supported.

Much of the complexity in seed and seedling survivorship patterns resulted from the presence of ungulate frugivores in the study area. White-lipped peccaries are distance-responsive seed predators and are responsible for some of the high mortality of seeds and for the mortality of seedlings around parent trees. In my study there was a higher mortality of seeds and seedlings around parent trees relative to tapir dung areas even though both had high seed densities. This is probably because white-lips key in on adult *Maximiliana* clumps. Tauris occur as solitaires and thus may be more difficult for foraging herds to locate. One would predict that the discovery of tauris would be a random process as the animals search for other food resources. For example, seed predation by white-lips at tapir defecations is probably higher at buritizais (clumps of buriti palms, *Mauritia flexuosa*) than tauri sites (Chapter 6). White-lips enter buritizais in search of buriti fruit (Fragoso in press), water, mud holes, soil invertebrates and fish trapped as these wetlands dry (pers. obs.). Buritizais are multiple-use areas and easily identified by the presence of water and aggregations of buriti. *Maximiliana* seeds defecated there should experience predation levels similar to those at parent trees, but less than that occurring at latrine trees, because they attract frugivores and granivores for the same reasons as *Maximiliana* palm clumps. This in fact appears to occur (Chapter 5). Vertebrate seed predators can locate patches of seeds located far from parent plants but perhaps only if they occur in another easily identifiable clump of trees (buritizais), as suggested by the regular visits of white-lipped peccary to *Mauritia* swamps (Chapter 6).

Many studies have tested the Janzen-Connell hypothesis and produced conflicting results. In La Selva, Costa Rica, Clark and Clark (1984) found that *Dipteryx panamensis* seedling survivorship increased with distance from parent plants. Howe (1993b) obtained the same result with *Virola nobilis* seeds and seedlings on BCI. Schupp (1992) in contrast, found that *Faramea occidentalis* seed survivorship increased with increasing adult density. Condit et al. (1992) examined the dispersion of 80 tree species on BCI and found that most recruitment patterns conflicted with the predictions of the Janzen-Connell model, as did earlier work by Hubbell and his co-researchers on BCI (Hubbell and Foster 1987). All the studies cited above shared key characteristics that may have influenced their results: their forests were strongly disturbed (within the last few decades), small remnant fragments almost completely surrounded by farms or impounded water (Eisenberg 1990). The study sites also lacked white-lipped peccaries (La Selva, BCI, Santa Rosa National Park; pers. comm. D. Clark, W. Hallwachs and J. Eisenberg, respectively), and lacked tapirs (La Selva) or had only a few tame tapirs derived from a reintroduction (BCI), a major seed disperser. Although both sites have collared peccaries, this smaller species has a very different social and ranging pattern and is thus not ecologically equivalent to the white-lipped peccary (Chapter 6). In addition, BCI appears to sustain unusually high densities of agoutis and pacas (Agouti paca) (Emmons 1984, Glanz 1990, Smythe 1978). These factors and methodological differences, such as the scale at which seed dispersal was studied, could help explain the discrepancy in results between the studies. If one examines the distribution of large adult trees at BCI, one finds that many species occur in conspecific clumps (Thorington et al. 1982). Some of this clumping probably reflects earlier interactions between tapirs, white-lips other biotic factors and trees, at the time when the trees were seeds or seedlings and ungulate diversity was higher at BCI.

Rodents are important secondary dispersers of seeds already dispersed by tapirs (Chapters 3, 4 and 5). They remove seeds defecated by tapirs, and generate a secondary seed shadow which results in higher seedling and sapling densities than those found around parent trees. White-lipped peccaries also forage in tapir feces, but they are mainly seed predators. Thus when rodents move seeds from tapir feces they provide a definite reproductive advantage to the plant because these seeds escape destruction by white-lipped peccaries. In the past rodents also may have been important secondary dispersers of seeds first dispersed by Gomphotheres or other large extinct Pleistocene mammals (Janzen 1982b). Tapirs and rodents continue an interactive dispersal syndrome that benefits *Maximiliana*, but one probably initiated by tapirs. Studies of ecological interactions in tropical forests missing large mammals add to the difficulty of deciphering already complex interactions (Janzen and Martin 1982).

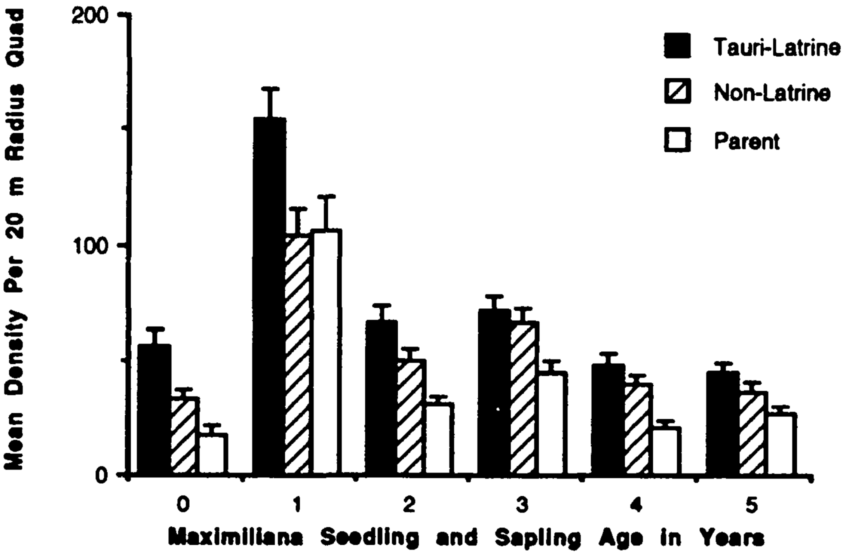

Fig. 3-1: The mean density and S.E. of *Maximiliana* seedlings and saplings per 1257 m^2 quad (20 m radius) at tauri-latrine (N=25), randomly-selected nonlatrine (N=25) and *Maximiliana* parent trees (N=25).

Table 3-1. The number of *Maximiliana* adults within 500 meters of study sites in the three site types.

No of Maximiliana Adults	Number of sites with N No. of adults Tauri	Non-Latrine Tree	Parent Tree
0	14	18	0
1	3	2	1
2	3	1	1
3	0	2	2
4	1	2	2
5	3	0	1
6 to 20	0	0	15
Unknown #	1	0	0

Summary Statistics			
Total Adults Per Site Type	28	18	201
Mean No. per Site Type	1.12	0.72	8.04
SE	0.35	0.27	0.91

Table 3-2: Probability values for *Maximiliana* seedling density comparisons among tauri-latrine, nonlatrine and *Maximiliana* parent trees. Nonsignificant comparisons are in bold numbers, all others are significant at $p < 0.05$.

SEEDLING AGE	P-Values for Among-Site Comparisons Tauri vs. Random	Tauri vs. *Maximiliana*	*Maximiliana* vs. Control
0	0.0039	0.0026	**0.8947**
1	0.0009	0.0001	**0.3088**
2	0.0173	0.0001	0.0340
3	0.0050	0.0001	0.0095
4	0.0007	0.0001	0.0268
5	0.0011	0.0001	**0.3591**

CHAPTER 4
REGENERATION DYNAMICS OF AN AMAZONIAN PALM. PART III. CREATION OF PATCHES

Introduction

Holling (1986, 1992) has suggested that a small number of plant, animal and abiotic processes with particular sizes and rates of activity may structure terrestrial biomes over various temporal and spatial scales. These structuring processes produce a landscape with "lumpy" geometries, temporal frequencies or periodicities, corresponding to the size and time characteristics of the organisms or processes that create them. Each lump or discrete grouping in a system has a particular range of grain sizes in space and time, and particular sizes, inter-object dimensions and fractal dimensions within that range. Here I use this same approach in an effort to understand the processes that structure the diversity of tropical forest plants. Because many tropical tree species occur in a patchy (clumped) distribution (Hubbell 1980, Leigh et al. 1993, Thorington et al. 1982), it is appropriate to ask whether this patchiness too is regular and scale-dependent.

Specifically, I consider the questions: 1) Is there lumpiness or discontinuity in this system as predicted by Holling (1992), 2) what are the processes that produce these lumps or discontinuities and 3) why some individuals occur as solitaires and others in high density conspecific aggregations?

Dominant seed predators and dispersers in Neotropical moist forests occur in a range of sizes from very large ungulates (tapirs, *Tapirus* sp., 250-300 Kg; white-lipped peccaries, *Tayassu pecari*, 30-40 Kg) through mid-size ungulates (collared peccaries, *Tayassu tajacu*, 10-25 Kg; and large rodents such as *Dasyprocta* sp., 4 Kg), to small rodents. The movement abilities, home ranges and number of seeds ingested per feeding site for these animals are directly correlated with their body sizes, while their longevity and population densities are inversely correlated (Eisenberg 1981, Robinson and Redford 1986). These factors lead to several predictions about the densities of conspecific tree patches that can be created by dispersers and modified by predators, and about the time frame during which patches can be maintained or replenished. First, certain densities will be more likely to occur, and these will persist through time. For example, low density patches, where little thinning through intraspecific competition occurs, will be fixed or constant through time. Second, initially high density patches will thin out through time, but will be maintained as relatively high density groupings relative to the other patches identified. Third, very high density patches may disappear, because these densities are sought out by seed and seedling predators.

I tested these predictions by examining the lump pattern (i.e., clustering of density data) exhibited by seedling, sapling and adult densities of the palm *Maximiliana maripa* at three site types. *M. maripa* is a large sub-canopy to canopy palm common throughout Amazonia (Kahn and de Granville 1992, Pesce 1985). Aggregations of seeds and seedlings are produced by the simultaneous ripening of large fruit crops that drop beneath the parent tree, and by the defecation of large numbers of seeds at repeatedly used tapir latrine sites (Chapter 2). These aggregations are subsequently attacked by predators such as bruchid beetles, rodents, white-lipped peccaries and collared peccaries. The adult trees frequently occur in patches of at least a hectare in area, as I discovered during 156 hours of flying over the forest. I defined an adult patch as any aggregation with a density of 13 or more trees per quarter hectare plot, based on the distribution of numbers of individuals found in randomly chosen patches sampled with randomly placed quarter hectare plots.

Methods, Study Species and Study Site

Study Site and Dates

This study took place on Maraca Island Ecological Reserve, an 110,000 ha area composed of one 60 by 25 km island and other smaller islands in the Uraricoera River, Roraima, Brazil (3°22'N 61°26'W). The forests are undisturbed and contiguous with those of greater Amazonia. The study site and species are described in detail in Chapter 2. The *M. maripa* seedling and sapling data were collected from October to December 1992.

Plants

I collected data on *Maximiliana* seedling, sapling and adult abundance from three site types: 25 randomly selected *M. maripa* adults that produced fruit in 1991 (all located within randomly selected conspecific patches); 25 tapir latrines around tauri trees (*Couratari multiflora*: Lecythidaceae), 19 of them located more than 500 m from *Maximiliana* patches, 3 more than 200 m from patches, and the remaining three closer than 200 m to patches; and 25 randomly selected nonlatrine-nonpalm emergent trees located more than 60 m from tauri-latrines and the same distances as the latrines from *Maximiliana* patches. Three to four trees were sampled per day. Details on the randomization of study plants are given in Chapter 3. The second and third site types had few to no adult *Maximiliana* in the vicinity. All seedlings, saplings and adults were counted within concentric circles (four 5 m radial increments) to a distance of 20 m from the tree trunk. To ensure accuracy in counting, I roped off the 20 m radius area into 12 equal parts. Each part was then searched by two or three people walking abreast. Juvenile *Maximiliana* individuals were classified into four known age groups (0,1, 2, and 3 year old) and three size classes (referred to as 4 and 5 year old saplings, and adult trees). The criteria for separating age classes are described in Chapter 3. The zero year seedling data were not used in the analysis described below because seeds had not yet completed their germination cycle and thus I could not account for pre-germination mortality.

Lump Estimation

In order to apply Holling's (1992) ideas of important scales of activity, a novel tact was taken to analyze the data. I used a version of the "kernel estimator" of data density (Silverman 1986, Chambers, et al. 1983) refined by P. Marples, of the Arthur Marshall Computer Lab, University of Florida, to search for consistent clusters amongst data sets of *Maximiliana* seedling densities.

The kernel estimator ("kerminator") produces a smeared histogram of data density: Figure 4-1 is a standard histogram of the density of first year seedlings An interval is defined over the seedling-density-axis (s) which completely encompasses the observed data. This information is used to produce a smeared histogram (Fig. 4-2). At each incremental location along the seedling-density-axis the frequency of occurrence (of observed densities) is calculated (f(s)). Within a window (the range of units within which data densities are calculated) or interval (of width h) the weighted frequency is calculated as

$$\sum_{i=a}^{b} f(s)_i \cdot \Delta s = 1$$

$$f(s) = \frac{1}{h \cdot N} \cdot \sum_{i=1}^{N} W\left(\frac{s - s_i}{h}\right)$$

$$W(u) = \begin{cases} 1 + \cos(2\pi u) & \text{if } |u| < 1/2 \\ 0 & \text{otherwise} \end{cases}$$

where s_i denotes the *i*th datum in the data-set and W is the weighted (by the cosine function) frequency function. Here frequency is defined as a cosine function but either constant or normal functions can be used. The increment (ds) along the seedling-density-axis must be finite (Ds) for computer computation yet must be small.

I examined a variety of window widths (h), each providing a successively coarser view of the data. Marples created a program that identifies intervals along the seedling-density-axis containing comparatively many data points as clusters (lumps), ignoring any cluster containing less than two data points. The program then summarizes clusters over multiple data-sets so that the consistency of cluster placement (lumping) can be evaluated (e.g., the data from the smeared distributions as in Figure 4-2 are summarized as in Figure 4-3.). If clusters and sparse-intervals occur over the same range of seedling-densities in multiple data-sets (trees or sites), then pattern has been established. Note that a lump is a persistent or repeatedly occurring grouping defined by the program.

Essentially, then, the program identifies the window width or scale at which pattern is visible. Wider windows destroy pattern by aggregating data, smaller windows destroy it by subdividing it too finely. It is then up to the researcher to identify biological processes that are acting on this scale and creating the pattern.

Results

Total densities of seedlings and saplings per area of 20 m radius ranged from 240 to 686 at latrines, from 46 to 533 at parents, and from 52 to 545 at nonlatrine trees, respectively. All replicates within all site types had seedlings of all age and size classes.

The tapir latrines (Site 1) held more lumps over a higher range of seedling and sapling densities than did the parent trees (Site 3), while the control sites (Site 2) were intermediate between the two (Figs. 4-3, 4-4 and 4-5). Density lumps were generally lost in the transition from younger to older plants, but these trends were more pronounced at certain sites. At latrines, high density lumps were lost in the progression from the one to the two and three year classes (from 240-260 to 130-140 to 80-110 same-age individuals per site, respectively, Fig. 4-3). They remained consistent between the third and fourth year classes (85-115), but declined to a mid-density lump (20-60) in the fifth year plants. At the nonlatrine-control sites, the highest density lumps were also lost in the progression from first to second year seedlings (200-220 to 85-110 respectively); however, the lumps in the two, three, four and five year plants changed little (70-110, Fig 4-4). At parent trees, the lower densities around the trunk appear to maintain themselves through time (Fig 4-5). For high density lumps, however, the pattern is somewhat similar to other sites, with the higher density lumps dropping off from the first to second year plants (165-190 to 45-55, respectively), and the mid-to-low density lumps (densities of 45 to 70) remaining constant from the two, to three and five year classes. For the fourth year class there is only a single, low density lump (5-25).

A visual comparison of the data for each year or size class among sites reveals the following contrasts (Figs. 4-6 through 4-10). Latrine sites supported more lumps at higher densities than did parent tree sites, and the nonlatrine-control sites held lumps of intermediate density compared to the two other site types. The one year old seedlings at latrines grouped into five density lumps, three mid-density (60 to 150) and two high density (200 to 265) (Fig 4-6). The nonlatrine sites support one or two high density lumps (200-220, with perhaps a second at 160-180), two mid-density lumps (45-80, and 75-95) and a low density lump (10-25). The parent trees also support a low density lump (0-40), two mid density (60-80 and 100-120), and one almost high density lump (165-185).

The number of density lumps decrease dramatically from the first to second year plants at all sites (Fig. 4-6 to 4-7). The latrines now hold only two mid-density (50-75 and 130-140), and one low (35-45) density lumps. The number of lumps at the nonlatrine and parent sites was reduced to two each, one low (30-55) and one mid (85-105) at the former, and one low (10-30) and one mid (50-65) in the latter. This pattern remains generally the same for third year plants, except for the one mid density lump dividing into two mid density lumps at nonlatrine-sites (Fig. 4-8). For the fourth year plants the lump pattern remains generally the same as in the third year, except that parent sites now hold only a low density lump (Fig 4-9). In contrast to the persistent lump pattern described for second, third and fourth year plants, for fifth year plants the latrine holds only a low density lump (20-55), while the nonlatrine sites support a low (20-40) and mid-density lump (65-95), as do the parent sites (5-35, and 60-75) (Fig. 4-10).

The pattern of adult density lumps differs radically from the seedling and sapling groups. The latrines hold only a very low lump of 0-1, as does the nonlatrine sites (Fig. 9). However, the parent tree sites hold two density lumps, one at 4-10 and another at 18-20.

Discussion

The kerminator program revealed that there is lumpiness in *M. maripa* seedling, sapling and adult densities across time (age classes) and landscapes. It distinguished lumps of low, medium and high densities. As predicted, only specific densities occurred and remained constant through time, indicated by the two to five year class lump pattern at control and parent trees. The second prediction that high density lumps would decrease in density through time, but would be maintained as relatively high density lumps relative to the other lumps identified was also supported. Low and medium density lumps were maintained in the transition to older age/size categories, while high density lumps generally were lost (e.g. latrine trees). The highest density lumps occurred at latrines, and to a lesser degree at nonlatrine-control sites, even though more seeds fall around parent plants then are dispersed to latrines (Chapter 2). However, *M. maripa* seeds dispersed by tapirs experience greater survival than those remaining beneath parent trees (Fragoso 1993). An unexpected result was the presence of high density lumps around nonlatrine-control trees and perseverance of mid-density lumps into the four and five year sapling classes. The closest seed source to the nonlatrine-control sites in most cases were the tapir dispersed seeds at latrines. The seedlings and saplings at control sites must have originated from seeds secondarily dispersed from tapir-latrine sites by rodents (and perhaps to a lesser degree through primary dispersal by primates and rodents).

The lowest density lumps were observed at parent sites. However, these sites also contained the highest density lumps of fifth year plants (however, latrine sites contained the greatest mean density for five-year class relative to other site-types; see chapter 3). Since the highest density plant lumps occurred at the other two site types in the younger age classes, and these were generally lost with age, how can one explain higher density lumps of older versus younger plants? This contradicts the directionality of most life tables, and counters the previous pattern of higher density lumps at latrine and latrine sites. One explanation is that the fifth year class encompasses trees of many ages, because it incorporated plants between four years and the age at which trunks develop (a period of 5-7 years for *Attalea* sp., Conner 1966; and 7 years for *Iriartea* sp., Pinard 1993). The younger age classes included only plants belonging to their cohort (0,1, 2 and 3 year old), or a smaller subset of older plants (the 4 year category, since everything larger would go into the next age class of 5 year plants). This inflation of density at the highest size class would not have occurred at latrines if tapirs had only recently begun defecating there; for example, within the last five to seven years (as evidenced by few plants in fifth year class).

This scenario seems logical given that the resident tapirs eventually die and their home ranges become occupied by new individuals. The new resident tapir may choose other latrine sites, or perhaps residents simply switch latrines over time for territorial or other social reasons. Based on that logic one would expect fewer five year plants at these sites because M. maripa seeds were not dispersed there in earlier years. At parent trees, in contrast, a few plants surviving each year for 10 to 15 years would inflate the number of individuals in the five year class of this site. This would not have occurred at latrine sites because of the paucity of adult M. maripa trees nearby as a seed source. The unanswered question is why the nonlatrine and parent trees maintained a mid-density lump of the five year class.

An alternative explanation for the inflation of density results from the fact that I did not follow seedlings through time. My classes are based primarily on plant size. Therefore differences in population size among years could also result from differences in fruit crop size and overall fruit production among years.

What I describe above is a process by which M. maripa clumps are created. When a tapir dies the rain of tapir-dispersed seeds to some latrines may end. However, the new resident tapir begins the cycle anew by defecating around the base of previously unused tauris, creating new high density aggregations of M. maripa. Eventually the tauri dies and tapirs no longer have the tree to defecate around. However, the seedlings and saplings at the site will grow into adults and eventually form new clumps or perhaps the tauri may have already been in the midst of an adult clump when it toppled over.

While there is a possibility that high density adult clumps originate from parent sites, this is unlikely since they held only a low density lump of fourth year plants (the oldest cohort that likely contains only plants of a single year class). More likely these sites eventually disappear as the adults die or they support single adults or low density clumps, because adult aggregations attract seed and seedling predators, probably resulting in lower recruitment rates into adult age classes. Recruitment may become so low within parent sites that more adults die than are recruited into that age class. Hence succession at such sites could result in a mixed forest with perhaps one, a few or no *M. maripa* adults. In contrast, succession at latrine and nonlatrine-control sites could result in the creation of high density aggregations of adult/parent *M. maripa*. The demography of *M. maripa*, including longevity and turnover, need to be studied before these hypotheses can be tested.

New low and high density clumps of *Maximiliana* are thus likely to be generated from latrine sites based on the presence of high density clumps of older age seedlings. Low and high density adult clumps may also be generated from the nonlatrine control sites, but the parent sites most likely produce single trees or very low density clumps, because at the fourth year age class they only generate low density lumps.

The role of seed predators in the lumping process is as follows. As the densities of *M. maripa* adults producing fruit increases, they begin to attract seed predators such as bruchid beetles and white-lipped peccaries (Chapter 3). White-lipped and collared peccaries also destroy seedlings. Eventually, predation rates are so high and recruitment so low that few plants reach adulthood. These *M. maripa* clumps eventually become mixed forest.

While rodents do disperse seeds away from parent trees, because of their small home range size most rodent-dispersed seeds probably remain within conspecific aggregations. Most of these seeds are eventually found and eaten by white-lipped peccaries or beetle larvae (Chapter 5). The few seeds successfully dispersed by rodents first do not produce aggregations of seedlings as dense as those formed at tapir latrines. Thus this class of seed disperser is more likely to produce solitary trees or low to mid density aggregations of *M. maripa*.

This is a self-organizing system in that all players in the system affect each others' population dynamics. *M. maripa* trees provide food for tapirs, who in turn create new aggregations of the plants. The original source clumps of fruit/seeds eventually becomes mixed forest because of low population recruitment due to high seed and seedling predation rates. Predation rates are high because seed and seedling predators key in on adult aggregations (Connell 1970, Janzen 1970, Hubbell 1980). The key player in this system may be tapirs. They enhance the fitness of M. maripa by consuming its fruit and successfully dispersing the seeds. Seed and seedling predators combine with tapirs to determine the dispersion of M. maripa across time and landscapes.

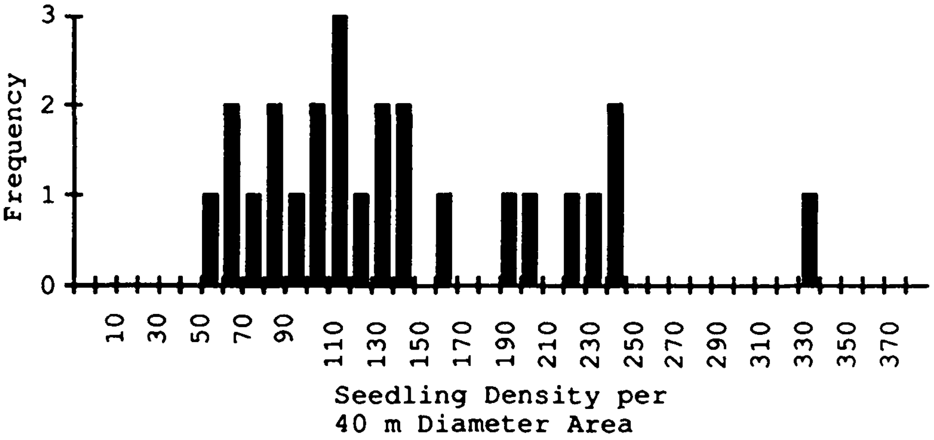

Figure 4-1: A normal histogram showing the frequency of first year *Maximiliana maripa* seedling densities at tauri tapir-latrine trees (Site 1).

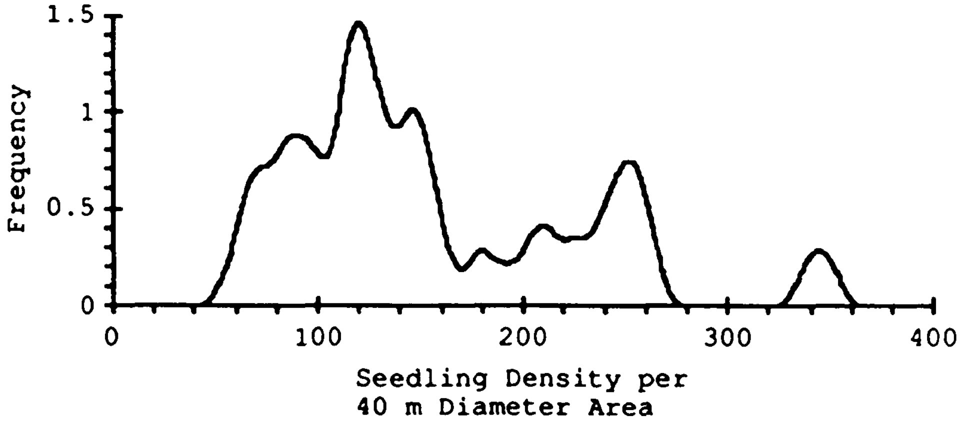

Figure 4-2: An example of a smooth histogram of converted frequency data for first year *Maximiliana maripa* seedling densities at tauri tapir-latrines (Site 1).

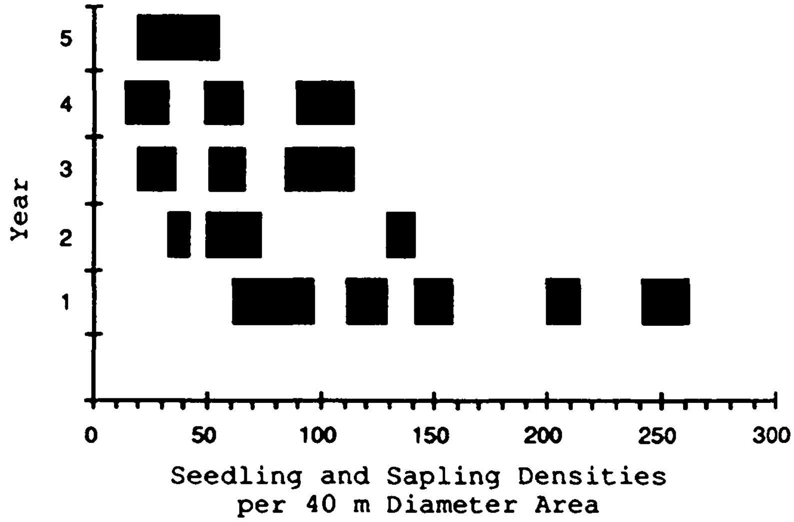

Figure 4-3: *Maximiliana maripa* seedling and sapling density groupings (lump structure) at ages 1 to 3 and size classes 4 and 5, as identified by the Kernel Estimator at tauri-latrine trees (Site 1).

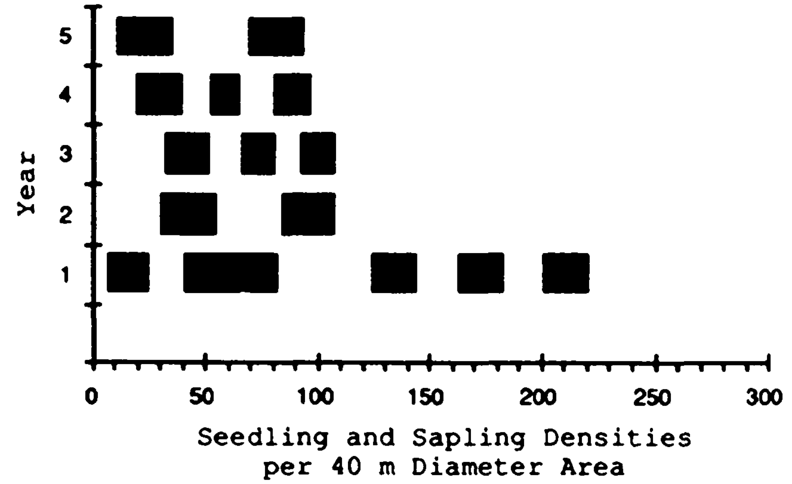

Figure 4-4: *Maximiliana maripa* seedling and sapling density groupings (lump structure) at ages 1 to 3 and size classes 4 and 5, as identified by the Kernel Estimator at latrine-control trees (Site 2).

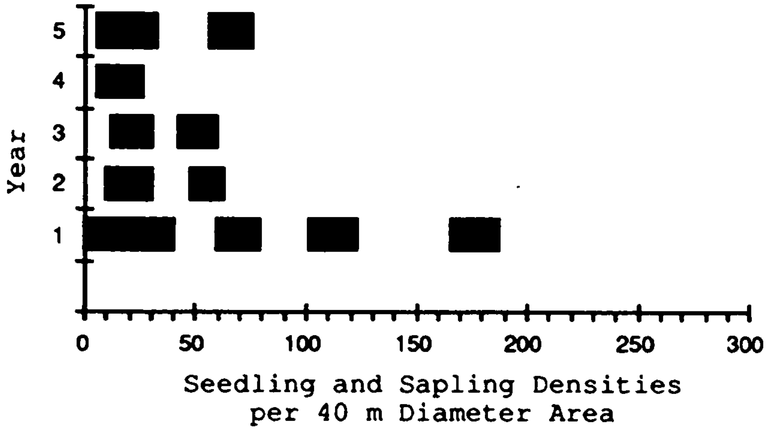

Figure 4-5: Maximiliana maripa seedling and sapling density groupings (lump structure) at ages 1 to 3 and size classes 4 and 5, as identified by the Kernel Estimator at parent trees (Site 3).

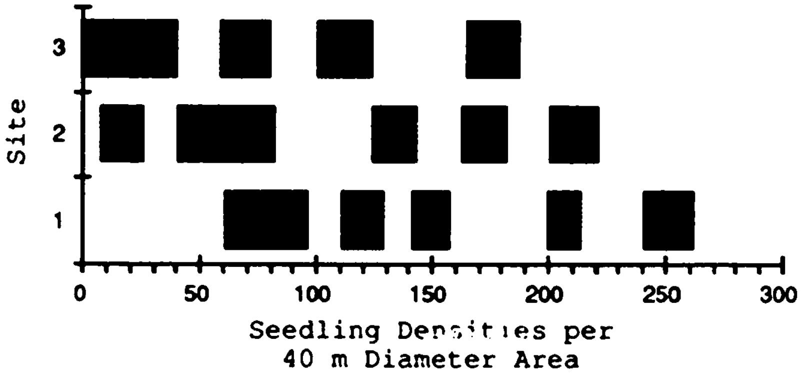

Figure 4-6: A comparison of one year old Maximiliana maripa seedling density lumps among three site types: tauri-tapir latrines (Site 1), latrine control trees (Site 2) and parent trees (Site 3)

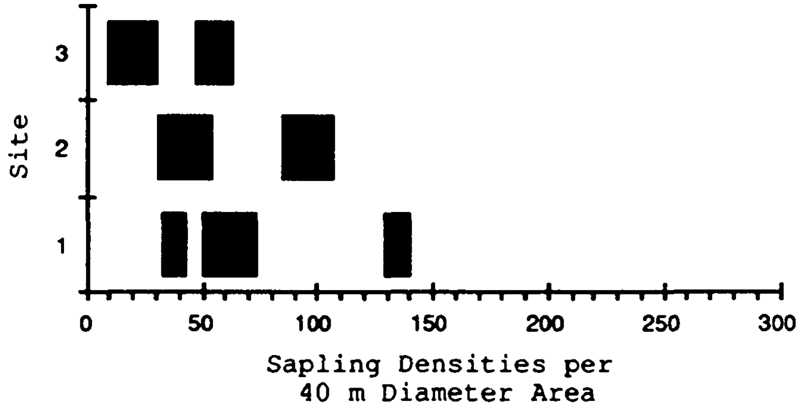

Figure 4-7: A comparison of two year old Maximiliana maripa sapling density lumps among three site types: tauri-tapir latrines (Site 1), latrine control trees (Site 2) and parent trees (Site 3)

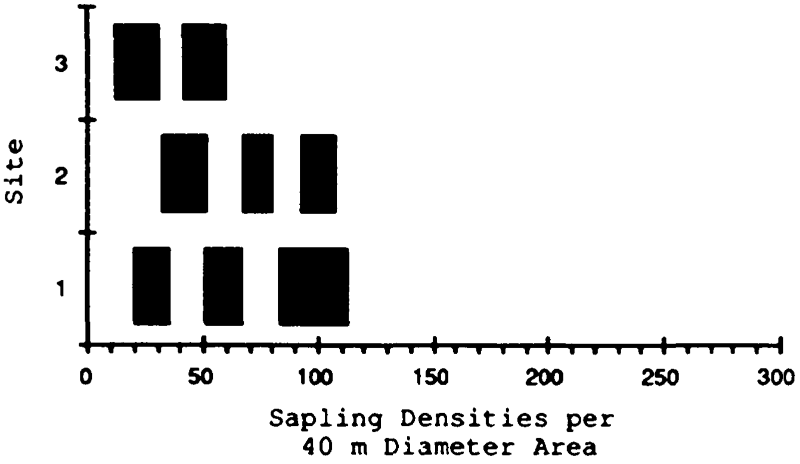

Figure 4-8: A comparison of three year old Maximiliana maripa sapling density lumps among three site types: tauri-tapir latrines (Site 1), latrine control trees (Site 2) and parent trees (Site 3)

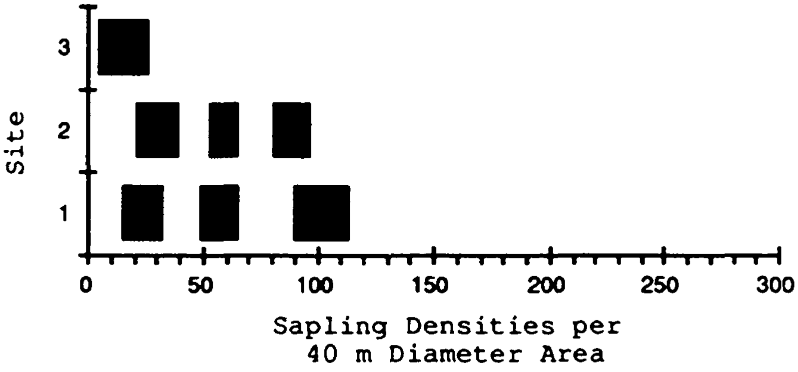

Figure 4-9: A comparison of four year old Maximiliana maripa sapling density lumps among three site types: tauri-tapir latrines (Site 1), latrine control trees (Site 2) and parent trees (Site 3)

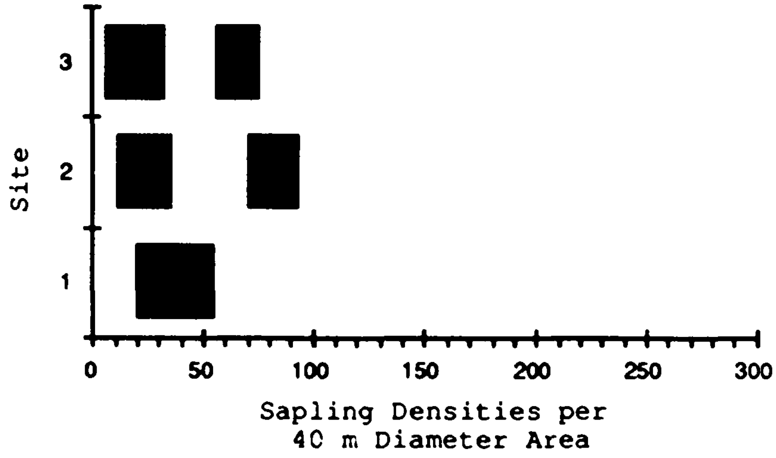

Figure 4-10: A comparison of five year old Maximiliana maripa sapling density lumps among three site types: tauri-tapir latrines (Site 1), latrine control trees (Site 2) and parent trees (Site 3).

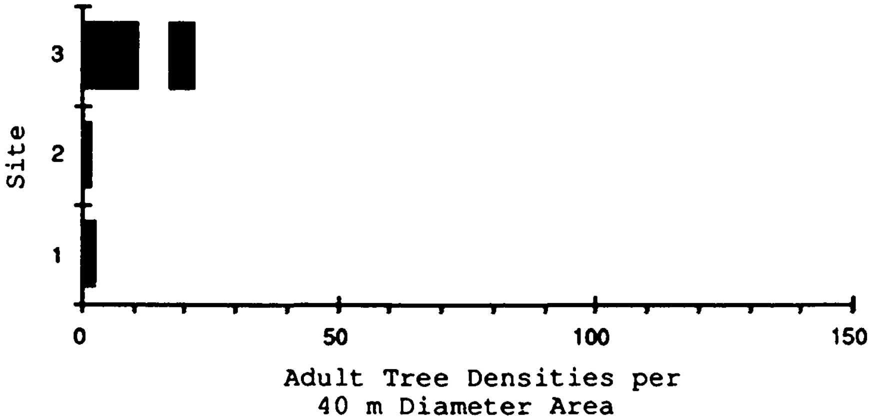

Figure 4-11: A comparison of adult Maximiliana maripa tree density lumps among three site types: tauri-tapir latrines (Site 1), latrine control trees (Site 2) and parent trees (Site 3).

CHAPTER 5
SCALE-DEPENDENT MODIFICATION OF SELECTIVE PRESSURE ON PALM SEED DEFENSES: INTERACTIONS AMONG SEED PREDATORS

Introduction

Seed consumption is a common feeding strategy among animals, and represents a selective factor that can significantly affect plant population ecology and plant evolution (e.g., Fleming and Estrada 1993, Harper 1977, Louda 1989). Selective pressures by seed predators should act to increase the frequency of seed traits that facilitate escape from predators (e.g., Howe 1986, Howe and Smallwood 1982, Janzen 1969). Evaluating how seed predation influences seed traits, however, has proved difficult (Harper 1977; review by Louda 1989). The different organisms influencing seed characteristics often remain hypothetical, especially in the tropics where the diversity of seed consumers is greatest (e.g., Louda 1989, Wright 1990). One reason for this uncertainty is that most seed populations are attacked by a variety of seed predators, often from different classes, orders, or even phyla and kingdoms (e.g., vertebrates and fungi), but most studies examine interactions between one or two seed predators and one species of seed (e.g., Bradford and Smith 1977, Wilson and Janzen 1972, Wright 1983, 1990). Studies that do address multiple interactions are usually interested in the consumer rather than the plant's point of view (e.g., Herrera 1989, Traveset 1993). It is unclear how a guild or several guilds of seed-predators influence seed traits of a given plant species. It is also difficult to identify past selective pressures from consumers that are now extinct (Janzen and Martin 1982). Thus, the fact that some seeds respond to predators by producing secondary compounds which repel predators (Janzen 1969, 1977, 1981a, 1985a), while others increase endocarp hardness or produce more endosperms (Bradford and Smith 1977, Wilson and Janzen 1972, Wright 1990), may be an indication not just of alternative solutions to the same predation pressure, but of optimal or compromise solutions to a multitude of conflicting pressures.

Palms, a dominant component of tropical lowland forests (Kahn and de Granville 1992, Uhl and Dransfield 1987), produce large seeds which tend to attract high levels of seed predation by both vertebrates and invertebrates (Janzen 1971, Terborgh 1983, 1986 a and b). Most studies of palm seed dynamics address only predation by bruchids and rodents (e.g., Bradford and Smith 1977, Forget 1991, 1992, Janzen 1971, 1972, Vandermeer 1979, Wilson and Janzen 1972, Wright 1983, 1990). Evolutionary relationships posited among large seeds, palms, rodents and beetles tend to be speculative (e.g., Bradford and Smith 1977, Wilson and Janzen 1972, Wright 1990). Here I examine the traits of *Maximiliana maripa* palm seeds entering and persisting in a seed bank. I consider how seed selection by tapirs (*Tapirus terrestris*, a seed disperser) and a guild of seed-predators could influence seed morphology. I then consider the potential influence of predation by three types of predators on the evolution and ecology of these seeds. Although I am not examining all the organisms that could be ifluencing *Maximiliana* seed traits, I have chosen those organisms that my data (Chapters 2, 3, and 4) suggest are responsible for the largest proportion of seed mortality and initial escape from mortality.

In the predator guild that utilizes *Maximiliana* seeds, each predator uses unique strategies, which reflect different adaptations to seed eating, to circumvent palm seed defenses: Beetle larvae bore through the endocarp surrounding the endosperm(s), while rodents gnaw through it and white-lipped peccaries (*Tayassu pecari*) simply crush it (Fragoso pers. obs., Bradford and Smith 1977, Janzen 1971, Wilson and Janzen 1972). Collared peccaries (*Tayassu tajacu*) are not considered because in this study they did not consume *Maximiliana* seeds during caged experiments or in the wild (Fragoso unpubl. data). Deer (*Odocoileus virginianus*, *Mazama* spp.) and tapirs both spit out the seeds or ingest them intact rather than crushing them.

I address the hypothesis that each seed predator species selects for different seed characteristics, and that the distribution of seed traits is a cumulative response to the interaction of these forces by examining a series of predictions. 1) Given that individual trees can produce both single and multiple endosperm (carpels) seeds, the proportions of these seed types produced by a palm population will depart significantly from an even distribution. Barring complicating genetic effects, the assumption is then that selection favors the dominant seed traits. I then consider whether tapirs, a seed-dispersing species, are responsible for the selective advantage of some seed traits by examining the prediction that 2) the number of endosperms per seed does not influence fruit ingestion by tapirs.

Seed traits are usually corelated with one another, and there are tradeoffs associated with energy investment in one or another (Janzen 1969, 1977). To determine correlations between Maximiliana seed traits that may enhance survival, I tested the prediction that 3) single-endosperm seeds have thicker endocarps than those with two or three endosperms. I consider the possibility that seed predators preferentially attack seeds with certain traits by testing the prediction that 4) the proportions of single and multiple endosperm seeds attacked do not differ among beetle larvae, rodents and white-lipped peccaries ("white-lips").

While seed predators may or may not attack seeds indiscriminately, the post-attack survival of endosperms may be a function of predator identity. I tested this hypotheis using the predictions that 5) multi-endosperm seeds are more likely to survive attack by larvae than by rodents or white-lipped peccaries; 6) the proportions of one, two and three endosperm seeds do not differ between those eaten by the seed predators and those remaining alive at feeding sites, or those originally located beneath parent trees; and 7) all species attack seeds with similarly thick endocarps. I then examine the distribution of single- and multi-endosperm seeds among both *Maximiliana* individuals (in aggregations) and among patches, and relate this distribution to the movement and feeding patterns of the different consumers to show how consumer ecology can exert selective pressure on the spatiotemporal distribution of seed traits as well as on the seed traits themselves.

Methods, Study Site and Species

Study Area

This study took place from December 1990 to December 1992, on Maraca Island Ecological Reserve, a 60 by 25 km island in the Urariquera River, (Fig. 2-1) located at $3^{\circ}22'$N $61^{\circ}26'$W in the moist tropical forest habitat of Roraima, Brazil. The study site is described in detail in Chapter 2.

Study Species

The Palm

Maximiliana maripa is a common, sub-canopy to canopy palm of the northern Amazon forest. It can grow to 35 m in height (Kahn and de Granville 1992, Pesce 1985). On Maraca the trees grow in patches with densities from 13 to 32 individuals per 1/4 ha (Fragoso pers. obs.; based on five randomly chosen patches). Some trees also grow as solitaires in the forest, but this analysis is concerned only with those growing in aggregations. Adult trees produce from 1 to 4 infructescences, each bearing from hundreds to over two thousand fruits (Fragoso pers. obs., K. Silvius unpublished data). Fruits weigh from 14 to 26 g, and measure 5 to 6.5 cm in length. Seeds weigh from 7 to 17 g. Details on the ecology of Maximiliana are given in Chapter 2.

I use the word seed to refer to the endocarp and enclosed endosperm(s). Other authors occasionally refer to this structure as the "nut" or "endocarp." Maximiliana seed endocarps are large, woody and extremely hard; they were not ingested by seed predators. When endosperms were consumed, seed predators left the endocarp or endocarp fragments (white-lips) at feeding sites.

Tapirs

Tapirs are solitary ungulates (Perissodactyla) that weigh up to 250 kg and feed mainly on browse and fruits (Eisenberg 1989). On Maraca they fed extensively on Maximiliana fruit and defecated entire seeds (Fragoso 1993, Chapters 2 and 3). Tapir feces consisted of aggregations of poorly digested plant matter, similar in appearance to horse dung. Feces were defined as all boluses defecated at one time. Tapirs defecated repeatedly over long periods of time at certain sites (Chapter 2), henceforth referred to as tapir latrines. I located six lowland latrines, distinct from the upland tauri latrines described earlier. The Forest Lake and Savanna Lake latrines were seasonal ponds, the Bactris Swamp, Trail 4 and Trail A latrines were seasonal streams, and the New Buritizal latrine was a seasonal wetland. Rodents and white-lips foraged on the accumulations of seeds at these latrines during dry periods, but infestation rates by beetle larvae were low, apparently because larvae may be killed by passage through the tapir's gut (Chapter 2).

Beetle Larvae

The beetle species has not yet been identified, but is probably in the family Bruchidae, and is similar to the species described by Janzen (1971) and Wright (1983). Adult beetles lay eggs on fruits, probably while they are still attached to the tree (A. Ribeiro, pers. comm.). After hatching, the larvae penetrate the endocarp of seeds, where they feed on the endosperm until emerging as adults up to nine months later (Fragoso pers. obs.). Usually only one larva or one adult beetle occur per seed, but I have found up to three larvae or two adult beetles in a single seed (Fragoso pers. obs.).

Rodents

Tooth marks on gnawed seeds indicated that agoutis (*Dasyprocta agouti*.), perhaps paca (*Agouti paca*), squirrels (*Sciurus* spp.) and possibly smaller terrestrial rodents consumed many *Maximiliana* seeds. The effects of different rodent species on seeds could not be distinguished, and all seeds with rodent tooth marks are grouped together. This grouping is justified by the lack of significant differences in endocarp thickness between seeds with small versus large teeth marks. Rodents dug into old, dry tapir feces in search of buried seeds, and the traces of this characteristic foraging behavior, combined with gnawed seeds, indicated when sites had been used by rodents.

White-lipped Peccaries

These mammals weigh up to 39 kg at Maraca (Chapter 6). They form large herds with tens to hundreds and possibly as many as two thousand individuals per group (Fragoso, pers. obs.; Kiltie 1983, Mayer and Wetzel 1987, Sowls 1984). Home range size increases with herd size (Chapter 6.). A herd with 130 individuals ranged over 109 km^2 (Chapter 6). White-lips leave unique signs when foraging: They furrow deeply into soils in search of buried seeds and roots, and the depth and extent of rooting is much greater than that of collared peccaries (Fragoso pers. obs.; Kiltie 1981a, Kiltie and Terborgh 1983, Sowls 1984). Their tracks, which are clearly visible in the recently rooted soils, are also much larger then those of collared peccaries (Fragoso pers. obs.; Sowls 1984).

Collared Peccaries

These ungulates co-occurred with white-lips in the study site. They averaged 20 kg in weight and foraged in the same regions as white-lips. They exhibit a territorial social structure, and herds can contain from about 8 to 50 individuals, depending on the site (Fragoso pers. obs.; Castellanos 1983, Sowls 1984). A feeding trial conducted with two wild-caught collared peccaries revealed that they could not crack open *Maximiliana* endocarps (Fragoso unpubl. data). This result was substantiated by observations of collared peccary feeding in areas of tapir latrines without eating *Maximiliana* seeds (Fragoso pers. obs.). The jaw structure of collared peccaries is less robust than that of white-lips, indicating that many palm seeds consumed by white-lips may be too thick for collared peccaries to open (Kiltie 1981b).

Methods

Seed Collection Sites and Dates

From October to November 1991, the end of the *Maximiliana* fruit-fall period, seeds were collected from beneath 20 randomly chosen (as described in Chapter 2) parent trees, distributed over five *Maximiliana* clumps randomly selected from among 24 study clumps. Ten seeds from freshly-fallen ripe fruit, rotted fruit, or fruit with pulp removed by consumers were randomly chosen from among the hundreds lying beneath trees by tossing a stick into the air and collecting the seed nearest a marked end.

From October 1991 to November 1992, seeds were collected randomly from tapir feces distributed over six tapir latrines. These seeds had been defecated in October and November, at the end of the 1991 fruiting season, and most had thus been lying in the latrines for 2 to 13 months. They included intact seeds, larvae-infested seeds, and seeds attacked by rodents and white-lips.

Whole seeds also were collected opportunistically from the forest floor, after dispersal by rodents and spider monkeys (Ateles belzebuth). The time elapsed between fruit-fall and collection was sufficient for beetle larvae to mature and for some adult beetles to develop in the seeds. These seeds were also exposed to predation by rodents and white-lips for six to seven months; therefore, intact seeds represent seeds not found or not chosen by vertebrates.

Additional seeds attacked and rejected (left behind after a herd passed through) by white-lips were collected from March to April and October to November 1992 from the latrines. Seeds gathered from April 9 to 12 were collected specifically to compare the thickness of seed endocarps attacked and left behind by white-lips, with that of seeds found at all latrines.

Seed Descriptions

The following were considered attacked seeds: 1) endocarps penetrated by rodents (as indicated by tooth marks) with or without surviving endosperms; 2) endocarps penetrated by beetle larvae with or without surviving endosperms; and 3) seeds cracked open (penetrated) by white-lips. For some comparisons there is a category termed "seeds rejected by white-lips". These are seeds that a captive white-lip attempted to but could not open (this attempt often left the endocarps scratched by teeth; see below). There is also a category described as "seeds left by white-lips." These seeds were left on the soil surface of latrines by foraging white-lips along with cracked seeds. I assume that these were available to and rejected by white-lips. The endocarps of some of these seeds were scratched in the manner described for the captive white-lip.

To describe the characteristics and verify the condition of seeds that appeared intact, I carefully cut the distal endocarp tip, and measured the thickest, thinnest and a mid-sized area of the exposed edges to the nearest 0.1 mm, using calipers. These measurements were averaged to obtain a single measurement per seed. The number of endosperms per seed also was noted. The remainder of the seed was dissected and searched for larvae. Endosperms were categorized as 1) alive and whole, 2) containing larvae, or 3) containing adult bruchid beetles or their exit holes. Not all measurements were taken on all seeds; sample sizes therefore vary for each trait measured. Sample sizes are given in the results.

Seeds cracked open by white-lipped peccaries were collected from tapir latrines within a day of consumption. They were examined and measured in the manner described above, together with a sample of the seeds left uneaten. Only seed tips or fragments including a tip were counted, ensuring that seeds were counted only once. In all cases the endosperm had been completely consumed. Rodent-attacked and rejected (apparently available but not chosen) seeds were collected simultaneously from feces soon after the time of consumption, and examined as above, as were larvae-attacked seeds.

The combined samples described above, together with additional seeds collected opportunistically from the forest floor, were used to describe the number of endosperms per seed for the entire seed population.

Captive Trials

To examine seed choice by white-lips in more detail, an adult wild-caught white-lip was caged and offered intact and larvae-infested *Maximiliana* seeds collected opportunistically from tapir feces and from the forest floor. The animal was maintained on a diet of fruits and seeds collected from the forest, usually from *Maximiliana*, because it refused all unfamiliar foods. The level of larvae infestation of the seeds fed to the white-lip was determined by opening and checking 30 to 35 seeds from each source. I then haphazardly selected from 5 to 70 seeds from each source and placed them on a tray in the cage. The seeds were checked hourly and the previous sample's opened and uneaten seeds were removed and fresh ones introduced. The thickness of crushed and uncrushed endocarp tips was measured as described above.

White-lip and Rodent Foraging at Tapir Latrines

All tapir latrines were visited in October and November 1991, and February, March, April, July, September and November 1992. During these visits I noted the presence of: 1) white-lip rooting in the soil; 2) seeds cracked by white-lips; 3) rodent-dug holes at tapir feces, and 4) rodent-gnawed seeds. Seeds cracked by white-lips and gnawed by rodents were collected and treated as described above.

Statistical Analysis

I compared endocarp thickness among seed populations attacked and left uneaten by different predators using one-factor ANOVAs. I used Fisher's Protected Least Signifcant Difference t-test (PLSD) or Scheffe's F-test when comparing individual data sets (Post-Hoc) identified by multi-category ANOVAs as showing significant differences (Abacus Concepts Superanova 1992). Contingency tables (X^2) were used to examine proportional differences in seed thickness and endosperm classes among seed populations used by different predators (Abacus Concepts Statview 1992). Occasionally two and three endosperm seeds were lumped together as multi-endosperm seeds, due to the small number of three endosperm seeds in some categories.

Results

Endocarp Thickness and Endosperm Number: Entire Population

I examined a total of 1814 seeds and ascertained the number of endosperms for 1455 of them (Fig. 5-1 and Table 5-1). Table 5-1 describes the date, origin and number of seeds collected. Joint measurements of endocarp thickness and endosperm number were obtained for 705 seeds from tapir latrines, including intact and vertebrate-attacked seeds. Endocarp thickness only was measured for the 329 seeds obtained from all latrines and from the trial with a captive white-lip.

The results with respect to the different predictions are as follows:

Prediction 1: The hard woody endocarp ranged in thickness from 1.5 to 6.5 mm for the entire seed population (n=1034). The proportion of seeds with one, two and three endosperms departed significantly from an even distribution of 1/3 each (df=4, X^2=2910, P=.0001). Most seeds (67 %) contained only one endosperm; however, 29 % and 4 % had two and three endosperms, respectively (Fig. 5-1).

Prediction 2: Endosperm number per seed did not appear to influence fruit selection by tapirs. The proportion of one, two and three endosperm seeds defecated did not differ significantly from that found in seeds below parent trees (df=2, X^2=4.61, P=.0998) (Fig 5-1). Thus, seed populations at tapir latrines were representative of those under parent trees.

Prediction 3: There were significant differences among the thicknesses of endocarps enclosing one, two and three endosperms (Fig. 5-2, df=2, F=110.42, P=.0001). Single-endosperm seeds (n=493) were significantly thicker than two endosperm (n=184, Scheffe's F=90.81, P<.01) or three endosperm seeds (n=28, Scheffe's F=30.78, P<.01). The thickness of two and three endosperm endocarps was similar (Scheffe's F=1.58, P>.05). Single-endosperm seeds ranged in thickness from 2 to 6 mm, but most were greater than 4 mm thick (Fig. 5-3). In contrast, most multi-endosperm seeds were less than 4 mm thick (Fig. 5-3). The proportion of one, two and three endosperm seeds in each thickness category departed significantly from an even distribution (df=8, X^2=179.82, P=.0001) (Fig 5-3).

Selection for Endosperm Number: Evidence from the Field

Prediction 4: Seeds attacked by beetle larvae, rodents and white-lips included similar distributions of one, two and three endosperm seeds, and these distributions were similar to those in live seeds at tapir feces and beneath parent trees immediately after fruit fall (Fig. 5-4; df=8, X^2=3.72, P=.8811). Therefore larvae, rodents and white-lips all fed on the same pool of seeds, and appeared to use the different endosperm classes in proportion to their occurrence in the seed bank.

Prediction 5: Complete endosperm mortality of attacked (penetrated) seeds, however, varied in relation to predator species. Based on data from latrines, beneath parent trees, and the forest floor (n=77 seeds), 29 % of the multi-endosperm seeds attacked by beetles survived with at least one endosperm intact, but all single-endosperm seeds were killed (Table 5-2). This result departed significantly from the expected proportions (df=2, X^2=51.56, P=.0001). Larvae would thus appear to exert selective pressure in favor of multi-endosperm seeds.

Rodents also killed all single-endosperm seeds they attacked at latrines (n=50), but occasionally (8 %) one endosperm survived in the multi-endosperm seeds (Table 5-2). This result also departed significantly from expected proportions (df=1, X^2=10.64, P=.0011). Rodents would thus also appear to push selection in the direction of multiple-endosperm seeds.

All endosperms in seeds penetrated by white-lips at latrines, on the other hand, were killed regardless of endosperm number (n=83) (Table 5-2). Because white-lips crush the entire nut, I could not always clearly identify the number of endosperms per seed. These seeds were excluded from the analysis, probably resulting in an underestimate of the number of multi-endosperm seeds killed by white-lips, since multi-endosperm seeds are thinner and more likely to be shattered.

Selection for Endocarp Thickness: Evidence from Captive Trials and the Field

Prediction 6 and 7: I presented a total of 204 Maximiliana seeds during 16 feeding trials to the captive white-lip. It ate 120 and rejected 84. For 15 trials I recorded the percentage of offered seeds infested with beetle larvae, but I did not record the proportion of infested and intact seeds eaten. However, the animal did eat both larvae-infested and uninfested seeds, because the mean percent infestation rate for seeds was 46.3 % (n=15 trials) and the white-lip ate a mean of 60.7 % of introduced seeds. Endocarps rejected (by spitting) by the caged animal were significantly thicker then those that were opened and eaten. It generally crushed only endocarps less than 4 mm thick (F=8.06, P=.0001, Figs. 5-5, 5-6 and 5-7).

A similar pattern was evident in seeds consumed and rejected by wild white-lips, suggesting that the main trait influencing seed consumption by white-lips was the thickness of endocarps. Intact endocarps at the Forest Lake latrine left by a foraging herd were significantly thicker than attacked endocarps (Fig. 5-5 and Table 5-3). Table 5-3 presents the statistical comparisons between white-lip, rodent, and larvae attacked seeds, and seeds left at their sources. The thickness of endocarps penetrated at Bactris Swamp latrines were not significntly different from those eaten during the experiment, but those opened at Forest Lake were significantly thicker. However, the seeds rejected during the captive trial had similar dimensions to those remaining at Forest Lake, Savanna Lake and Bactris Swamp latrines. The endocarps which remained at Forest Lake did not differ in thickness from those left at Savanna Lake or Bactris Swamp latrines, but were significantly thicker then those left at the New Buritizal latrine.

Larvae-infested seeds had significantly thinner endocarps than the live, uninfested seeds remaining at the Forest lake latrine, but they did not differ from the live seeds at Savanna Lake, New Buritizal or Bactris Lake latrines. Larvae-infested seeds had significantly thicker endocarps than those cracked by the experimental white-lip, and by white-lips at Bactris Swamp latrine, but significantly thinner than those endocarps cracked at Forest Lake.

A comparison of data from specific latrines shows that rodent-attacked seeds did not differ in thickness from intact seeds remaining at Forest, Savanna and Bactris latrines, but they were significantly thicker than those found at the New Buritizal latrine (Table 5-3, Fig. 5-5). Rodents attacked all available seeds regardless of endocarp thickness, and actually appeared to eat thick seeds at a higher proportion than their occurrence in the population, although this trend was not significant.

Selection Differences Among Seed Consumers

Based on the combined data from 1992 for latrines, from 1991 for trees, and from both years for forest floor, there were significant differences in the thickness of endocarps penetrated by white-lips, beetle larvae, rodents and the remaining live seeds (Fig. 5-6, df=3, F=13.89, P=.0001). Seeds cracked by white-lips were significantly thinner than those penetrated by larvae (Fishers PLSD=.13, P<.01). They were also thinner than those attacked by rodents (Fishers PLSD=.13, P=<.05), and live seeds (Fishers PLSD=.13, P<.05). White-lips thus appear to use thin seeds more frequently than other predators, and than their occurrence in the wild (Fig. 5-3 versus 5-7).

I failed to reject the prediction that rodents feed on seeds of all thicknesses. The seeds they ate were significantly thicker than those still alive at latrines (Fig. 5-6, Table 5-3). They were also significantly thicker than those penetrated by larvae (Fig. 5-6, Fishers PLSD=.13, P<.01), and those remaining alive (Fishers PLSD=.13, P<.05). I also failed to reject the prediction that beetle larvae penetrate the entire range of endocarp thicknesses found in seed populations; overall, larvae-infested and non-infested seeds from the same feces were of similar dimensions (Fig. 5-6, Fishers PLSD=.13, P>.05).

White-lip and Rodent Foraging at Tapir Latrines

Not all latrines were visited at the same time by all seed predators (Table 5-4). The Forest Lake latrine was hit repeatedly by peccaries, more frequently than the other latrines (Table 5-4). White-lips first visited the site in November 1991, when tapirs were still defecating *Maximiliana* seeds. However, white-lip-cracked *Maximiliana* seeds were not found at Forest Lake until February 1992, indicating that seeds were not eaten immediately after defecation. Two months passed before cracked seeds were found at another latrine (Bactris Swamp), and it was not until September that white-lip-cracked seeds where found at the New Buritizal latrine (Table 5-4). However, by November 1992, white-lips had visited and consumed seeds at all latrines. Thus, the white-lip - seed trait relationship described for Forest Lake (after at least four white-lip foraging bouts), is eventually repeated at the other latrines. As time passes, the endocarps also deteriorate and peccaries are able to open thicker and thicker seeds (Fragoso pers. obs).

Rodents began visiting all latrines in February 1992 (Table 5-4). This was also when the first rodent-gnawed seeds where found, suggesting that rodents also do not consume seeds immediately after defecation by tapirs. The Savanna Lake latrine, followed by the Bactris Swamp latrine, had more seeds consumed by rodents (based on finding gnawed seeds) from February to April 1992, than all other latrines.

Production of Endosperm Classes by Different Trees and Tree Clumps

Based only on seeds collected beneath parent trees, individual trees produced a mean of 69.5% single, 27.5% double and 3% triple endosperm seeds (Fig. 5-8). Two trees produced only single-endosperm seeds, but most produced variable proportions of single and multi-endosperm seeds (Fig. 5-8). The proportions of each seed type varied significantly among trees (Fig 5-8; df=19, F=2.96, P=.0001), but not amongst the five conspecific clumps (Fig 5-9; df=4, F=2.33, P=.0574).

Discussion

In this study seed predators chose seeds differentially, and determined the average value of key characteristics of surviving seeds as well as the spatial distribution of variation in these characteristics. Ignoring for the moment selection from factors other than predation, such as germination success (review by Bazzaz and Ackerly 1992, Foster 1986, Harper et al. 1970, but see Silverton 1989), we can predict the expected value of seed traits in a population under selection by individual seed predators species. While all predators attacked all palm seeds regardless of physical differences, seeds that lost all endosperms differed in their physical characteristics from those in which at least one endosperm survived. White-lips killed all endosperms in two and three endosperm seeds, because they could easily crush the thin endocarps. A seed population responding only to the selective pressure exerted by white-lips should be dominated by thick-endocarp, single-endosperm seeds. On the other hand, the direction of selection exerted by beetle larvae and rodents is towards multi-endosperm seeds, regardless of endocarp thickness, because they kill all single-endosperm seeds they penetrate. Therefore, if seed traits were a response to predation by beetle larvae or rodents, the population should be dominated by two or three endosperm seeds. The Maraca Island Maximiliana seed population as a whole was dominated by single-endosperm seeds, suggesting that past selective pressures favored the development of single over multi-endosperm seeds. Since single-seeded seeds are killed by beetles and rodents, but often survive white-lip attacks (if they have thick endocarps), this observation indicates that white-lips (and other recently extinct seed predators that crushed endocarps) have been the dominant force influencing seed traits.

The proportions of single versus multi-endosperm seeds should change to reflect changing selective pressures. For example, if white-lips become extinct and beetle larvae or rodents dominate the seed-eating guild, there should be a concomitant change in the proportion of one, two and three endosperm seeds in seed banks. Similar studies to this one have been conducted in Costa Rica and Panama with Scheelea rostrata, a palm similar to Maximiliana, in areas lacking white-lips but where rodents and beetle larvae are common (e.g., Bradford and Smith 1977, Janzen 1971, Wright 1983, 1990). Bradford and Smith (1977) found that endosperm survivorship within attacked seeds of S. rostrata in Costa Rica and Panama increased as the number of endosperms per seed increased. The mean distribution of single- and multi-endosperm seeds per S. rostrata tree on Barro Colorado Island (BCI), Panama was 94% single-endosperm, 5% two and 1% three (n=3). In Costa Rica, the corresponding figures were 73%, 24% and 5% (n=5). In my study the figures are 69.5%, 27.5%, and 3% respectively (n=20). The figures suggest that trees in Panama and Costa Rica are or were under equal or greater pressure to produce single-endosperm seeds relative to Maraca Maximiliana populations.

However, one would not expect extant adult palm tree seed production to reflect recent changes in the selective pressure exerted by a new seed predator guild (c.f. Janzen and Martin 1982). The current generation of reproductive trees would reflect the selective pressures of past years, when white-lips still occurred in the Central American study sites. White-lips have been absent from BCI since the early 1930's (Eisenberg, pers. comm.) and from La Selva since at least 1970 (Clark 1994). No continuous data are available on the longevity and age at first reproduction for wild palm trees, but most data on trees aged by leaf scars indicate they mature late and are long-lived. Coconut palms, for example, do not flower until they are 10-15 years old (Conner 1966). One study of another neotropical arborescent palm (Euterpe globosa in Puerto Rico) followed seedlings for 210 days, calculated age until trunk development based on growth rate, and then used leaf scars to estimate the age of trees with trunks (Van Valen 1975). Individuals reached reproductive maturity at about 50-60 years of age (9-12 m in height), reached the forest canopy at 104 to 130 years of age (14-16 m), and were senescent at 156 or more years (18-20 m). Given the long life-span and long time to reproductive maturity of palm trees, few palm trees in the population would have started producing fruit since the disappearance of white-lips from these two sites.

One would predict, however, that the seeds surviving in the Costa Rican seed bank after predation by rodents or beetles would show a larger proportion of multi-endosperm seeds than those on Maraca, where white-lips easily destroy them. Bradford and Smith (1977; Table 5-3) report that 57% of the surviving seeds had single-endosperms and 43% had two or three endosperms, compared to 71% and 29%, respectively, on Maraca. Bradford and Smith (1977) concluded that there is selective pressure for trees to produce multi-endosperm seeds, because they did not consider the recent presence of white-lips at their study sites. I conclude that where the species composition of tropical Neotropical seed-predator guilds remain intact, as at Maraca, selection favors thick-endocarp, single-endosperm seeds. Due to a difference in our awareness of seed consumers, we interpret similar data in very different ways.

The great variance among trees but not among clumps of trees in the number of endosperms produced per seed suggests that the greatest selective pressure occurs at the within clump rather than the larger among clump scale. This suggests that all the seed predator types considered here appear to reach and influence all clumps. Some trees within clumps, on the other hand, escape predation by white-lips, perhaps by dropping fruit asynchronously at the tails of the fruit-drop period and away from the peak in fruit-fall, when a white-lip herd is less likely to visit the clump (Fragoso, unpubl. data). Most of these seeds may be dispersed by tapirs or rodents before a herd visits or re-visits the clump where such a tree is located. However, these trees would not escape the attention of beetle larvae or rodents, and both predators may occur continuously within clumps and have activity ranges with a scale smaller than or equal to that of the clump (Smythe 1978, for rodents; Wright 1990, 1983, for larvae). These seed predators consume seeds within the clump throughout the entire fruit-drop period, albeit at a much slower rate relative to a herd of white-lips. A visit by tens to hundreds of white-lips to specific clumps, while less frequent and more irregular, is more catastrophic for seeds already on the ground. They can destroy hundreds to thousands of seeds in one foraging bout. The strategy of a plant responding to the selective pressures exerted by white-lips, other than by increasing endocarp thickness, should therefore be to either drop seeds over a longer period than its neighbors, or to drop seeds at the tails of the fruit-fall distribution. These strategies would decrease the risk of white-lip attack, because large herds of white-lips probably respond to the peak in fruit-fall within clumps, when the food supply is sufficient to feed an entire herd (Kiltie and Terborgh 1983).

However, these trees would still have to contend with beetle larvae and rodents. The adaptive response in this case would be to increase the number of endosperms per seed, since some of the seeds in these nuts will survive the attacks of these predators. Perhaps the best strategy when the timing of predator-species attacks is highly unpredictable, is a mixed one, where individual trees produce both single and multi-endosperm seeds. This scenario would explain why the variation within Maximiliana clumps in the number of endosperms produced per seed per tree is greater than that between clumps: all clumps are attacked by all seed predators, but the rate, level of impact, and timing of each species visit differs, selecting for greater variance within clumps.

The ecology of each species of seed predator influences the selective pressure it exerts on plants. White-lips move through forests as units of tens to hundreds of individuals, they have overlapping home ranges, each of which can be hundreds of square kilometers (Chapter 6). One herd's home range would encompass many clumps of Maximiliana. The large numbers of individuals per herd and the many clumps of Maximiliana per home range would result in white-lips spending little time within a clump before moving on (from five minutes to four hours; Fragoso unpubl. data). In contrast, agoutis are territorial and tend to locate their territories in and around rich food sources (Smythe 1978). This is probably true of many other rodents as well (Eisenberg 1981, Emmons 1984). An agouti's home range may be smaller than a single Maximiliana clump. These animals visit trees within their clump on a daily if not hourly basis in search of fruits and seeds (Forget 1990, 1992a), each time scatterhoarding or eating a few seeds. During peak fruit-fall within a clump these animals would be overwhelmed by fruit availability, because each tree drops hundreds to thousands of fruits. Thus many seeds would escape predation by territorial as well as smaller non-territorial rodents, which cannot reproduce quickly enough to take advantage of the crop, and cannot aggregate to any great degree because of their solitary-territorial social structure (Janzen 1974, Smythe 1978).

On the other hand, although beetle larvae can take advantage of large seed crops due to their high reproductive rates and population densities (Janzen, 1971, Wilson and Janzen 1972, Wright 1990, 1983), their impact on seed traits is probably reduced by predation by white-lips. My experimental data with a caged white-lip suggest that beetle larvae are readily eaten by white-lips. White-lips may in fact prefer infested seeds; they forage on seeds once they have aged on the ground, perhaps because a) larvae have higher nutritional value, or b) old or infested seeds are easier to crack. For a larva to escape consumption by white-lips it would have to inhabit a seed unbreakable by white-lips (i.e. single-endosperm seeds with thick endocarps). Therefore, even if multi-endosperm seeds are more likely to survive a beetle attack, these are the seeds most likely to be eaten by white-lips, and a white-lip will eat larvae within seeds. This reasoning suggests that most larvae that survive to adulthood do so in single-endosperm seeds with thick endocarps. The interaction between these two species of seed predators can alter the selective outcome of predation. White-lips provide additive selective pressure for thick, single-endosperm seeds through their consumption of larvae, not only by effectively neutralizing the effect of larvae, but also by exerting selective pressure on beetles to oviposit on the thick endocarp, single-endosperm seeds that are most likely to escape consumption by white-lips. White-lips and beetles then both exert selection in the same direction.

My hypotheses suggest that large-seeded trees should exhibit a mixed evolutionary strategy. Most trees should respond to white-lips, but some should also respond to beetle larvae or rodents. The mixed strategy would be stable, because complete synchrony could result in high mortality by peccaries, while complete asynchrony could result in high mortality by rodents. A population composed solely of single-endosperm seeds could also be destroyed by rodents and larvae, while one containing only multiple endosperm seeds would be destroyed by peccaries. This mixed strategy is even more critical when we consider that white-lip, rodent and beetle populations may fluctuate asynchronously in size over time (Fragoso and Emmons in prep, Leigh et al. 1982, Smythe et al. 1982, Wright 1990, Young 1994). Given the variation in seed traits already present in the population, the response to a change in selection direction could occur quickly.

Table 5-1: Date of collection, site of origin and treatment category of all Maximiliana seeds examined in this study. Seeds from parent trees were chosen randomly, seeds from the forest floor and tapir latrines were chosen opportunistically, as were seeds attacked and rejected by white-lips. See methods for more details.

Date	Origin or Group	Category	Data Collected	No. Seeds Measured
1991 Oct.-Dec.	Forest Lake[1]	Whole	○	30
	Forest Lake	Whole	○◆	70
	Forest Floor	Whole	◆□	50
	All Latrines	All Seeds	◆□	330
	Parent Trees	All Seeds	◆□	170
	Parent Trees	Whole	○◆□	30
1992 Mar. 3	New Buritizal	White-lip Left	◆□	80
	Forest Floor	Whole	◆□	20
1992 Apr. 9-12	1-Forest Lake	White-lip Eaten	▲	6
Apr. 9-12	1-Forest Lake	White-lip Left	▲	25
Apr. 9-12	1-Savanna Lake[1]	Whole	▲	42
Apr. 9-12	1-Bactris Swamp[1]	Whole	▲	20
Apr. 9-12	1-Trail 4[1]	Whole	▲	10
Apr. 9-12	1-Trail A[1]	Whole	▲	5
Apr. 9-12	1-New Buritizal[1]	Whole	▲	75
Apr. 9-12	1-White-Lip Experiment	White-lip Eaten	▲	48
Apr. 9-12	1-White-lip Experiment	White-lip Rejected	▲	11
Mar. 26-Apr. 9	2-Forest Lake	White-lip Eaten	◆□▲	65
Mar. 26-Apr. 9	2-Forest Lake	White-lip Eaten	▲	87
Mar. 26-Apr. 9	2-All Latrines	Live	◆□▲	189
Mar. 26-Apr. 9	2-All Latrines	Larvae Killed	◆□▲	197
Jan. 1 & Mar. 10	2-All Latrines	Rodent Eaten	◆□▲	180
Oct. 26	3-Bactris Swamp	White-lip Eaten	◆□▲	18
Oct. 26	3-Bactris Swamp	White-lip Left	◆□▲	14
Nov. 5	3-New Buritizal	White-lip Left	◆□▲	42
TOTAL SEEDS				**1814**

○ =Weight, ◆ =No. of Endosperms, □ =No. of Endosperms Alive, ▲ = Endocarp Thickness, and [1] indicates a latrine site.

Table 5-2: The percentage of one- and two- or three-endosperm *Maximiliana* seeds attacked by beetle larvae, rodents and white-lipped peccaries, where at least one endosperm survived per seed.

Endosperms Per Seed	**Larvae %**	**Rodent %**	**White-lip %**
1	0	0	0
2 or 3	29	8	0

Table 5-3: A comparison of the endocarp thickness of *Maximiliana* groups identified by an ANOVA as statistically significant. Data sets are paired and statistically compared using Fisher's PLSD. An * indicates a significant difference at P<.05, while > or < equals direction of greater thickness, = indicates no significant difference with the column label read first. WLP equals white-lipped peccaries.

Seed Group		1	2	3	4	5	6	7	8	9	10
WLP Eaten in Cage	**1**										
WLP Eaten at Forest Lake	**2**	* >									
WLP Rejected in Cage	**3**	* >	* >								
WLP Left at Forest Lake	**4**	* >	* >	=							
Savanna Lake Latrine **X**	**5**	* >	* >	=	=						
New Buritizal Latrine	**6**	* >	=	* <	* <	* <					
Bactris Swamp Latrine **X**	**7**	* >	* >	=	=	=	=				
WLP Eaten at Bactris Swamp	**8**	=	* <	* <	* <	* <	* <	* <			
Rodent Attacked	**9**	* >	* >	* <	=	=	* >		* >		
Larvae Attacked	**10**	* >	=	* <	* <	* <	=	=	* >	* <	
Live	**11**	* >	* >	* <	* <	=	=	=	* >	* <	=

X = Rodents foraged heavily in these latrines. Seeds used in the analysis identified by notation: "1-site" for latrines and white-lips, "2-all latrines"-for larvae and rodent killed; from Table 1.

Table 5-4: Seed consumption at tapir latrines: Latrine sites and dates at which white-lips were recorded rooting for Maximiliana seeds, and/or white-lip cracked or rodent gnawed seeds were found.

Date			**Latrine**		
	Forest Lake	Savanna Lake	Bactris Swamp	Trail 4	New Buritizal
1991- October				▼	
November	▼				
1992-February	▼✚O	O	O	▼O	▼O
March	▼✚O	O	O	▼	O
April	▼✚O	O	▼✚O	▼	O
July				▼	▼
September				▼	▼✚
November	▼✚	▼✚	▼✚	▼✚	▼✚

▼ = White-lip rooting, ✚ = Seeds cracked by white-lips, O = Rodent burrowing and gnawed seeds.

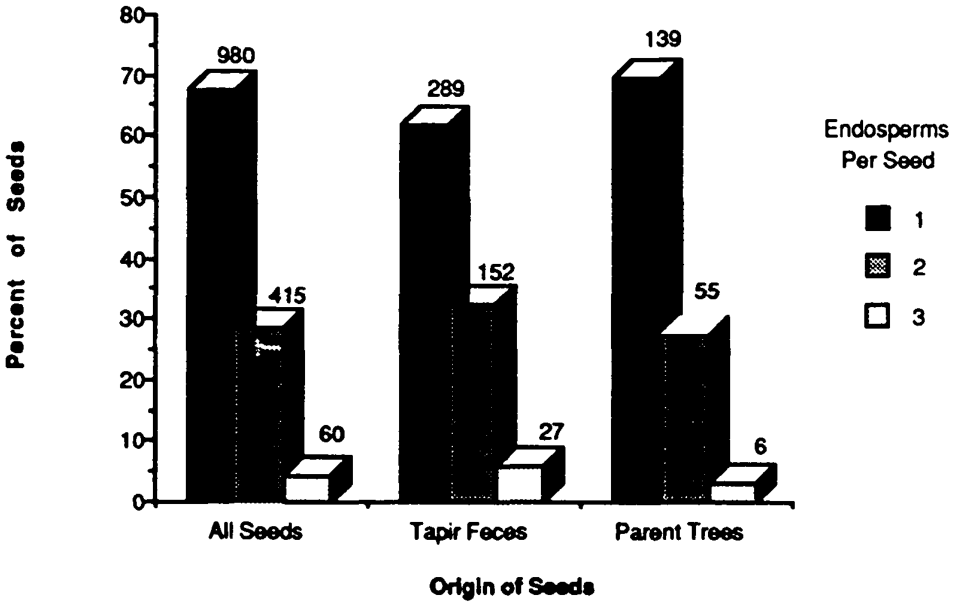

Fig. 5-1: The number of endosperms per *Maximiliana* seed in populations beneath parent trees (n=200), those defecated by tapirs (n=468) and for all seeds collected (n=1455). Numbers above columns are number of seeds per category.

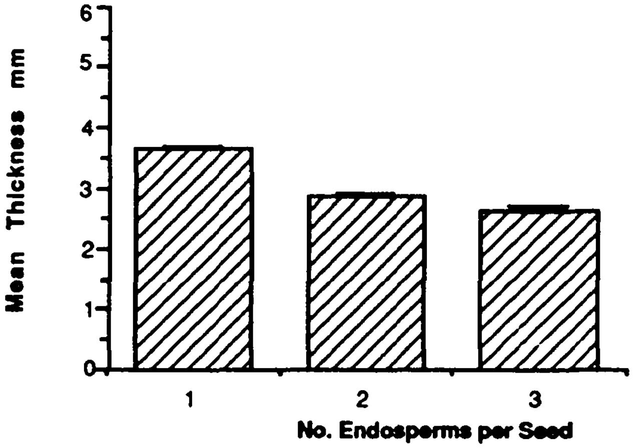

Fig. 5-2: The thickness of Maximiliana endocarps in relation to the number of endosperms per seed (SE bars shown). Sample sizes are 493 seeds, 184 seeds and 28 seeds for one-, two- and three-endosperms seeds, respectively.

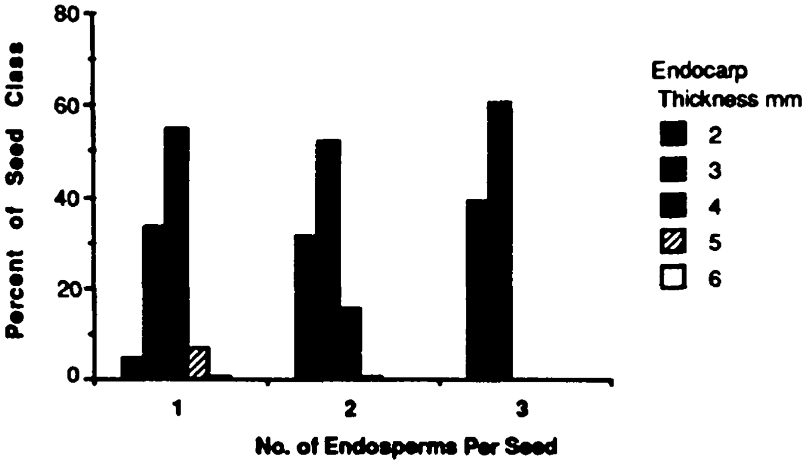

Fig. 5-3: The proportion of one, two and three endosperm Maximiliana seeds in each of six 1 mm increment endocarp thickness categories.

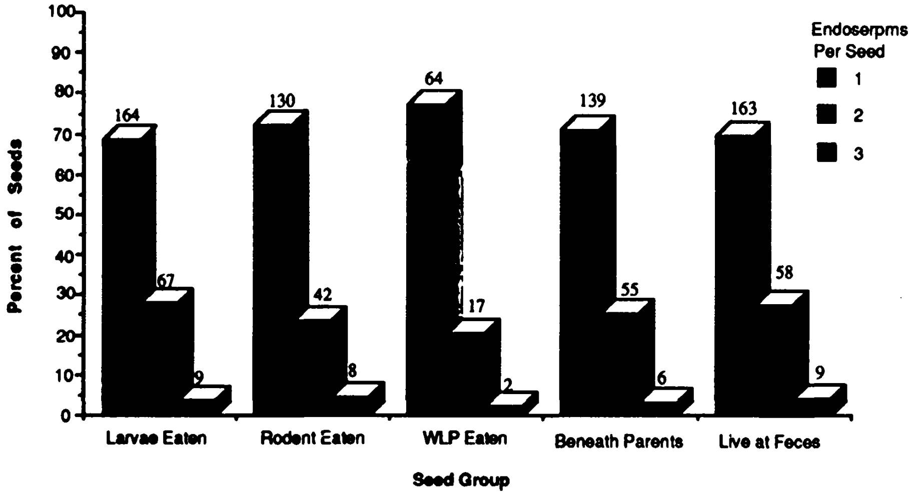

Fig. 5-4: The distribution of one, two and three endosperm Maximiliana seeds attacked by beetle larvae, rodents, and white-lips, and live at feces.

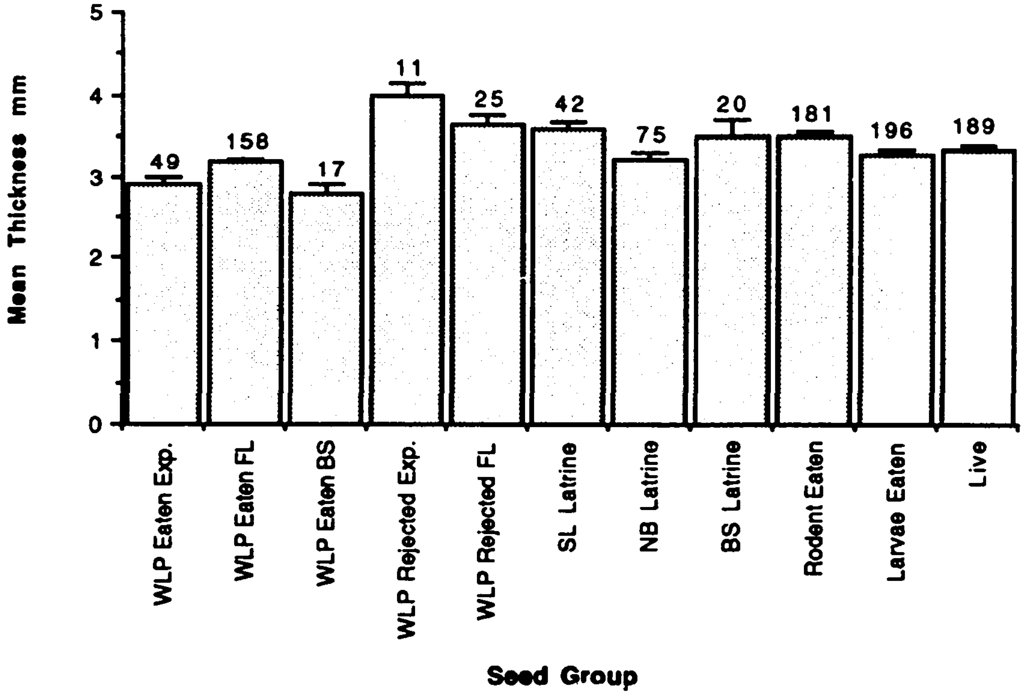

Fig. 5-5: The number (N above SE bars) and mean thickness of *Maximiliana* endocarps of seeds: 1) attacked by a white-lip (WLP) during the experiment, 2) attacked by a white-lip herd at the Forest Lake latrine (FL), 3) attacked by a white-lip herd at Bactris Swamp latrine (BS), 4) rejected by the white-lip during the experiment, 5) left unopened at the Forest Lake latrine by the white-lip herd that ate the group 2 seeds, 6) whole from Savanna Lake latrine (SL), a site where seeds were eaten only by rodents at the time seeds were collected, 7) whole at the New Buritizal latrine (NB), 8) whole at Bactris Swamp latrine, (9) attacked by rodents, 10) killed by beetle larvae, and 11) live at latrines.

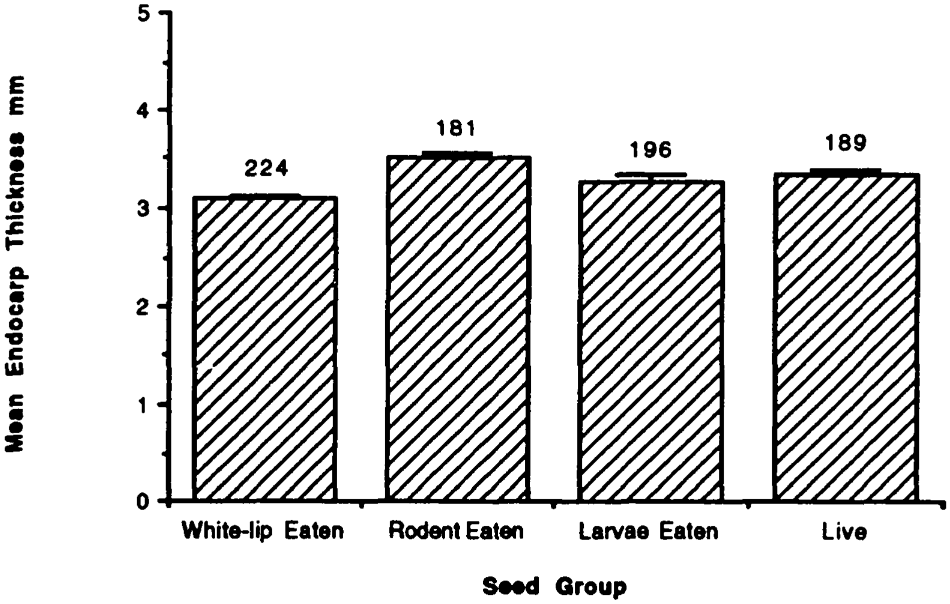

Fig. 5-6: A comparison of the mean thickness of Maximiliana endocarps penetrated by white-lips (WLP), beetle larvae, rodents, and those found alive in the field (SE and sample size above bars).

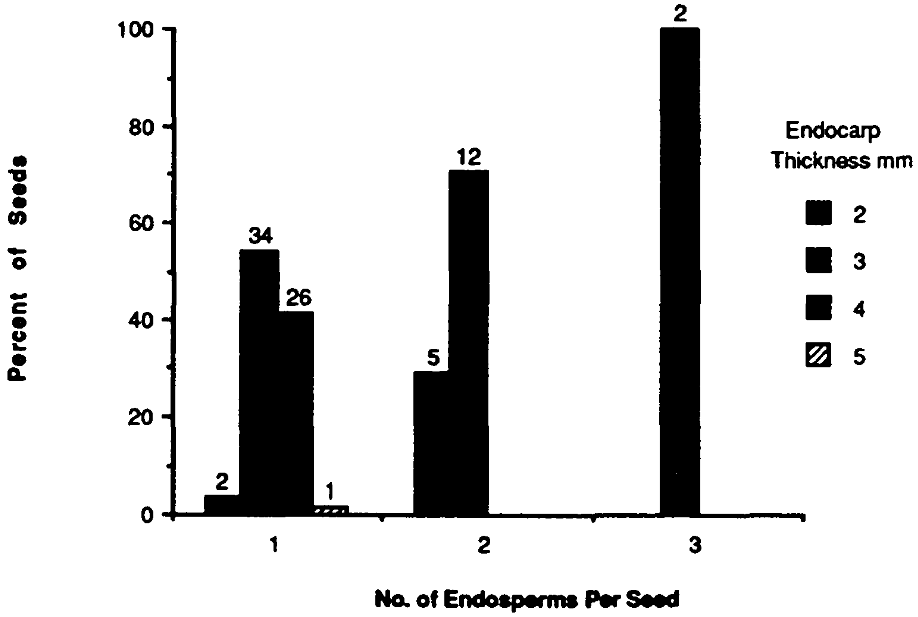

Fig. 5-7: The thickness of Maximiliana endocarps cracked open within each endosperm category by white-lipped peccaries. The number of seeds per category is listed above columns.

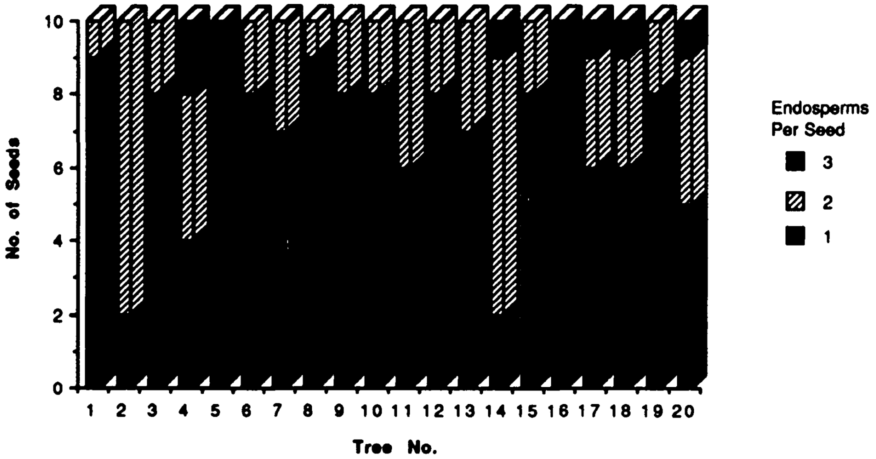

Fig. 5-8: The number of seeds with one, two and three endosperms below 20 Maximiliana trees. Seeds were collected randomly from beneath 20 randomly chosen trees from October to November 1991, the end of the fruit-drop season.

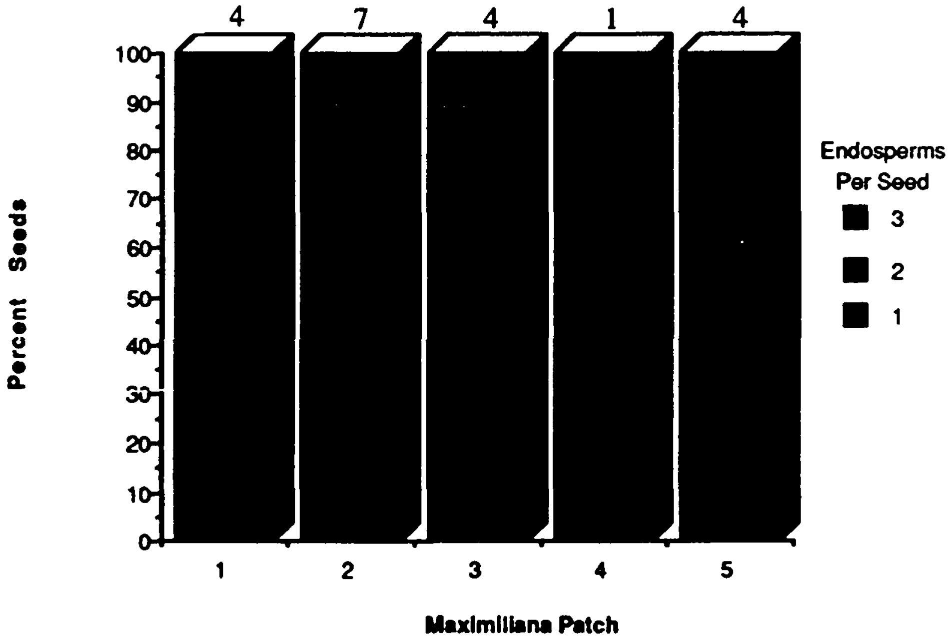

Fig. 5-9: The percentage of seeds with 1-, 2- and 3-endosperms at five Maximiliana clumps. The number of trees sampled per clump is listed above columns.

CHAPTER 6
THE NATURAL HISTORY OF COLLARED AND WHITE-LIPPED PECCARIES IN AN AMAZONIAN RAIN FOREST

Introduction

The white-lipped peccary (*Tayassu pecari*) remains one of the least known large mammals of the New World (Sowls 1984, Eisenberg 1989). What we know of its biology derives mainly from two pioneering studies. The first study was Kiltie's examination of niche separation between white-lipped and collared peccaries (*Tayassu tajacu*) based on the jaw morphology and mechanics of museum specimens; and his description of white-lip behavioral ecology derived from signs left by passing herds and from number of visits to a single site (Kiltie 1980, 1981a, 1981b, 1981c, 1982, Kiltie and Terborgh 1983). The second study is Bodmer's (1889a and b, 1990b, 1991a and b, 1992, 1993a, in press) analysis of the stomach contents of hunter-killed animals and his estimation of population densities using these kills and counts along transects. Additionally, Sowls (1984) provided an anecdotal description of white-lip behavior from brief observations of a herd feeding at bait station in the Atlantic Forest of Brazil. Mayer and Wetzel (1987) and March (1993) summarized what little is known about white-lips. White-lips, however, are key factors in tropical forest dynamics, and also supply most of the meat consumed by many subsistence peoples (Bodmer et al. in press, Vickers 1991). Because of this biological and economic importance, researchers have tried to infer as much information as possible from the limited data available. Some inferences have been accepted as fact, as in the case of the widely held belief that peccaries carry out long-distance migrations (e.g., respectively: Bodmer 1990b citing Terborgh pers. comm., Vickers 1991 incorrectly citing Kiltie 1980 and Kiltie and Terborgh 1983).

White-lips are one of three species of peccaries (Tayassuidae) inhabiting the Neotropics (Eisenberg 1989). They are among the largest ungulates in tropical South and Central America (25-40 kg, Robinson and Redford 1986), smaller than tapirs (Tapirus spp.), but about the same size as Mazama deer. They range throughout the wet and dry tropical forest regions from southern Mexico to northern Argentina (Eisenberg 1989, Leopold 1959, Mayer and Wetzel 1987, Redford and Eisenberg 1992, Sowls 1984). Although Sowls (1984) reported that white-lips required old-growth forest for their survival, they also inhabit savanna-woodland regions of South America (Eisenberg 1989, Mayer and Wetzel 1987, Olmos 1993), and savanna-wetland Pantanal of Brazil (Fragoso, unpublished data, Schaller 1983).

White-lips are one of only two species of tropical forest ungulates that form large herds containing at least 200 individuals (Sowls 1984). There are anecdotal accounts of herds with 1000-2000 individuals (Mayer and Wetzel 1987). The other species that exhibits large herding behavior is the bearded pig (Sus barbatus) of Southeast Asia (Caldecott 1988, 1992, Caldecott et al. 1993). Several researchers have suggested that white-lips are migratory (e.g., Bodmer 1989, 1990b, Sowls 1984), while others have suggested that they are nomadic (e.g., Kiltie 1980, Kiltie and Terborgh 1983). To date there is no evidence to support or disprove either migration or nomadism.

I studied a wild population of white-lipped peccaries in Amazonian Brazil, and examined the ranging behavior of herds. I test the hypothesis that white-lips migrate by comparing dry and wet season home ranges. If white-lip herds do migrate the two ranges should be spatially distinct (c.f Baker 1978). I also test the hypothesis of irregularity in movements (nomadism) by looking for a pattern of consistently repeated visits to sites within a distinct home range. If white-lips repeatedly return to distinct spots they are not nomadic. Managing white-lip populations has become an objective in many countries due to the commercial importance of white-lip skins and their use as food by subsistence peoples (e.g., Bodmer et al. 1993). The only age structure and sex ratio data available for white-lips originate from hunter-killed animals (e.g., Bodmer et al. 1993). This type of information may not be representative of free-ranging populations, and use of it alone for developing management plans can lead to the overhunting of certain age classes and sexes (Ralls et al. 1980). Therefore, I also examined the age structure and sex ratios of wild herds and compared this information to similar data collected from hunter-killed animals. The large size of white-lip herds is unusual for a forest-dwelling ungulate (Kiltie and Terborgh 1983). I discuss how this social organization may have evolved in white-lips and compare it to that of collared peccaries. Because so little is known about the social and other behavior of white-lips in the wild, I also describe the social organization of herds, their susceptibility and response to predation, their between-herd interactions and other aspects of their behavior and ecology.

I compare white-lip-home range and group sizes with those of collared peccaries (Tayassu tajacu) coexisting in the study area. Despite a superficial similarity, the ecology and behavior of white-lips and collareds are very different. For example, collareds form smaller herds, do not move as far as white-lips (Sowls 1984), and, most importantly, in areas where white-lip peccary populations decline, those of collared peccaries remain stable or even increase (Emmons, pers. comm.; Fragoso, pers. obs.). The ecology of the collared peccaries is also poorly known in tropical rain forest (Bodmer 1989, Kiltie 1981a, 1981b, Kiltie and Terborgh 1983, McCoy 1984, Suarez 1993), but has been extensively studied in the southwestern U.S.(review by Sowls 1984, Corn and Warren 1985, Green and Grant 1984) and to some extent in the Llanos of Venezuela (Castellanos 1983, Hernandez 1988, Robinson and Eisenberg 1985). A comparison between the two species may aid in elucidating the ecology of both and the habitat requirements that may be critical to white-lip survival. In particular, I focus on key body size differences, which through their relation to home range size and herd size, lead to a different perception of the landscape by the two species. By differences in "perception" I mean that the same environment that is coarse grained to the white-lip is fine grained to the collared peccary (c.f. Weiss and Murphy 1988). This different perception not only has the potential to reduce competition and cause differences in responses to environmental disturbance between the two species, it also has important implications for how the two species differentially affect the fruiting plants they feed on.

Methods and Study Site

Study Area and Date

Maraca Island Ecological Reserve lies at 3°25'N and 61°40'W, at the northern edge of the Amazon River basin in Roraima State, Brazil (Fig. 2-1). It is formed by the branching of the Uraricoera river, a tributary of the Rio Branco (Amazon drainage). All 110,000 ha of tropical rain forest, wetlands, and isolated savannas forming the reserve are protected by I.B.A.M.A. (the Brazilian Secretariat for Wildlife, Ecological Reserves and Parks) as a site for research and forest protection. The dominant vegetation of the region is primary, tropical evergreen lowland rain forest (Moskovits 1985), contiguous with the great Amazon rain forest (Milliken and Ratter 1989). Maraca supports populations of white-lips, pumas (*Felis concolor*), jaguars (*Panthera onca*) and other animals typical of a Neotropical rain forest area undisturbed by Europeans and their descendants (Fragoso 1989, Moskovits 1985, Milliken and Ratter 1989b). There have been no human settlememts on the island within historical time, and it has never been logged. Approximately eight isolated families lived at different times along the river banks of the eastern tip up until 1977. Illegal hunting does occur on the outskirts of the reserve along navigable areas of the river, although hunters avoid the area around the research station. The study site is described in detail in Chapter 2. The study of collared and white-lipped peccaries extended from December 1990 to January 1993. The study area included only the eastern half of the island, about 114 km^{2}, the area used by the two study herds.

Habitats and Plant Communities of Eastern Maraca

The habitats and plant communities described here were those used by white-lips in the study area. The descriptions are based on qualitative assessments of the vegetation and flooding regimes over two years as seen from the ground and airplane (December 1990 to December 1992). To produce a detailed description of plant communities, I combined my own descriptions and locations with those of Milliken and Ratter (1989) from the same area. In the following descriptions, "high" and "low" refer to canopy height.

Mauritia Wetland--The Mauritia Wetland community consisted of seasonally inundated, practically monospecific, stands of *Mauritia flexuosa* palms. *Virola surinamensis*, *Cecropia* sp., *Bactris maraja*, and *Euterpe precatoria* were common beneath the *M. flexuosa* canopy. The shrub layer generally consisted of *Renealmia alpinia* and bromeliads (*Ananas* sp.).

Mauritia Wetland-High Forest--This is the ecotone between the Mauritia Wetland community and the Terra Firme High Forest vegetation (see below).

Low Maximiliana Palm Forest--These were almost mono-dominant stands of low (<5m) *Maximiliana maripa* palms with no overstory of other species.

Low Riverine Shrub--This community was dominated by 2 - 3 m high shrubs, which formed an almost completely closed canopy. This community had a very high density of stems per unit area, and these were occasionally interspersed by high grasses (Poaceae) or interlaced by lianas. This community floods yearly.

Low Riverine Forest--The Riverine Forest was typified by a 15 - 25 m canopy. Characteristic canopy trees include *Ceiba pentandra*, *Enterolobium cyclocarpum*, *Spondias mombin*, *Bactris maraia*, *Triplaris gardneriana*, *Cecropia* sp. and *M. maripa*. The understory is occasionally dominated by patches of *Heliconia* spp.. During exceptionally high water periods (e.g. once every 10 - 50 years; pers. comms. J. Alves and G. de Olivieira) the ground beneath this community is under water.

Mid to High Riverine Forest--Similar to the previous category, but with a more broken canopy.

Savanna (including Ponds and Forest Patches)--The Savanna consists of a number of seasonally inundated grasslands, the largest of which was 8.5 by 1 km in dimension. The ground is covered by dense grasses (Poaceae). Seasonal ponds (Ponds) and tree islands (Forest Patches) utilized by white-lips occurred throughout the savannas. Characteristic trees of the tree island included *Curatella americana*, *Genipa americana*, and *Humiria balsamifera*.

Terra Firme High Forest--Most of the study region was covered by Terra Firme High Forest. This plant community was dominated by 30 - 50 m high trees with occasional palm patches dispersed throughout. It also had a well developed sapling understory. Some characteristic tree species were *Pradosia surinamensis*, *Pouteria venosa*, *Ecclinusa* *guianensis*, *Tabebuia uleana*, *Couratari multiflora*, and *Hymenaea courbaril*.

Terra Firme High Forest with Inaja--Occasionally I noted areas of Terra Firme High Forest dominated by stands of 20 - 30 m tall *M. maripa* palms in and beneath the canopy; this community is described as Terra Firme High Forest with Inaja.

Terra Firme High and Low Canopy Forest--Terra Firme High and Low Canopy Forest is similar to the Terra Firme High Forest but with a more broken canopy and a thicker understory, often dominated by bromeliads.

Shrub Thicket--Two types of thicket were identified, both of which were seasonally inundated by water: the Shrub Wet-Thicket (also known as Vazante) consisted of tall herbs (e.g., *Thalia gardneriana*) and low shrubs such as *Mimosa pigra*, *Senna alata*, *Canna glauca* and grasses such as *Eriochloa punctata*.

Bactris Thicket: The Bactris Thicket consisted almost exclusively of *B. maraja* palms.

During the wet season much of the area covered by Mauritia Wetland, Savanna and Shrub Thicket habitats is inundated by water. Some of the lower lying regions of the Riverine Forest may also flood every year, and all of it floods during exceptionally high water (approximately once every 50 to 75 years; estimated from discussions with J. Alves and G. de Olivieira). The Terra Firme forests remains unflooded during this period, although occasional pools may form on the soil surface.

The above habitat categories were used when animals were located from the air or the ground. To estimate the actual area covered by the habitats within the peccaries' home ranges, I combined them into the more general categories of: Terra Firme Forests, Riverine Habitats, Mauritia Wetlands, Shrub-Thicket and Savanna. I measured their extent on an aerial photograph, and confirmed their extent and location from an airplane. The coverage for each plant community was determined by overlaying a grid of squares, each equivalent to a 310 X 310 m area, over a plant community map drawn from the photograph and summing the number of squares in each plant community. For a square to be counted toward a plant community, that community had to cover more than half the square. This methodology provided a reliable measure of the extent of different vegetation cover in the home ranges of white-lips.

White-lip Captures and Tracking

To determine the presence of white-lips or their sign (tracks, rooting and scent) in the study area, 60 kms of trail were searched every two days (by two teams operating separately) from January 1991 to December 1992. Occasionally days were missed due to unforeseen circumstances. More intensive searches were conducted for sign (tracks or rooted soil) along preferred areas such as Mauritia flexuosa swamps and creek beds. If a herd or fresh sign were encountered, the group was stalked and individuals darted. Individuals were tranquilized with 2.5 cc of Ketamine and 0.5 cc Azaperone delivered by means of a Tele-inject gun. Animals that were not completely tranquilized by the first injection were administered an additional 0.5 cc of Ketamine. I was assisted in the tracking and capturing by a Macuxi Amerindian hunter. For each individual captured, I recorded standard body measurements, sex, age (young, juvenile, or adult), reproductive condition, herd size, time, date, and location. Captured animals were marked with an individually numbered ear tag of a color unique to each herd, and a Telonics radio collar placed around their necks. The animals were monitored until recovered sufficiently (range from 1-3 hours) from tranquilization to walk beyond sight. To determine if captured white-lips rejoined their herds and to monitor herd movements I placed radios on at least two individuals per herd and visually located the individuals a few days after their capture. Activity monitors on the radio-transmitters allowed me to determine when the animals were active or inactive.

I usually located radio-collared white-lips twice weekly from the air using a Challenger Ultralight airplane. Two Telonics H-antennae, one on each wing of the plane, were used to locate the signals from radio-collared animals. Standard aerial-tracking techniques were used to locate animals from the air, with searches beginning by circling over the last location for an animal, and flying parallel lines separated by 2 km from that point until the signal was located. I immediately plotted locations. Due to hazardous climatic and flying conditions, and the type of airplane used, flying was limited to 0600 to 0930 hours in the morning and 1500 to 1800 hours in the evening. Whenever possible follow-up visual-ground locations were conducted throughout the day using a three-element Yagi antenna. In some instances animals where located only from the ground.

Collared Peccary Capture and Tracking

Collared peccaries could be captured more easily than white-lips due to their habit of sheltering in holes or logs when chased. The Amerindian hunter, his four dogs and I would search the trail system for collared peccaries. When the dogs encountered a collared peccary or fresh scent they pursued the herd until the peccaries entered a giant armadillo (Priodontes giganteus) burrow or hollow log. The baying dogs kept the animals within the burrows until our arrival. We then blocked the entrance with stakes and dug a hole through the roof approximately 50 cm behind the entrance. We then inserted a 3-4 m long palm leaf into the burrow until it contacted the animal, which reacted by running towards the entrance. The peccary was then injected in the rump with a mix of 1.5 cc of Ketamine and 0.5 cc

Azaperone delivered in a syringe by means of a Tele-inject pistol. The post-capture treatment and data collection were as described above for white-lips. Radio-collared individuals were closely monitored to avoid capturing animals from herds with two or more radio-collared individuals. To ensure the capture of individuals from all herds in the eastern end of the island, we avoided hunting within the home ranges of herds that were already marked.

White-lip Behavior and Activity

Radio and visual tracking of white-lips indicated that they repeatedly visited the same food-rich sites. To determine the frequency of white-lip visits to such sites, I conducted detailed observations of their activity at one such site, a drying pond full of eels and other fish (Savanna-Pond). I checked visually and, through radio telemetry, for the presence of white-lips at four times per day every day (at approximately 0700, 1200, 1800 and 2000 hours) from January 26 to March 29, 1992. I noted the time herds visited the pond, their length of stay, their departure time and their activities. Herds in or by the pond were observed visually using 10 x 40 Zeiss binoculars, from an observation platform located 4 m up a tree and 50 m from Savanna-Pond. The un-vegetated borders of the pond, and its location in an open savanna by the side of a road provided excellent views of the herd. I correlated the visually observed activities of radio-collared individuals and the herd with changes in the activity signal transmitted by radios. This was done by scan-sampling the behavior of radio-collared individuals, and the herd at 5 minute intervals while simultaneously noting the change of radio-pulses per minute, from slow to fast or vice versa, and the frequency of changes for two minute periods at half hour intervals. This correlation allowed me to deduce actual herd activity from radio signals when animals were monitored only by telemetry. These data were used to construct a daily activity cycle for white-lips. Herd social organization was determined by watching all animals (occasionally focusing on those that were radio-collared and ear-tagged) and noting the position and behavior of individuals in reference to one another.

White-lip Herds: Age Classes, Sex Ratios and Social Structure

I determined the sex, age, and number of individuals in one herd through counts from the observation platform and a blind located 10 m from the pond. Data on the sex, age and number of individuals for another herd not visiting the pond were obtained through counts as they crossed trails. White-lips were classified into four age categories based on their coloration, size, and reproductive state. Adult white-lips were full-sized individuals with white-chins and blackish-gray body color. Adult males had enlarged testes. Sub-adults were approximately two-thirds to three-quarters adult size and maintained the reddish-brown coloration of young animals; on subadult males testes were small. Juveniles consisted of reddish-brown animals approximately half the size of adults but which were weaned; infants were approximately 1/4 of adult length and were still suckling. The captured white-lips were aged using the above criteria and additionally by tooth wear (molars) by measuring the height of crowns from the gumline. Old animals had very worn molars that reached up to 2 mm above the gumline, the crowns on middle-aged adults ranged from 2 to 3 mm above the gumline, adults and young-adults had crowns 3 to 4 mm above gumlines, juvenile-adults were animals that had adult characteristics (e.g. slightly-enlarged testes) but retained some subadult coloration and had little tooth wear (crowns extend 4 to 5 mm above gumline). Sowls (1984) discussed the pros and cons of using tooth wear to age peccaries. Although tooth wear depends on diet, in this study tooth wear is a valid aging method because the animals' herd and herds used the same area, suggesting they consumed the same food items in similar proportions.

Collared Peccary Herds: Age Classes, Sex Ratios and Social Structure

Collared peccary herd behavior, social structure, age classes and sex ratios were noted opportunistically whenever herds were encountered along peccary-search transects and during ground monitoring of the radio-collared herds. Sex and age were noted as for white-lips, modified by the following criteria: only adult animals had a distinctive and complete pale band of hair surrounding their necks; infants lacked this band and were generally redder, as were the larger weaned juveniles.

White-lip and Collared Peccary Habitat Use and Diet

I recorded the type of habitat or plant community for each peccary location. I used this information to compare habitat preferences between seasons, between herds and with that of collared peccaries using X^2 analysis. The diet of white-lips and collareds was described from opportunistic visual observation of individuals feeding in the wild.

Peccaries and Predators

A combination of a prolonged inactive signal and the location of an individual far from its herd usually indicated the death of that animal. Deaths were confirmed by ground location of carcasses and their radio-collars, usually within a day to a few days of death. The area surrounding the dead animal was searched for signs of the predator by a local Amerindian hunter who specialized in tracking and hunting wild cats. Predators were identified to species whenever possible through a combination of tracks, the attack-bite location on the body, tooth marks on bones and the post-kill treatment of carcasses. Kill sites were characterized qualitatively using vegetation type and density.

Home Range Analysis

I used the percent convex polygon method of the computer program HOME RANGE (Ackerman et al. 1991) to compute home range size based on the placement of locations within a 310 by 310 m square of land. I present home range sizes using both 100 percent of the locations (100 % contour line) and 95 percent of locations (95 % contour line). Ackerman et al. (1991) discuss the advantages and disadvantages of using the different contour lines for estimating home range size. I rely on the 100 % contour line because it incorporates the maximum number of locations when calculating home ranges.

Results

Habitats

The Terra Firme forests covered 71.4 km ^{2}, and was the most extensive vegetation type within the white-lip home ranges. It was followed in order by the Riverine Habitat, Mauritia Wetland, Savanna and Shrub Thicket plant communities (Table 6-1). The total area cover for all the vegetation types derived from the map was 105.9 km^2, an amount very similar to that encompassed by the combined home ranges of the two white-lip herds, 113.65 km^2. This close match indicates the robustness of the methodology used to measure the extent of vegetation cover.

White-lip Observations, Captures, Tracking Periods, and Locations

I first observed a white-lip herd of 30 - 40 animals on January 8, 1991, near Savanna Pond (Fig 2-1). A herd with a similar number of individuals (30 to 50) was encountered on June 28 at Forest Lake (Fig 2-1), and again on July 5 and 15th. On December 1, 1991, 46 white-lips were seen near Forest Lake, and 40 individuals at Savanna Pond on January 26 1992. On January 30, I captured the first individual (a female, no. 108) from the above group (henceforth herd A), that was still at Savanna Pond. I then captured a male (146) on February 7, two males on the 10th (109 and 105) and lastly male W6 on the 22nd. The similarity between the number of white-lips observed in the herd(s) early in the study and herd A suggested that it was the same group. This is supported by the home range analysis (see below), which indicates that all of the pre-capture herd observations occurred within herd A's home range.

With the exception of one observation of a herd of between 100-200 individuals on September 6, 1991, herd A was the only white-lipped group encountered on and east of the trail system from the time of the first white-lip capture until July 13, 1992, when a second herd entered the region. On July 16, I captured a female belonging to the latter herd (herd B), followed shortly by another female (Table 6-2). This herd contained approximately 130 animals and could have been responsible for the September 6 observation.

I thus captured a total of 7 white-lips, 5 in herd A and 2 in herd B. Only 4 of the herd A individuals were radio-tagged, male W-6 was only ear-tagged. Individual white-lips were radio-tracked on from 3 to 13 months, and the number of locations per animal ranged from 27 to 67 (Table 6-2). I obtained location data for herd A from January 26, 1992 to January 8, 1993 (but the pre-tracking observation data indicated the herd probably inhabited the area for at least 27 months) and B on 5 months (probably 10 months due to the September 1991 sighting). The variation in tracking time and number of locations among individuals occurred because of the death or loss of collars of some animals.

Collared Peccary Captures, Tracking Periods, and Locations

I captured the first collared peccary in July 1991, but did not begin radio-tracking this species until the second capture in April, 1992 due to the expense of flying the airplane. In total, 12 collared peccaries were captured belonging to two herds (Table 6-2). These were the only two herds regularly using the trail area and the region to the east. Individuals from both herds were tracked for varying lengths of time. The variation in tracking time and location number for individuals and herds occurred because of the death or loss of collars of some animals.

White-lip Herd Composition, Social Structure, Organization, Between-Herd Dynamics and Dispersal

White-lip herd A initially contained 39 individuals (based on January to March 1992 observations at Savanna Pond): 9 (23 %) adult males, 16 (41 %) adult females, and 15 (36 %) juveniles/sub-adults and infants (Fig. 6-1). At a last count in November 1992, the herd had grown to 53 individuals. Herd B contained 96 adults and 8 infants (n = 1 count); however, from the amount and location of noise made by individuals that had crossed the trail before I started counting, I estimated that there were an additional 20 to 30 individuals in this herd. Herd A had an adult sex ratio of 1:1.8 (male:female). This ratio is not significantly different than 1:1 (df=1, $X^2=2$, P>.05), but note my small sample size (n=25 adults) diminished the power of the test. The sex ratio for Herd B could not be determined due to its ranging pattern, large size, and avoidance of open areas. The sex ratio for the captured animals was 1.3 to 1 (male:female), based on a small sample (n=7). The discrepancy between sex ratios obtained by different methods suggests that further research on adult sex ratios is necessary especially if hunting schedules for sustainable use are to be developed.

During the hours of observation of herd A at Savanna-Pond (Table 6-3) I noted that the oldest radio-collared individual (based on tooth wear) could be considered an alpha male. He was the only male that regularly copulated with females (for example, he was observed copulating six times in three hours during one 23 hour observation period when copulation data were recorded systematically), and through aggressive encounters kept all other males but one from copulating. The latter male copulated only once, and this as the alpha stood near by. Other males tried to copulate but were chased off by the alpha; including male 105, the largest male captured (3.2 kg heavier than the presumed alpha male; 33.2 versus 36.4 kg).

Sub-groups were recognizable within herd A. Individuals in these groups foraged, slept, and traveled closer to each other than to members of other subgroups. Foraging sub-groups would often be separated by up to 25 m from other sub-groups. When napping or mud-wallowing, members of sub-groups were more likely to be in physical contact with each other than with individuals from other sub-groups, and these could be separated by 2 to 50 m. Sub-groups consisted of equal sized juveniles (there were at least two such groups), same sex subadults (two to three groups), young-adult males (each with 2-4 individuals), and adult females and their young (each with 2-4 individuals). One male (146) did not belong to any sub group: during all but one observation (see below) of the herd (both at Savanna-Pond and in the forest) he was always 10 to 15 m distance from the herd. Other than by the consistent sex and age composition, however, I could not determine the permanence of subgroups.

The female subgroups, and their infants were usually located within the center of the herd, along with the alpha male. They where encircled by the subadult and adult male sub groups. Adult males usually emerged first from the forest (slightly dispersed), followed by the females and young and then one or two males. This ordering also occurred when herds were traveling in single file. For example, when observing herd A, I noted that an adult radio-collared male (perhaps the alpha) led the group as they traveled between locations. This male was followed in line by another radio collared male, then came the radio-collared female, followed by other females. At the end of the line were a few males, and the second to last one was also radio-collared, perhaps number 146.

Generally the two white-lip herds remained apart. However, on three occasions they spent the night together, as indicated by aerial locations just before sunset and a confirming location just after sunrise the following day. White-lips do not usually travel at night (see below). The nature of these encounters could not be determined from the airplane, but at 0700 hours the morning after the first night together (July 18), radio signals indicated that the alpha male from herd A was active while female 117 from herd B was inactive (resting or sleeping). The two herds were again together from 1714 until at least 1745 hours on August 29th. During that location all three radio-collared individuals in the two herds were active. The herds were again together from November 3 to 4, during which time they slept and foraged near one another. After the first two nights together the herds separated and moved in approximately opposite directions. During the third meeting they foraged and traveled within hearing and smelling distance (approximately 50-100 m) of one another for at least two days.

After the first herd meeting, the subadult male W6, originally of herd A, was seen traveling and foraging with herd B on two separate occasions when A was 4 km distant. W6 thus seemed to have dispersed from his natal herd to a larger group after the two herds had come into contact.

Collared Peccary Herd Composition, Social Structure, Organization, and Between-Herd Dynamics

Reliable counts of collared peccary herd A were made as it crossed trails. This herd contained at least 28 adults and 6 infants for a total of 34 animals (n=4 counts). On one occasion I noted the sex of 23 adults belonging to this group: 10 were males and 13 females. I did not observe group B crossing a trail, but I counted 12 animals (10 adults and 2 infants) on one occasion while the animals foraged in a somewhat open forest. However, I suspect there were more animals in this group than noted during this count.

Generally, collared herds were less cohesive than white-lip herds. Collared herds traveled as dispersed groups with individuals or sub-groups often located 100 meters or more from one another. In the early morning, collared herds often splintered into sub-groups of 2 to 10 individuals, some of which could be located 500 to 1000 m from each other. The radio-tracking data indicated that collared sub-groups coalesced back into a herd at dusk. There were also times during the tracking period when the radio-collared individuals splintered into subgroups for days and weeks, with herd A separating into at least three subgroups, and herd B into at least two.

On two occasions the collared peccary herds were seen approximately 100 m from one another, near enough to smell, hear and occasionally see one another. On one of these occasions the herds were feeding on super-abundant _Pouteria venosa_ seeds within a clump of adult trees extending across the boundary of both herd's territories (see below). However, the herds kept approximately 100 m from one another, and did not mix over a 4-hour observation period. The herds were located approximately 100 m from one another on another occasion, during which they were observed for 3 hours. Individuals in both herds lay on the ground, or foraged in place, but did not move towards one another. The following day the herds were approximately 1.5 km from one another. On four occasions I watched herd A crossing a trail. They were traveling in a dispersed fashion, not in a single file. The first two animals to cross the trail on both occasions were adult males. They were followed approximately 8 m behind by two females with young, and for various time periods and distances by other adults and young.

Collared peccary Herd B contained 3 adult males, 4 adult females and 2 infants, for a 1:1.3 sex ratio. The adult sex ratio for the captured population was similar, 1:1.4.

White-lipped and Collared Age and Body Size

On average white-lips weighed twice as much as collareds, with no overlap between adult weights of the two species (Tables 6-4 and 6-5). Although the smallest white-lip was shorter in total body length than the longest of the collared peccaries, the white-lips with the shortest fore and hind legs still had longer limbs than the longest of the collared peccaries. Thus, while there was some overlap between the two species in their lengths, white-lips were heavier and had longer legs.

Adult female white-lips were generally heavier and longer than males, averaging 37.71 Kg versus 32.75 Kg for males, but males had longer ears, tails, hind and foreleg lengths (Table 6-5). For both sexes hind legs were generally longer then fore legs.

Collared males and females had similar weights (Table 6-5); however the male:female pattern in the other body dimensions described for white-lips repeated itself in collareds: females have greater total lengths than males but males had longer legs.

Foraging Pattern and Activity Cycles

White-lip herd A repeatedly returned to a food-rich pond (Savanna Pond) in the savanna from January 26 to March 29th, 1992 (Fig. 6-2). These visits ranged in length from a few hours to six days, for a total of 23 days (Table 6-3). I monitored the herd at the pond visually and by radio simultaneously for 119 hours and 36 minutes, and by radio only for 91 hours and 51 minutes (Table 6-3). Continuous monitoring periods ranged in length form 2 to 31 hours and 45 minutes.

Herd A visited Savanna Pond seven times from January 26 to March 29th (Fig. 6-2). During this period the water in the pond evaporated, exposing more eels and other fish to the white-lips than they could eat. On the few occasions when the peccaries left Savanna-Pond, they went to a Mauritia Wetland (Forest Lake) in Terra Firme Forest or a creek flowing through the Riverine Forest. These were brief visits from which they always returned to Savanna-Pond. This pattern of visits to the pond decreased in frequency and length in March, a change correlated with the almost complete drying of the pond and the absence of fresh fish.

The herd last visited the pond during this cycle on March 29, when it had almost completely dried. After this they began spending more time in the Mauritia Wetlands (11 out of 44 locations for this period) and in the Terra Firme High Forest (11 out of 44 locations). In early September they began utilizing the Riverine habitats to a greater degree and continued doing so until November (well into the dry season; 10 out of 44 locations for this period), when they once again began using the ponds in the savannas. They first visited the shallower, smaller ponds. They only returned to the larger and deeper Savanna-Pond on January 1993, when the site was once again in the initial stages of drying out.

Figure 6-3 shows herd A's movements between consecutive locations over the 13-month tracking period. Figure 6-4 does the same for herd B over a 5-month period. Both herds moved within a well-defined area (home range) and both herds repeatedly travelled the same trajectory to return to previously visited sites.

A general activity pattern emerged from the observations at Savanna Pond (n=23 days); illustrated by figure 6-5, which was constructed from data collected during the February 14 to 15 monitoring period. The herd slept through the night in a dense thicket of Bactris spp. thorn-palms within the Riverine forest adjacent to Savanna-Pond. They usually slept in pairs or small groups, in physical contact with one another. The radio signals indicated that the white-lips "tossed and turned" in the bedding area for about an hour before becoming fully active at dawn. Although active at sunrise, they remained in and around the bedding area for one to one-and-half hours before emerging at 0730 hours from the forest and entering the pond. Once at the pond they fed continuously, stopping occasionally to rub their heads against the rear-dorsal scent glands of other herd members, to copulate, nurse their young, or chase one another. These activities continued until 1000 or 1100 hundred hours. At about 1100 hours they retreated to the bedding area, or to a nearby tree island, or thick vegetation bordering one side of the pond, for a nap in the shade. They returned to the pond at approximately 1400 hours, to eat, wallow in the mud, copulate, and nurse. At dusk, they re-entered to the bedding area. They did not immediately lie down to sleep. Before settling for the night they often moved between bedding-niches and sleeping partners for about an hour before settling into a more continuous sleep.

White-lipped Peccary Home Ranges and Population Densities

Radio-collared white-lips from the same herd remained together from the onset of tracking until they died. The one exception was subadult W6, previously described as dispersing from one herd to another. Therefore, in this study, the home range of a herd consisted of the locations for the longest surviving herd member (see Table 6-2). Home range size was positively related with herd size (Tables 6-6 and 6-7): herd A with 39 white-lips (53 individuals at the end of the study) roamed over 21.77 km^2, while B with 124 to 134 individuals ranged over 109.6 km^2. On average, the individuals in the larger herd traveled further between locations than those in the smaller group (Tables 6-6 and 6-7).

With increasing herd size the number of individuals per km^2 decreased, from 2.4 for herd A (n=53) to 1.2 for B (n=134). These figures cannot be density estimates for the population because herds had overlapping home ranges, with A's home range being almost completely encompassed by B's (Fig. 6-6). Since we know that herd A's home range supported two white-lip herds, we can determine population density for this area by dividing the number of white-lips in the two herds by the area (177/21.77). This gives 8.13 white-lips per km^2. Similarly, we can also estimate the density for the remaining 87.85 km^2 of herd B's home range by dividing 124 animals into the 87.85 km^2. This assumes that no other herds ranged over the area. This gives 1.4 white-lips per km^2. Thus, the white-lip population density for eastern Maraca can range from 1.4 to 8.13 white-lips per km^2.

Home range size varied between seasons. This was most evident for herd A, the only group for which there is sufficient data for a seasonal comparison (Table 6-7). For herd A home range size almost doubled from the dry (January to June 1992) to the wet season (July 1992 to January 1993), from 12.54 to 21.67 km^2 (100 % contour intervals, 95 % intervals equal 11.39 and 17.59 respectively). This increase resulted from an expansion outward around the entire dry season home range boundary and not from a seasonal movement into a new and discrete wet season range (Fig. 6-7). The herd continued using their dry season range along with the wet season extension. Herd B made one long trip into a new area to the west of the island on September 23 (Fig. 6-4), and this may have been correlated with changing rainfall patterns; however by September 30 they had returned to their previous foraging area. Since this herd did not move into this foraging area until July 13, it is not surprising to discover their use of a more distant region of their home range. Again as with herd A, although B moved into a new area, it continued to use the old one as well.

The earlier observations of a herd with a similar number of animals as in white-lip herd A, within what was later identified as Herd A's home range, suggest that these were the same groups. Thus herd A may have inhabited the same area for at least 27 months, from the beginning to beyond the end of the study, when the last radio-collared animal died (# 109 was last seen on April 1993; pers. comm. G. de Oliviera).

Collared Peccary Home Ranges and Population Densities

To obtain a more complete herd home range size for collared peccaries I pooled locations for individuals from one herd with little overlap in their tracking dates into one data set. Thus, the data for individuals 192, 108c and 113-2 were pooled to determine the home range for herd A, and that of 115, 102, 116-2 and 113-1 were pooled to form that of herd B. Consequently, herd A was tracked for eight months (March to October 1992) and B for six months (April to September) (Tables 6-7 and 6-8).

The two collared herds had similar home range sizes, with A's at 10.14 km^2 slightly smaller than B's at 11.68 km^2 (Table 6-8). The similar size of the home ranges suggests the number of individuals per herd was probably similar. There was almost no overlap in the home ranges of the two herds indicating that this species is territorial (Fig. 6-6). An examination of the locations of the herds in the overlap area reveals that the two herds encountered one another along a border with almost no crossing into one another's areas (Fig. 6-8). This encounter area consisted of a super-abundant fruit patch that straddled the territory of both herds. It also appeared to be a territorial marking/display area. When the herds were simultaneously in this border area they did not mix.

A between-species comparison reveals that although collared herd A had a similar number of individuals (n=34) as white-lip herd A (n=39), the latter's home range was twice as large as that of the collareds (Table 6-8).

White-lip Use of Habitats

White-lips did not use the plant communities and habitats within their home ranges evenly (Table 6-9, Fig. 6-9). The Mauritia Wetlands, Terra Firme High Forest, and savanna ponds where the most frequently used habitats. Within the Terra Firme High Forest, white-lips foraged extensively in M. maripa clumps.

The home range analysis indicated that herd A nearly doubled the size of its home range from the dry to the wet season, and that these increases were in the form of an expansion outward along the entire boundary of the dry season range. This type of range increase is reflected in the equal use of some habitats between the seasons with a concomitant increase in the use of more seasonal resources (Fig. 6-9). For example, the Mauritia Wetlands were used in similar proportions during both seasons, but the Riverine and Terra Firme habitats were used significantly more often in the wet season, and the Savanna habitats in the dry (df=3, X^2=8.08, P=.0443). Note that in Fig. 6-9 and for the X^2 analysis I use the combined habitat categories presented in Table 6-1.

There were large differences in the time spent by herds A and B in different habitats during the wet season, the only period for which I have data for herd B (Fig 6-9). Herd B spent significantly more time in Mauritia Wetlands and Terra Firme Forest than herd A; but herd A spent significantly more time in Riverine and Savanna habitats (df=3, X^2=16.78, P=.0008). Interestingly, the area used exclusively by herd A (Fig. 6-6), consisted of a large 9 by 1 km savanna (and adjacent Riverine forests) that separated the Terra Firme from Riverine forests. Herd B remained almost exclusively within the Terra Firme forest region (Table 6-9).

Collared Peccary Use of Habitats

Collared peccaries were found almost exclusively within the Terra-Firme High Forest, with a few locations in Mauritia habitats (Table 6-9). They did not use the savanna habitats, and rarely entered the Thickets and Riverine communities. This pattern of habitat use limited a comparison between the two herds to Terra Firme forests and Mauritia communities; these were used in similar proportions by the two herds (df=1, X^2=.51, P=.476).

Habitat Partitioning by White-lips and Collared Peccaries

There were significant differences between the two species in their use of the Mauritia communities, Terra Firme forest, Riverine communities, and Savanna habitats (df=3, X^2=51.32, P=.0001). Seventy-three percent (n=36) of the observations within the Mauritia habitat were of white-lips, compared to only 27 % for collared peccaries. Similarly, white-lips accounted for 83 % (n=24) and 100 % (n=30) of the observations in Riverine and Savanna habitats respectively, in comparison to only 17 (n=5) and 0 % respectively for collareds. In contrast collared peccaries occurred much more frequently in Terra Firme forests, 62 % (n=65) versus 38 % (n=40) for white-lips.

White-lip Diets

White-lip diets varied with habitat and seasons. From January to March, herd A foraged almost exclusively at Savanna-Pond, where they ate eels and other fish exposed as the pond dried. They also occasionally foraged in Mauritia Wetlands, where they ate the endosperm of M. maripa seeds defecated by tapirs, uprooted and ate the M. flexuosa nuts attached to seedlings and ate the soft pulp of very ripe M. flexuosa fruit and M. flexuosa seeds. In Terra Firme forests they rooted around adult M. maripa in search of old, ungerminated seeds. They also ate the base of germinated M. maripa seedlings and seeds buried in and around M. maripa patches. M. maripa seeds remain in the seed bank for more than one year before germinating (Fragoso unpublished data), and were thus used year round. In June, the white-lips were in the Terra Firme Forest, where they fed extensively of the fruit pulp and seeds of masting Pouteria venosa, the ripe fruit pulp of masting M. maripa (they did not eat the new seeds), and also on Ilex jenmani fruits. Table 6-10 lists some of the items eaten by white- lips and their corresponding habitats.

Collared Peccary Diets

Collared peccaries ate most of the foods consumed by white-lips with the exception of M. maripa and M. flexuosa seeds (Table 6-11). This observation was confirmed in an experiment with wild caught collared and white-lip peccaries at Maraca (Chapter 2). However, like white-lips, collared peccaries uprooted the seedlings of both species and ate the attached root, and the nut in the case of *M. flexuosa* . They also consumed the ripe fruit pulp for both species. Collared peccaries also ate the seeds of *Pouteria venosa*, *Pradosia. surinamensis* and *Enterolobium cyclocarpum*

Anti-Predator Behavior

The anti-predator responses of white-lip and collared peccaries are different, even for similar sized herds. If humans are the threat, white-lips on Maraca bunch up and run off in a single file (this occurred in 48 encounters, in all of which the herds either observed me first or else I was hunting them; includes 36 encounters from Fragoso 1989). A sub-unit of adults may also conduct bluff charges before running (n=3; Fragoso 1989). If the predators are dogs, the white-lips coalesce into a group and chase the dogs (n=3). I followed a herd of white-lips for 2 hours on July 3 1992, during a capture attempt. This herd walked and ran almost continuously in single file in a large circular pattern for the entire period. Once I observed a jaguar stealthily approaching white-lip herd A as they foraged at Savanna Pond. The white-lips must have detected the jaguar when it was still 20 m distance across the pond, probably by scent because the jaguar was hidden by shrubbery. They responded by coalescing and running as a group into the forest.

Collared peccaries scattered when confronted by humans or dogs (n=52 encounters), with individuals running as subunits of one to 5 individuals. Collareds always ran from the dogs (n=26). We tracked 11 individuals to their final destination after a chase. In each case they avoided the dogs by entering a giant armadillo burrow (n=6), or hollow log (n=5). During one chase the dogs trapped four collared peccaries in a single log.

White-lip Mortality and Predation

White-lips on Maraca suffered high rates of mortality. Seventy-one percent (n=5) of the seven radio-collared individuals from both herds died; 43 % (n=3) were killed by jaguars or pumas. Specifically, of the five radio-collared white-lips in herd A, one was killed by a jaguar or puma (evidence: teeth marks on bones, canine puncture marks on collar, bones chipped); the cause of death for another male could not be determined (there were no teeth marks on bone nor were there pieces chipped off the bones). However, the latter individual's remains were near those of the previous animal, and both died within a few days of one another. The female white-lip from herd A lost its collar, thus its fate is unknown. The male marked only by an ear tag was alive and part of herd B when last seen on July 16, 1992. One year after its capture, Herd A's alpha male was still alive, but in April 1993 it was killed by a human hunter (pers. comm. G. de Oliviera). The females from Herd B were killed within three weeks of one another, one by either a jaguar or puma and the other by a female puma accompanied by its cub (identified from fresh tracks and treatment of carcass). Three of the kills occurred in the shrub thickets either in Riverine-Shrub thickets or shrub thickets in Mauritia Wetland-Savanna ecotone. One white-lip kill occurred in High Terra Firme Forest with almost no understory vegetation. During the two-year study, I or my assistants encountered jaguars twice and pumas three times.

Collared Peccary Mortality and Predation

At least 25 % (n=3) of the marked collared peccaries were killed by either pumas or jaguars (Table 6-12). The covering of the carcasses of one individual with dirt and leaves, suggests that it was killed by a puma, since this behavioral trait is unique to this species in this area. Kills occurred in dense shrub-thickets at ecotones with Mauritia wetlands and Terra Firme forest or Shrub Thickets in Riverine forests. Two collared peccaries died as a result of infections developing in legs entangled in radio-collars ("collar-related death"). There were no radio-tagged peccaries alive at the end of the study, although the fate of two ear-tagged individuals and two which lost their radio-collars and two whose batteries expired remained unknown.

Discussion

Two white-lip herds were monitored by radio-telemetry at Maraca, one on 13 months and the other on 5 months. The first of these herds may have been in the same region for at least 12 months before telemetry began, and for 3 months afterward, and the second may have been encountered once 10 months before being radio tracked. Two herds of collared peccaries were followed for a period of 8 months. I located visually or by radio seven white-lipped peccaries from two herds 280 times from January 1992 to January 1993. I observed one of the herds visually over three months for 23 days. This latter herd was radio-tracked for a year, both in the dry and wet seasons, while the other herd was followed only for the dry season. This is the most complete study of white-lip ecology to date, and the only study to successfully radio-track and observe wild herds directly for long periods of time. The length and intensity of observation provided representative picture of one herd's social structure, age structure, sex ratio, group dynamics, movements and activity patterns. The data for the second herd, although covering a shorter period of time in only one season, supported the patterns and dynamics observed for the first group. It also provided insights on the dependence of peccary ecology on herd size.

I found that white-lipped peccary herds were very cohesive year round, in contrast to the well-known fissioning pattern of collared herds. While the sex ratio was not statistically biased for either species, in one white-lip herd (the herd for which I have detailed counts of animals) females outnumbered males by a ratio of 1.8:1. For white-lips, home range size appeared to be related to herd size. One white-lip herd had a larger home range than a collared peccary's of the same size, confirming the relationship of home range size with biomass rather than just herd size (Eisenberg 1981). White-lips exhibited regular and predictable movements within a well-defined home range. Despite changes in food availability over the year, the white-lips did not move in a migratory (c.f. Baker 1978) or nomadic manner.

Peccary Social Structure

White-lipped peccary herds had overlapping home ranges, indicating that they do not maintain exclusive use of areas. In contrast, collared peccaries maintained non-overlapping territories. The two collared peccary territories and almost all of the home range of white-lip herd A were encompassed by the range of white-lip herd B. This is similar to the situation found by Taber et al. (1994) for sympatric Chacoan peccaries and collared peccaries in the Paraguayan Chaco. Although the four Chacoan peccary herds Taber et al. (1994) followed showed very little overlap in territory, collared peccary home ranges were almost completely encompassed within the larger Chacoan territories.

Obtaining a census of the age and sex distributions for a wild mammal population in a tropical rain forest habitat is difficult. At Maraca, I successfully obtained full counts after repeated long-term observation for one white-lipped peccary herd. Thirty-six percent of the animals belonged to three classes of non-adult animals. Even though no other study had previously obtained a complete age class representation of white-lips in the wild, management guidelines have been recommended based on truncated life tables derived from hunter killed adult animals (e.g., Bodmer in press).

As in the case for age classes, a closer consideration of sex ratios may also be important for designing management plans. Ideally, sex ratios should be based on observation of intact herds in protected areas, not on samples collected from hunters, since the two sexes may not be equally vulnerable to hunters. This situation can have serious long term impacts on mammalian populations (Ralls et al. 1980). For example, the assumption of equal sex ratios when determining harvesting rates for various whale species, may have contributed to the decline of populations, since most populations had female-biased sex ratios (Ralls et al. 1980). Based on the assumption of an even sex ratio and their knowledge of adult age classes, Bodmer et al. (in press) compared the over-hunted status of white-lips in a lightly hunted and a heavily hunted area. Based on the above argument, however, this may not be possible. Although it is difficult to study large mammals in tropical rain forests, especially highly mobile species such as white-lips, it is dangerous to extrapolate from limited data sets collected from hunter killed animals to develop a management plan that may weaken a population.

White-lips and Collared Herding Behavior: Implications for the Evolution of Herd Size

All of the captured white-lips successfully rejoined their herds, and all but one remained with them until their deaths. Although there were identifiable sub-groups within white-lip herds, the herd remained together throughout the year. White-lip herds were extremely cohesive units; individuals were never alone or beyond the hearing and scent range of the group. Nor did they fission as seasons changed or food availability declined. The cohesiveness of white-lip herds contrasts with the fusion and fission pattern observed in collared peccaries. In this study collared peccaries often splintered into distinct sub-groups that foraged hundreds of meters from other herd sub-groups during the course of a day. These sub-groups occasionally remained as independent social units for days and weeks.

The fissioning of collared peccary herds is not unique to the rain forest habitat. In the gallery forests of the Llanos region of Venezuela, collared peccaries also occur in large herds of up to 40 or 50 animals and these splinter into groups of 6 to 15 (Barreto and Hernandez 1988, Castellanos

1983, Robinson and Eisenberg 1985). Splintering is related to the seasonal decline in food availability (Barreto and Hernandez 1988, Castellanos 1983, Robinson and Eisenberg 1985). A similar splintering pattern occurs in collared peccaries in the south-western desert areas of the United States (Sowls 1984). Many tropical primate species groups also fission when food availability is reduced or becomes more patchy (e.g., Chapman et al. in review, Symmington 1990, Terborgh 1983) .

The only other herding tropical rain forest ungulate forming herds comparable in size to those of white-lips is the bearded pig (*Sus barbatus*) of southeast Asia (Caldecott 1988). In this species, solitary males and small female-offspring units are the norm, with larger herds forming irregularly, apparently in response to spatially and temporally localized high densities of fruits. In contrast, white-lip herd size remained large and fairly constant over time and among seasons. This suggests that white-lips experienced no severe food scarcity over two years, a counterintuitive conclusion given the large biomass of a peccary herd and the evidence for regular lean seasons, in some Neotropical areas (Glanz 1982, Milton 1990, Terborgh 1983, van Schaik et al. 1993).

While the ability to move long distances over an extensive home range may allow white-lips to encounter enough food to maintain a large herd size, the differences in body size, leg length, and anti-predator behavior between collared and white-lipped peccaries suggest that the larger white-lip herd size is actually a secondary and indirect consequence of anti-predator adaptations. Jaguars and pumas, the primary non-human predators on both species of peccaries (H. Quigley and P. Crashaw pers. comm. for the Pantanal, Taber pers. comm. for the Chaco, and Fragoso pers. obs.), have home ranges somewhat larger than collared peccary herds (about 10 km^2 for females, 28 to 40 km^2 for males, with some individuals using areas of only 2.5 km^2 for two weeks, Rabinowitz and Nottingham 1986), but much smaller than that of white-lip herds. Collared peccaries can thus become "stuck" in a jaguar's home range, where they will be easily located and monitored. Collared peccaries respond to predation attempts by jaguars by splitting up and running in several directions to find shelter. A collared peccary with long legs has the ability to move long distances without stopping, and to do so frequently, would be able to move out of a jaguar's home range. Even if it moved into another jaguar's home range, it would not have to stay there long enough for the jaguar to discover it. A collared peccary with the ability to move far is essentially a long-legged white-lipped peccary. Once white-lipped peccaries were able to move to reduce predation risk, they were also able to find scattered landscape level fruit patches. By increasing their access to food, they would have reduced the limitation on herd size set by the limited size or number of fruit patches within single habitats. At this point, any adavantages to large herd size, such as group-mediated anti-predator behaviors (Kiltie and Terborgh 1983, Roosevelt 1920) could lead to the evolution of large herd size.

Additional support for predation as an important force in the peccary evolution, is the cryptic coloration of both species, which was easily affected by the use of radio collars. Forty three percent of the radio-collared white-lips in this study and at least 25 % of the collared peccaries were killed by large cats. The broad white radio-collars probably made these animals more conspicuous to predators trying to focus on a single animal in a herd. The implication is that mortality from predation is high, and likely to have affected the evolution of many peccary traits.

The large herd size of white-lips has an additional implication, in relation to the habitat it lives in. Large white-lip herds can strongly affect plant regeneration, not only through direct predation on seeds and seedlings, but through the incidental destruction of seedlings by trampling and rooting. If peccary movements are indeed predictable, as discussed below, they may have over the long term affected fruiting strategies of plants, such as the timing and synchrony of fruit drop. If, in addition, white-lip populations fluctuate in numbers (Fragoso pers. obs., L. Emmons pers. comm.) then regeneration of plants used by white-lips may occur in bursts at the time of peccary population lows. The unique social structure of this animal could thus have been an important force shaping the structure of Neotropical forests.

White-lip Home Ranges

Herd A with 39 white-lips ranged over 22 km^2 and B with 130 individuals ranged over 109 km^2. Kiltie and Terborgh (1983) estimated herd densities at one per 60 to 200 km^2 in Manu National Park Peru. This has been interpreted by other researchers as being synonymous to the home range size of the 90 to 138 white-lips observed by Kiltie and Terborgh (e.g., March 1993, Nowak 1991). The methodology used to derive these numbers consisted of observers remaining in one place and counting herds as they passed through (Kiltie and Terborgh 1983). Home range size was then calculated using the frequency of visits and an estimated distance traveled per day.

In the Chaco habitat of Paraguay, Taber et al. (1994) tracked a white-lip for a day and noted that it moved 10 km in a straight line before they lost track of it. It is unclear whether this was a normal movement for the animal or whether it was attempting to evade the trackers by moving continuously, as white-lips are wont to do (Fragoso, pers. obs.).

In the same habitat, Taber et al. (1994) reported a home range size of 6.85 km^2 for one radio-tagged collared peccary followed for 165 days. This estimate is reduced to 1.96 km^2 if the methodology is based on 1-ha grid cells rather than on minimum convex polygons. Eisenberg (unpublished data) estimated a home range of 0.8 km^2 for a group of 11 collared peccaries on BCI, based on encounters rather than on radio tracking. In the rain forest isolate of La Selva in Costa Rica, Suarez (1993) estimated by radio tracking three collared peccary herds a mean annual home range size of 0.7 km^2 (80 % contour lines, minimum convex polygon). This includes a mean monthly home range size of 0.5 km^2 for two herds in secondary forest, and of 1.19 km^2 for a herd in primary forest. The home range sizes may have been this small because the animals were feeding on yucca crops in the agricultural fields surrounding the reserve.

The home ranges I report for collared peccaries on Maraca (10.1 and 11.7 km^2) are thus one order of magnitude larger than those reported elsewhere, but only slightly larger than Taber et al.'s (1994) estimate based on the minimum convex polygon method. Some of the differences may be due to the different habitats being studied, and some to differences in herd size. Suarez' (1993) herds, for example, averaged 18 animals, as opposed to my 34. In the Chaco, Taber et al.'s (1994) herds ranged in size from 4 to at least 11 individuals. Smaller herds would be expected to have smaller ranges. In each case, the researchers also could have been following only one of the subgroups of the herd, and therefore missed identifying parts of the range used by other subgroups.

Much of the difference, however, is probably due to the fact that I was able to track the peccaries continuously from the air and thus obtain a more detailed picture of the area used than is possible by ground tracking alone. It is true that in foot tracking one has a smaller scale of resolution and is able to use a smaller cell size than can be used from an airplane (e.g., Taber et al.'s 1-ha grids compared to my 310 x 310 m grids); however, the accuracy of triangulation does not really permit use of a grid size smaller than 5-ha, especially in forested habitats (Tommy Smith, pers. comm.). Animals' home ranges also may be distorted by ground locations, partly because if one approaches the animal closely to get a more accurate fix, the animal may be scared away to an artificial location. Additionally, researchers on foot are limited in how far they can move, and can easily miss any long distance movements the animals make.

White-lip Population Densities

The small size of white-lip herd A contrasts with sizes reported in the literature, with the exception of Sowls' (1984) count of 60 animals for a herd in a remnant patch of the Atlantic Forest in southern Brazil, and two small "satellite" groups observed by Kiltie and Terborgh (1983). In 1988, I found that white-lip densities in eastern Maraca were the highest reported in the literature (Fragoso 1989). I obtained complete transect data for density estimates by walking 122 km between June 12 and July 3 1988. In addition, I recorded the number of times herds were encountered along transects for 227 days sampled from June 1988 to June 1989 (Fragoso and Emmons in prep.). During this latter period I enountered herds 478 times. From the June to July 1988 transect data, I estimated densities at between 139 (King method) and 542 (Webb method) individuals per km^2. This is much higher than the estimated density of between 1.4 and 8.13 peccaries per km^2 for 1990-1993. Based on indirect evidence, I concluded that the white-lip population in the region may have experienced a major decline probably due to a pandemic disease (Fragoso 1993b, report to World Wildlife Fund USA). If true, this could explain the small size of herd A (and herd B relative to the hundreds of animals estimated for herds pre 1989; pers. comms. J. Alves, Dr. J. Thomphson, G. de Olivieira) and the low population density in 1990-1992 compared to 1988-1989. White-lip population density estimates for other Neotropical regions include 1.3 individuals per km^2 (Bodmer et al. 1988) in a hunted site in the Peruvian Amazon (estimated from hunter kills), and 4.9 per km^2 in an unidentified Neotropical site (Robinson and Redford 1986). These estimates and those from Maraca in 1992 are extremely low relative to the 1988 to 1989 on Maraca (Fragoso 1989), suggesting that white-lip peccary populations have either been recently reduced in many sites in Amazonia, or that they undergo population fluctuations.

Biologists tend to associate population fluctuations with small mammals, yet Young (1994) provides evidence from the literature that catastrophic mortality is common among large mammals, including forest mammals. Wild Sus scrofa populations in Asia can fluctuate dramatically; for example, S. scrofa were rarely seen in 1974 but by 1980 the population had attained a density of 10 indiviuals per km^2 (pers. comm. M. Sunquist).

On Maraca, it is unlikely that the decline in white-lip densities from 1989 to 1992 was due to a movement of the animals out of the area, because very large herds could not be found in any of the areas were they could reasonably be expected to have moved to. During September 1992, I searched the central and western area of the island, went 200 km along the Uraricaa river up to its junction with the Erico river, to a Yanomami Indian village 150 km northwest of Maraca, and there were no signs of white-lips in the area. I later traveled within the Yanomami reserve (9,400,000 ha in Brazil), hunting with the Indians, and found out personally and through interviews with Indians and Indian agency officials that no white-lips had been seen or hunted for two to five years. Before this period they regulalry killed white-lips. Similarly, a survey of approximately 50 Macuxi Amerindian hunters in a village near the main study site found that only one hunting party had killed white-lips (n=7) from 1992 to 1993. In contrast, in June of 1988, 4 hunters interviewed in the same village were averaging 3 to 5 white-lips per month (Fragoso and Emmons in prep.).

Peccary densities may thus fluctuate or oscillate on several scales: the large, multi-year scale of population cycles, and the smaller within year scale as a herd moves tens of kilometers within its home range. The usual transect methodology used to measure densities cannot distinguish between these two scales of variation, unless transects are carried out repeatedly over the long term and used only for within site among year comparison. Short-term studies used to compare widely separate sites (e.g., Emmons 1984, Gentry 1992) may not produce reliable results.

White-lip Movements

White-lips in this study exhibited a strong site fidelity, in the sense that they consistently returned to feeding, bedding and watering sites. Return visits were both short term (1 day to a few weeks within a season) and long term (from one year to another). When the Savanna-Pond contained abundant food, herd A visited it repeatedly, often remaining there for several days. This pattern of visits continued for three months in 1992. During this period, when the herd left the site it did so only for brief periods before returning. However, once the site dried up and no longer held food the white-lips ignored it, until the same time the following year when eels and other fish were once again available and they returned. Herd B also showed regularity and patterning in its movements (based on a visual examination of movement patterns as depicted in Figure 6-4), returning to the same foraging areas even after an extended trip of over 30 km. The same return visits characterized white-lip relations with palm patches. The Forest Pond, an almost monospecific *Mauritia flexuosa* palm clump, was visited as regularly as the Savanna-Pond. Here the white-lips ate from the thousands of *Maximiliana maripa* seed defecated by tapirs (*Tapirus terrestris*), and the fruit pulp, seeds and seedlings of *Mauritia*. White-lip herds also foraged repeatedly in clumps of *Maximiliana* palms. When a herd of white-lips entered a clump of *Maximiliana* during the mast period they often ate the pulp from all the thousands of fruit on the ground and spit out the seeds (Fragoso unpublished data). *Maximiliana* seeds were eaten only months after the end of the mast period, when the white-lips would again visit the clumps and root around adult palms in search of the more breakable buried *Maximiliana* seeds and recently germinated seedlings.

The only other descriptions of white-lip movements in the literature are those of Kiltie (1980), Kiltie and Terborgh (1983), and Bodmer (1989, 1990b). Based on the same observation methodology as used for describing "herd densities", Kiltie (1980), and Kiltie and Terborgh (1983) compared rates of visits to one site with the results from a random model, and reported that "[f]or practical purposes, then, appearances of *T. pecari* herds at the site were random events, occurring with a constant probability from day to day within a season. This result agrees with anthropologists' reports that *T. pecari* is a prey species which aboriginal hunters encounter unpredictably" (pg. 250, Kiltie and Terborgh 1983). In this study Kiltie and Terborgh (1983), wondered whether or not white-lips "possess home ranges at all". Bodmer's (1989) analysis of sites where hunters killed white-lips led him to conclude that white-lips were migratory, although he based this conclusion on movements of only about 10 km. Bodmer (1990b) supports his endorsement of the migration hypothesis, by citing local inhabitants' reports that white-lips were more likely to be found near "varzea" towns during the dry period than were collared peccaries. Migration in this sense implies movement away from a focus with a subsequent return.

Throughout their range, white-lip populations have been noted to occasionally disappear or decline sharply in numbers (e.g., Kiltie and Terborgh 1983, Vickers 1991, Stearman 1992, Fragoso and Emmons in prep.). One explanation for these disappearances is that the animals have moved out of their usual area while tracking fruit resources (Sowls 1984, Kiltie 1980, Bodmer 1989a), and they at times have therefore been considered either nomadic or migratory (Sowls 1984). At this point in time there is no way of distinguishing between in situ population declines and long-distance nonseasonal movements (those that take animals outside of their usual home range for reasons not associated with seasonal changes) as causes of the large scale disappearance of white-lips for the areas reported above.

This does not of course rule out occasional dispersal movements during certain phases of the animals' population cycle. If individually recognized white-lip herds are not tracked continuously for long periods of time, their ranging patterns could easily be misinterpreted as nomadism or migrations.

Baker (1978) discusses the difficulty associated with differentiating migration from regular movements within a home range. However, the range expansion by white lips on Maraca from the dry to wet seasons, and the seasonally simultaneous use of both ranges cannot be considered a migration even in the broadest sense as defined by Baker (1978). On Maraca, the two herds stayed within well defined home ranges during the study period, and they found sufficient food within this limited but heterogeneous home range. If we extrapolate from the Maraca data, a herd of 400 individuals would have a home range of about 380 km^2. A white-lip herd moving over a home range of this extent, when observed from only a few points, could easily give the impression of migrating or wandering, when in reality it might only be regularly covering many points in its vast home range. Whether white-lips in other areas have similar ranging patterns remains to be studied.

Habitat Partitioning and the Coexistence of Peccary Species

The two white-lip herds differed in their use of habitats even though both had access to the same area. This suggests that white-lips from different herds differ in what they accept as suitable or necessary habitat, or, that many habitats are suitable for white-lipped peccaries and not all are necessary. The only constraint might be (with increasing herd size) that the food patch size must increase, or visitation to patches increase or both. The larger herd B remained almost exclusively in the Terra Firme Forest communities. The savanna habitat they used only once consisted of a small patch within the forest. Herd A , on the other hand, traveled and foraged extensively in a savanna of large extent. Thus white-lip herd A used savanna habitats preferentially while white-lip herd B avoided them although both had access to them. Apart from this complete avoidance of one habitat by herd B, the two herds also differed in the extent to which they used shared habitats. One conclusion that can be drawn is that both white-lips and I distinguished habitats at the same scale, that is, individual herds chose among the habitats as I defined them. As a population (both herds combined) however, white-lips used all the habitats available to them. .

In contrast, the two collared peccary herds did not differ in their use of habitats. Essentially both collared herds used or preferred the same type of terra firme forest habitat. They were never observed in the Savanna habitat and rarely used the Riverine habitats and *Mauritia* wetland areas. White-lips and collareds may thus be responding to different levels of vegetation organization, with collareds partitioning their habitats at finer scales of resolution than I used to define the study area habitats. At my scale, collareds appear to be habitat specialists relative to white-lips. A study of collared peccary use of vegetation communities would have required a finer scale view of sub-habitats within Terra Firme forests than I was able to define.

White-lips and collared peccaries coexisting in the same area may thus not perceive and/or react to habitats (or their boundaries) or resources in the same way (c.f. Weiss and Murphy 1988). Thus this difference in response to habitats may simply be a consequence of their difference in body size and step-length, which affect their movement abilities and home range size (Eisenberg 1981, Holling 1992). If, as suggested earlier, body size and ranging differences are the result of selection for anti-predator behavior rather than for optimizing food availability or a combination of both selective forces, then body size differences may provide an additional explanation for the marked ecological differences observed when the two species are compared as previously noted by Kiltie (1981b). This provides an additional hypothesis to the proposal by Kiltie (1981b) that differences in bite-force and subsequent food selection reduce competition between two such similar species.

We must keep in mind that this study examined differences in a single habitat, the humid, closed canopy rain forest. Once we examine differences among collared and white-lips coexisting in the open Pantanal habitat and Cerrado, or Chacoan peccaries, white-lips and collareds coexisting in the Chaco habitat (Taber et al. 1994), we may be able to understand whether these differences in habitat grain size are indeed correlated with body size differences and other aspects of their biology.

Table 6-1. The amount of area covered by habitats used by two white-lip herds.

Habitat	Km^2	%
Riverine Vegetation	13.6	12.8
Mauritia Wetlands	10.0	9.4
Terra Firme Forests	71.4	67.2
Savanna	8.0	7.5
Shrub-Thicket	3.2	3.1
Total	106.2	100.0

Table 6-2: White-lipped and Collared peccary captures per herd, number of locations, number of months tracked (number of months on which locations were obtained) and the date of the first and last location per individual.

Species	Herd	Individual No.	No. Months Tracked	No. of Locations	First Location Month/Day/ Year	Last Location Month/Day / Year
White-lip	A	108	3	33	Jan/26/92	Mar/2/92
White-lip	A	146	7	42	Jan/26/92	Jul/15/92
White-lip	A	109	13	67	Jan/26/92	Jan/08/93
White-lip	A	105	7	34	Jan/26/92	Jul/15/92
White-lip	A	W6	8	27	Jan/26/92	Aug/06/92
White-lip	B	117	5	46	Jul/16/92	Nov/16/92
White-lip	B	101	3	31	Aug/06/92	Oct/30/92
Collared	A	107	2	2	Jul/02/91	May/06/92
Collared	A	108c	4	25	Jul/03/92	Oct/31/92
Collared	A	192	5	12	Mar/16/92	Aug/07/92
Collared	A	102-1	1	3	May/5/92	May/19/92
Collared	A	113-2	4	27	Jul/07/92	Oct/31/92
Collared	A	R3Y3	*	1	May/19/92	May/19/92
Collared	A	WY11	*	1	May/07/92	May/07/92
Collared	B	102-2	3	15	Jul/07/92	Sep/18/92
Collared	B	113-1	2	8	Apr/24/92	May/18/92
Collared	B	115	5	20	Apr/12/92	Aug/17/92
Collared	B	116-1	3	10	Apr/20/92	Jun/31/92
Collared	B	116-2	3	15	Jul/08/92	Sep/18/92

Table 6-3: Dates of telemetry and visual monitoring of white-lipped peccary herd A at Savanna Pond. Also presented are the number of hours per observation period, and the days/nights of 24 hour monitoring.

	Observation Type			
Date	Telemetry & Visual (Hrs:Min)	Visual Only	Telemetry Only (Hrs:Min)	Night Telemetry
Jan-26		2		
Jan-29		3		
Jan-31			4:00	
Feb-03	5:00			
Feb-04	11:47		4:13	
Feb-05	12:05			
Feb-07	3:39		1:43	
Feb-08	11:00		1:28	
Feb-09	3:35		7:20	
Feb-10			9:55	
Feb-11	12:00		2:30	
Feb-12	12:00		3:00	
Feb-13			3:00	
Feb-14	5:26		5:19	Yes
Feb-15	11:30		9:30	Yes
Feb-16	2:23			
Feb-23	5:45		5:30	
Feb-24	9:45		4:00	
Feb-25	11:27			
Mar-19			3:45	Yes
Mar-20			17:00	Yes
Mar-28			9:00	
Mar-29	3:30		0:38	
Total	119:36	5	91:51	

Table 6-4: The weight and body dimensions of white-lipped and collared peccaries. OAD=old adult, MAD=middle age adult, YAD=young adult, JAD=juvenile adult. * These measurements were not recorded.

					Length Measurements (cm)				
Species	Sex	Individual	Weight Kg	Age	Total	Tail	Hind leg	Fore leg	Ear
White-lip	F	101	39.5	OAD	*	*	*	*	*
White-lip	F	117	38.6	MAD	116	12	45	43	7.5
White-lip	F	108	35.04	MAD	111	7	49	47	8
White-lip	M	146	32.34	MAD	122	*	64	48	*
White-lip	M	109	33.24	OAD	97	8.5	53	52	8
White-lip	M	105	36.44	YAD	105	10.5	49	50	7.5
White-lip	M	W6	30.04	JAD	101	15	48.5	43.5	7
Collared	F	113-1	17.2	YAD	97	9	44	37	8
Collared	F	102-1	20.9	AD	100	11	46	37.5	7.5
Collared	F	WY11	10.4	JAD	91	8.5	41	34	7.5
Collared	F	116-1	18.6	MAD	94	9.5	40.5	37.5	9
Collared	F	113-2	21.3	AD	91	9	42	33	7
Collared	F	102-2	21.3	AD	102	6	40	31	7.5
Collared	F	116-2	16.8	AD	93	8	45	36	8
Collared	M	115	21.3	MAD	94	6	47	38	9
Collared	M	R3Y3	15.9	YAD	92	6	46	41	8.5
Collared	M	108.1	12.7	YAD	74	8	43	33	8
Collared	M	107	27.2	MAD	104	8	48	46	8
Collared	M	192	10.9	JAD	*	*	*	*	*

Table 6-5: Summary statistics of the body dimensions of white-lipped and collared peccaries. (M = males, F = females)

		White-lip F	White-lip M	Collared F	Collared M	White-lips M + F	Collared M + F
Weight (Kg)	Mean	38	32.75	18	17.6	35	17.83
	N	3	4	7	5	7	12
	SE	1.53	1.25	1.5	2.89	1.38	1.41
Total Length (cm)	Mean	113.5	106.25	95.43	91	108.67	93.82
	N	2	4	7	4	6	11
	SE	2.5	4.5	1.65	6.24	3.85	2.4
Tail (cm)	Mean	9.5	11	8.71	6.67	10.4	8.1
	N	2	3	7	4	5	10
	SE	2.5	2.08	0.61	0.67	1.44	0.55
Hind Leg (cm)	Mean	47	53.5	42.57	46	51.33	43.82
	N	2	4	7	4	6	11
	SE	2	3.66	0.92	1.08	2.74	0.85
Foreleg (cm)	Mean	45	48.5	35.29	39.5	47.33	36.82
	N	2	4	7	4	6	11
	SE	2	1.71	1.02	2.72	1.41	1.27
Ear (cm)	Mean	8	7.67	8	8.25	7.8	8.09
	N	2	3	7	4	5	11
	SE	2	0.33	0.22	0.25	0.2	0.16

Table 6-6: The home range sizes of white-lipped peccaries from two herds at the 100 and 95 percent contour intervals. Also shown are the number of locations for each animal, the number of locations defining the boundary of the home range, and the mean distance between consecutive locations. White-lip W6. N-100 %, 95 % indicates number of locations for 95 and 100 % contours, respectively. Differences in individual home ranges for peccaries in the same herd result from differences in length of tracking times.

Herd	Individual	Home Range Size-100% (km^2)	Home Range Size-95 % (km^2)	N-100 %	N-95 %	Mean Km Between Consecutive Locations
A	108	11.5	11.9	33	31	1.2
A	146	18.6	16.7	42	39	1.6
A	109	21.8	17.7	66	62	1.5
A	105	13.2	13.0	33	31	1.6
B	117	109.6	59.3	8	43	2.4
B	101	87.5	51.4	9	29	2.6

Table 6-7: The home range size of peccary herds and the number of locations per herd (N=number).

Sp./Herd	Individual	No. in Herd	Home Range Size-100% (km^2)	Home Range Size-95 % (km^2)	No. at 100 %	No. 95 %	Start Track	End Track
White-lip A	109	39	21.8	17.7	66	62	Jan/26 /92	Jan/08 /93
White-lip B	117	130	109.6	59.3	46	43	Jul/16 /92	Nov/16 /92
Collared A	192, 108c, 113-2	34	10.1	7.3	64	60	Apr/16 /92	Oct/31 /92
Collared B	115, 102, 116-2, 113-1	12	11.7	8.1	65	61	Apr/12 /92	Sep/18 /92
White-lip A-Dry Season	109	39	12.5	11.4	29	27	Jan/26 /92	Jun/02 /92
White-lip A-Wet Season	109	53	21.7	17.6	37	35	Jul/14 /92	Jan/08 /93

Table 6-8: The home range sizes of collared peccaries from two herds at the 100 and 95 percent contour intervals. Also shown are the number of locations for each animal, the number of locations defining the boundary of the home range, and the mean distance between consecutive locations (Loc.).

Herd	Individual	Home Range Size 100 % (km^2)	Home-Range Size 95 % (km^2)	Total Locations	Mean Km Between Consecutive Locations
A	108c	9.8	4.7	25	1.7
A	113-2	9.8	4.5	27	1.7
A	192	7.7		12	2.0
B	102	6.0	4.8	15	1.6
B	113-1	4.8	2.1	8	2.0
B	115	8.0	5.9	20	1.5
B	116-2	6.1	5.6	15	1.6

Table 6-9: The number of times and period the two white-lip herds where located in different plant communities (January to June 1992-dry season, and June 1992 to January 1993 wet season), and similar data for the collared peccary herds.

	No. of Telemetry Locations and Dates				
Plant Community	White-lip Herd A Jan.-Jun. 92	White-lip Herd A Jul.92-Jan. 93	White-lip Herd B Jul.92-Nov. 92	Collard Herd A Mar.92-Dec 92	Collard Herd B Mar92-Sep.92
Mauritia Wetland	8	7	17	3	2
Mauritia Wetland-High Forest Edge	0	1	3	4	4
Maiximiliana Palm Forest-Low	0	1	1	1	6
Riverine Shrubs-Low	0	5	2	0	3
Riverine Forest-Low	0	8	0	0	0
Riverine Forest-Mid to High	9	0	0	1	1
Savanna-Ponds	20	7	1	0	0
Savanna-Forest Patch	1	0	1	0	0
Terra Firme-High Forest	8	10	14	22	25
Terra Firme-High Forest with Inaja	1	1	3	3	4
Terra Firme-High & Low Forest	0	1	1	1	5
Terra Firme-Low Forest	0	1	3	2	3
Thicket-Shrub Wet	0	0	1	0	1
Thicket-Bactris Palm	1	0	0	0	1
Total	**48**	**42**	**47**	**37**	**55**

Table 6-10: Species and parts eaten by white-lips.

Item	Part Eaten	Habitat
Maximiliana maripa	Ripe fruit pulp	Terra Firme Forests, Maximilliana Clumps
Maximiliana maripa	Seeds in seed bank	Terra Firme Forest, Mauritia Wetlands
Maximiliana maripa	Seeds attached to seedlings	Terra Firme Forest
Mauritia flexuosa	Very ripe pulp	Mauritia Wetlands
Mauritia flexuosa	Ripe but semi-soft seeds	Mauritia Wetlands
Mauritia flexuosa	Seeds attached to seedlings	Mauritia Wetlands
Pouteria venosa	Ripe pulp	Terra Firme Forests
Pouteria venosa	Seeds	Terra Firme Forests
Ilex jenmani	Ripe fruit	Terra Firme Forests
Pradosia surinamensis	Seeds	Terra Firme Forests
Poaceae	Root bases	Shrub Thicket
Snake	Entire body	Terra Firme Forest
Fish	Entire body	Savanna ponds
Eels	Entire body	Savanna ponds

Table 6-11. Diet of Collared Peccaries

Species	Part Eaten
Enterolobium cyclocarpum	Seeds
Maximiliana maripa	Ripe fruit pulp, and the root base of newly germinated seedlings
Pradosia surinemensis	Mature and green seeds
Mauritia flexuosa	Ripe fruit pulp, and the germinated seed attached to seedling
Swartzia sp.	Mature and green seeds, and seeds attached to seedlings
Psidium sp.	Entire fruit
Bactris sp.	Seed
Pouteria venosa	Fruit pulp, mature seeds, and seeds attached to seedlings

Table 6-12: The fate of radio and ear-tagged collared peccaries.

Status	No. of Peccaries	% of Peccaries
Killed by Jaguar or Puma	3	25
Radio-Collar Related Death	2	17
Unknown Cause of Death	1	7
Escaped Radio-collar	2	17
Battery Died	2	17
Fate Unknown-Ear Tagged Only	2	17
Alive	0	0
Total	12	100

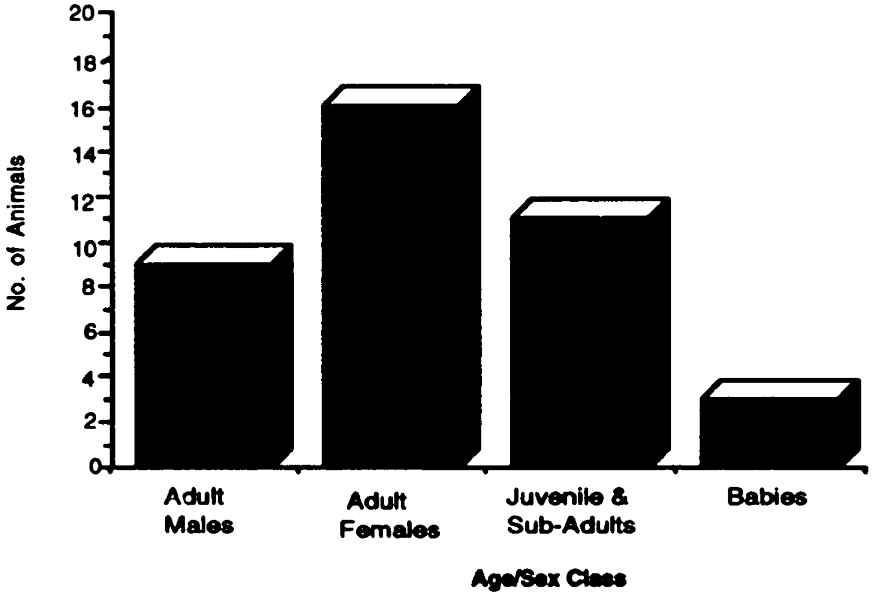

Fig. 6-1: The number, sex and age of white-lipped peccaries in herd A.

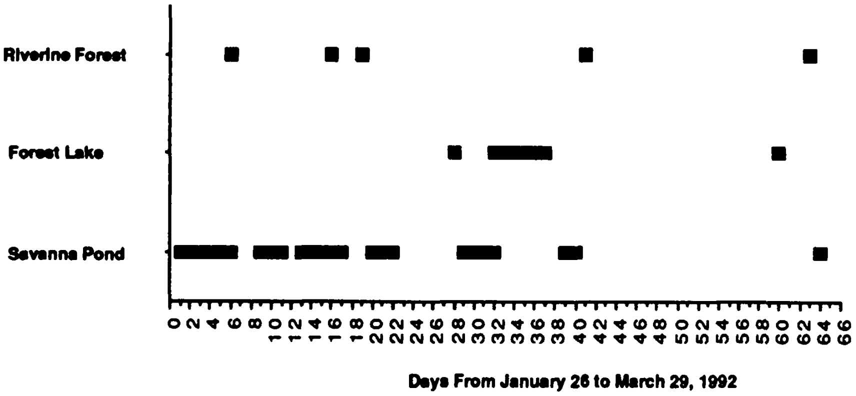

Fig. 6-2. The frequency and periodicity of white-lip herd A's foraging visits to two drying ponds (or lakes) and the riverine forest adjacent Savanna Pond.

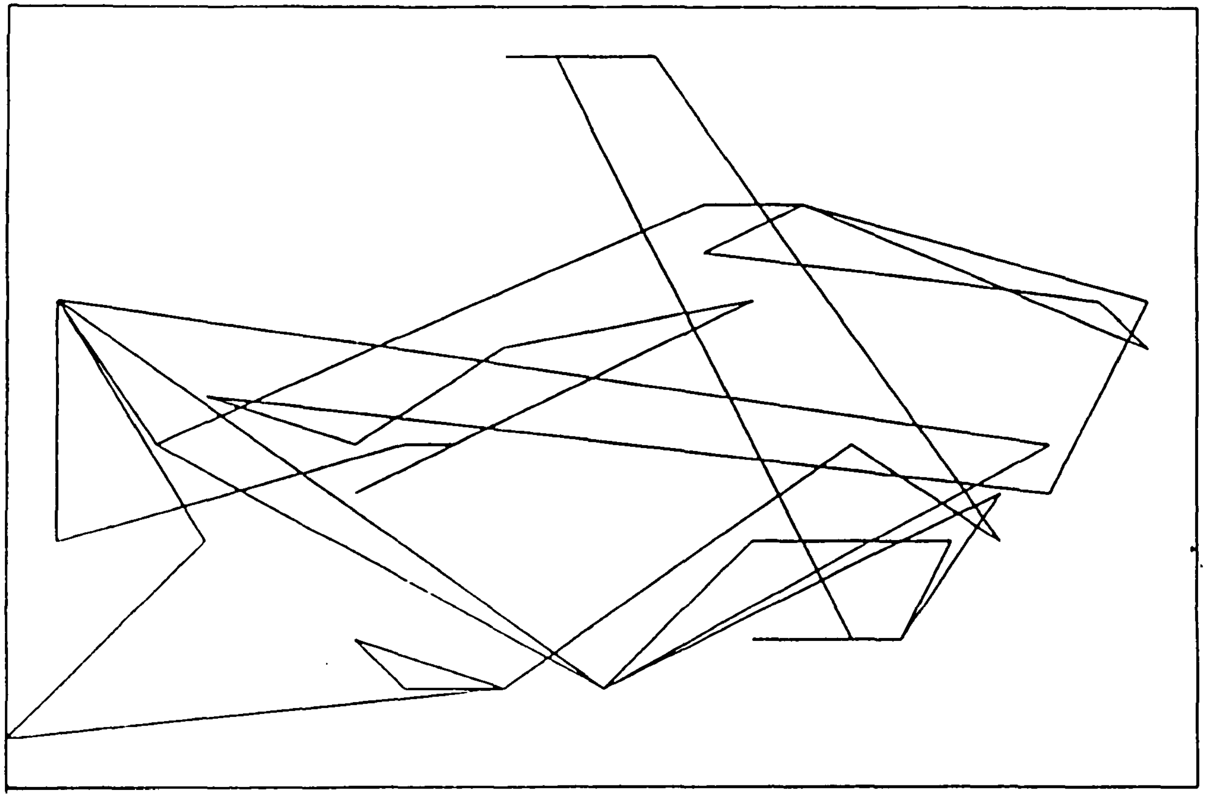

Figure 6-3: The straight-line movements of white-lip herd A as determined from consecutive radio-telemetry locations.

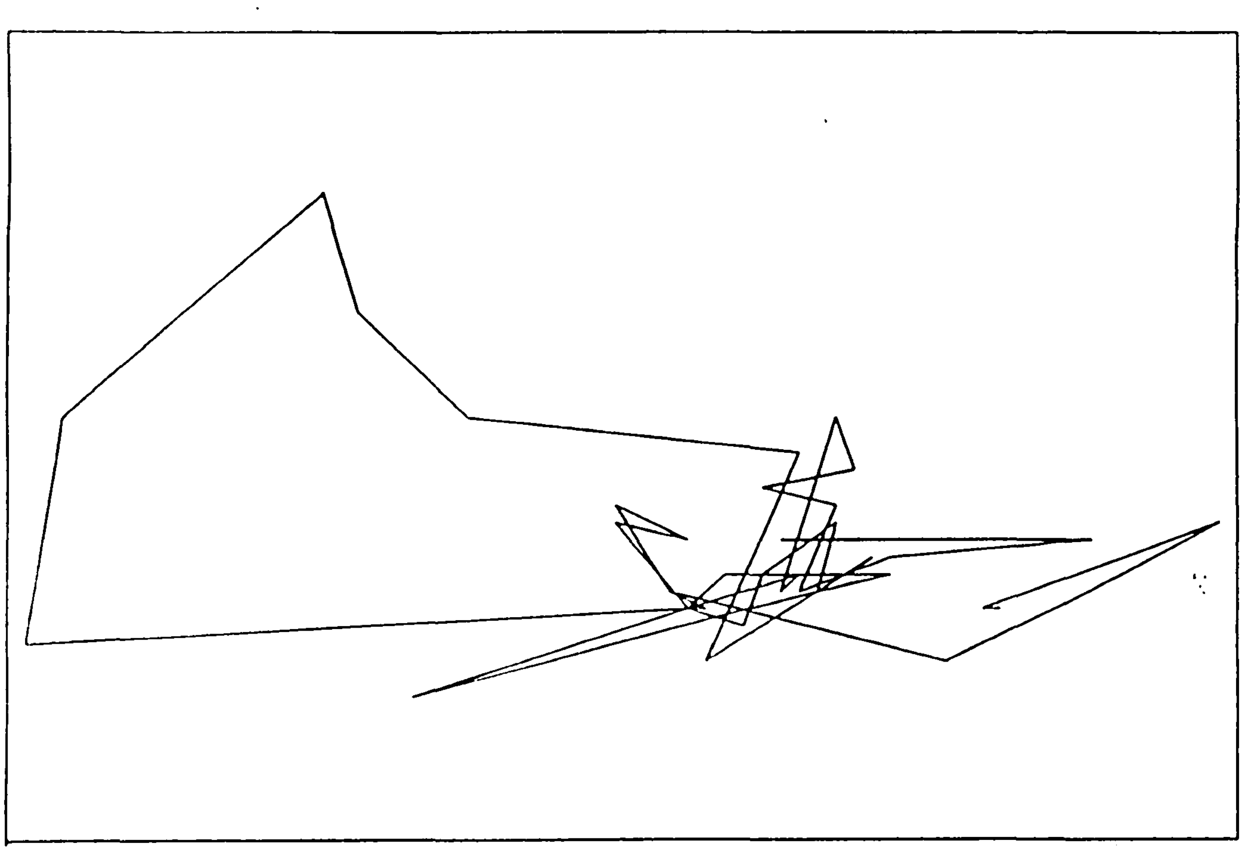

Figure 6-4: The straight-line movements of white-lip herd B as determined from consecutive radio-telemtry locations.

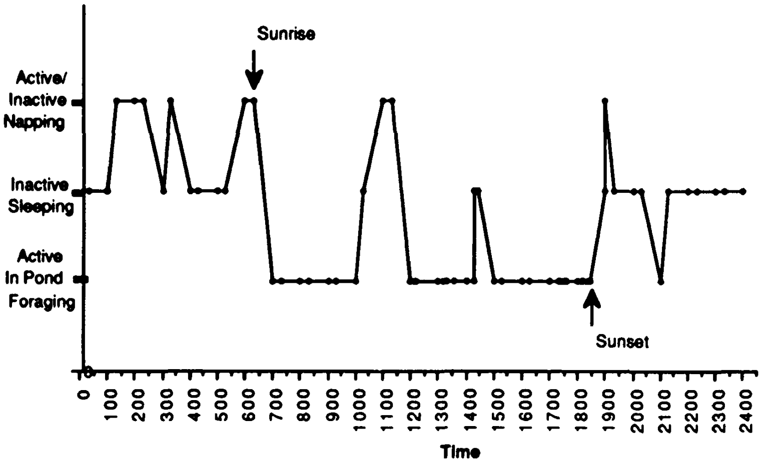

Fig. 6-5: The activity cycle for White-lip herd A over 24 hours from Febuary 14 to 15, based on simultaneous visual and telemetry observations during daylight and radio signals at night.

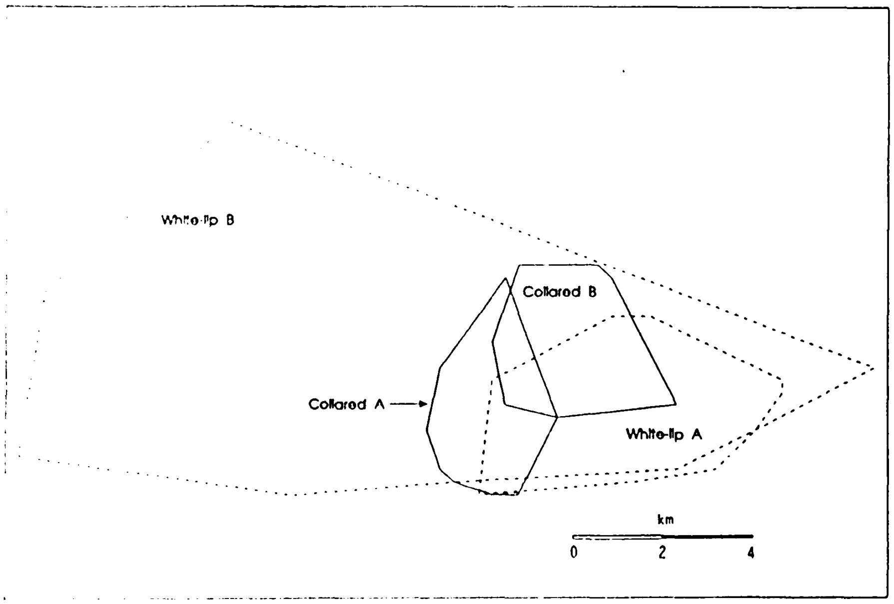

Figure 6-6: The spatial extent and relationship of two white-lipped and two collared peccary herd home ranges.

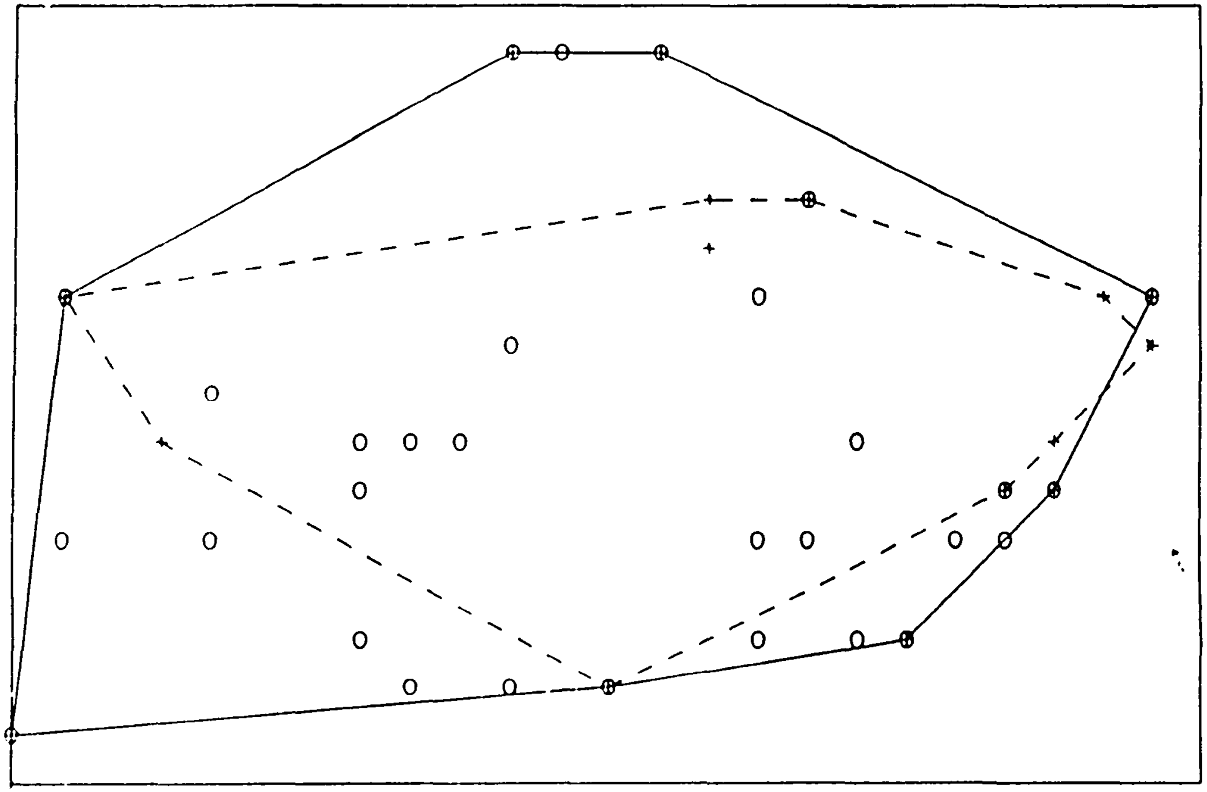

Figure 6-7: The dry (+) and wet (o) season locations for white-lip herd A and the extent of the dry (---) and wet season (__) home range.

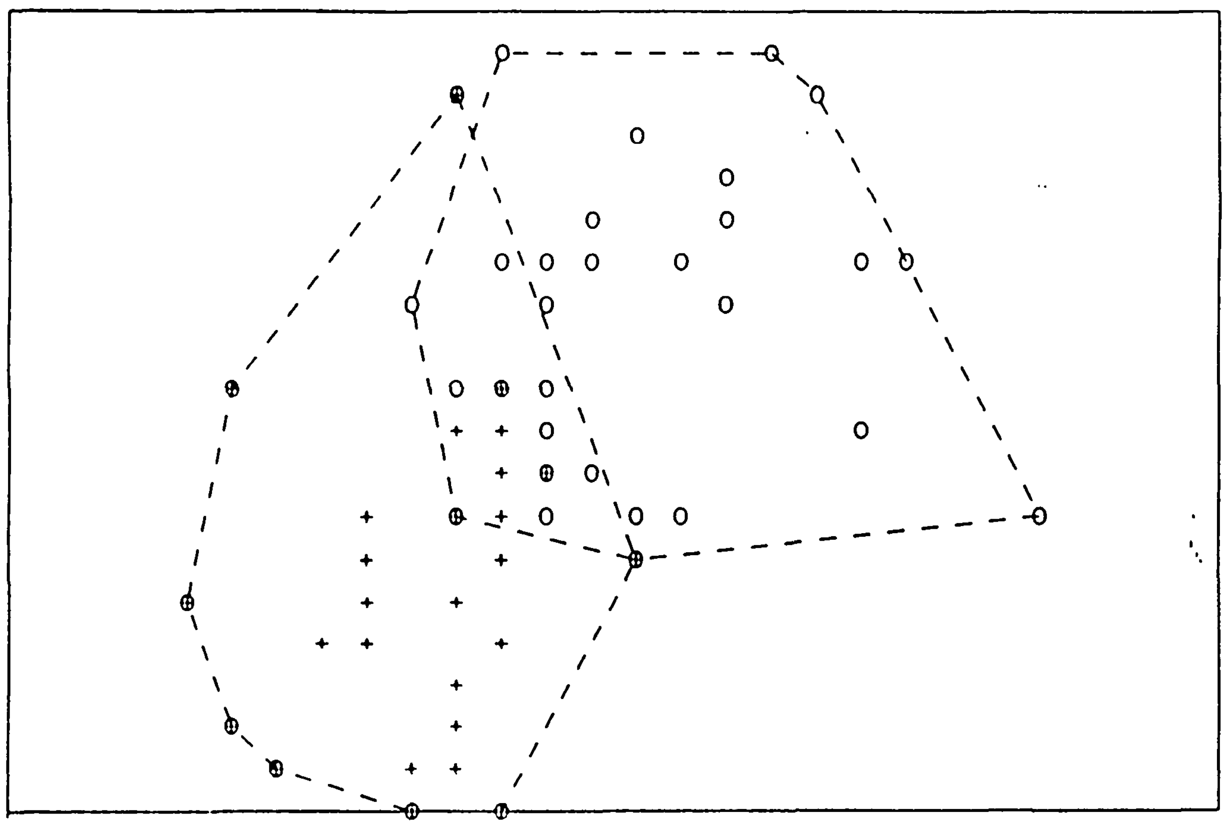

Figure 6-8: The locations and home range overlap for collared peccary herds A (+) and B (o).

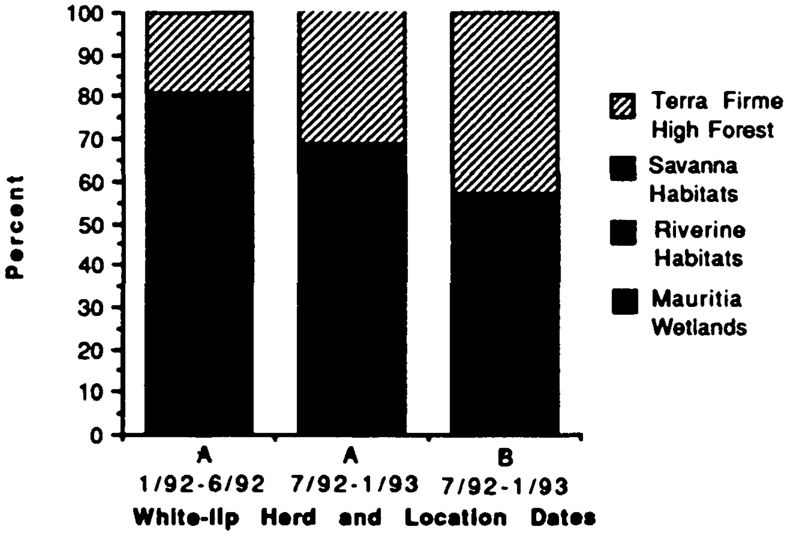

Figure 6-9. The percentage of radio-telemetry locations for white-lip herds A and B in four habitats and from January to June 1992 (dry season), and July 1992 to January 1993 (wet season) for herd A.

CHAPTER 7
CONCLUSIONS

White-lipped peccaries were a striking element in the forest dynamics of Maraca during this study. They directly destroyed seeds and seedlings, and both directly and indirectly appear to be affecting the evolution of seed traits. The soil in areas of tens of square meters of forest where the animals had been foraging for a few days was completely turned over and bereft of seedlings, in stark contrast to the surrounding carpets of seeds and seedlings. These are the same types of impacts that need to be considered when interpreting data from study sites where recently common and widespread megafauna are missing. At the same time, the white-lip population on Maraca was at an extreme low during this study, apparently recovering from a drastic and sudden decline that occurred during 1989. The ranging behavior, herd size, herd density and consequent impact of white-lips on palm regeneration at a population high may be qualitatively or quantitatively different, or both, from those observations presented here.

This study uncovered important differences between sympatric populations of collared and white-lipped peccaries in behavior, social structure, habitat preferences, food habits and perhaps the resolution at which they separate their landscapes. White-lips range over much larger areas and these herds have overlapping home ranges. In contrast, collared peccaries can be territorial, and even when herds are similar in size to those of white-lips, white-lip home ranges are still much larger. While there is overlap in the diet of the two peccary species, white-lips but not collareds prey on seeds of common Amazonian palms such as *Maximiliana maripa* and *Mauritia flexuosa*. However, both species appear to thin seedlings around parents.

Just as peccaries were key seed predators, another remnant member of the megafauna, the tapir, was a key seed disperser. Frugivorous species varied qualitatively and quantitatively in their role as seed dispersers. Almost all *Maximiliana* seeds spat out by medium to small-bodied terrestrial frugivores remained below the crowns of parent trees. This occurred even though rodents, collared peccaries and monkeys ate the pulp from large numbers of fruit and spat out the seeds intact. These short-distance dispersers left the seeds beneath the crowns of parent trees, where they were subject to high mortality from beetle larvae infestation, and where they would later be susceptible to beetle larvae and white-lipped peccaries. Tapirs, in contrast, removed large numbers of *Maximiliana* seeds away from the parent plant and clump. These results indicate that on Maraca, the relationship between non-tapir frugivores and *Maximiliana* provides less benefit to the plant in terms of numbers of seeds moved away from high mortality sites. Tapir seed dispersal resulted in a clumping of seeds and the initiation of new seed-seed consumer interactions away from the parent plant.

Tapir seed dispersal also led to higher seed escape from beetle larvae at tapir latrines, secondary dispersal from latrines to non-latrine trees by rodents, and lower level of predation at tauri-latrines than at parent trees. In addition, tapirs created unexpected seed shadows, one where the parent was no longer the focus of the shadow.

The result of tapir dispersal and predator foraging patterns was a lowering of recruitment near adults. The Maximiliana age data clearly show that for all age classes densities were much higher at latrine than parent trees. They also show that for three age classes densities were higher at random sites than by parent trees. Seeds under parent trees are undispersed seeds, or seeds moved short distances by rodents or spat out by ungulates. Seeds under control trees presumably were moved there by rodents, especially scatter-hoarding agoutis. In many cases tapir latrines were the closest seed source, so that rodent dispersal probably represents secondary dispersal of seeds already moved by tapirs.

Although these results support the Janzen-Connell model, in the sense that seedling mortality is highest near parent trees due to the activities of seed and seedling specific predators, they also show that recruitment patterns are more complex than those described by the model. Seedling recruitment was lowest near parent trees, but neither seed nor seedling mortality was complete. In addition, high survivorship at non-palm sites conflicts with the prediction of the Janzen-Connell hypothesis in that the pattern of mortality near parent trees increases tree diversity through an increase in spacing. Seed dispersal by tapirs created new high-density clumps of seedlings and saplings and reduced space for other species.

Thus, the scale at which one measures diversity plays a critical role in understanding the dynamics that affect diversity. For plants whose seeds are dispersed or destroyed by terrestrial frugivores such as tapirs and white-lipped peccaries, scale-dependent phenomena may be more apparent in forests sustaining large vertebrate frugivores and seed predators.

The above interaction appears to create lumpiness in the distribution of seedling and adult densities (*sensu* Holling 1992). There is a characteristic distribution of seedling densities, that may be related to the body (e.g., stomach) size of the dispersers. Using the framework developed by Holling (1992), I describe a process by which variable density *M. maripa* clumps are created. A key player in this process is the tapir who initiates clumps by defecating seeds at specific sites. However, when a tapir dies the rain of tapir-dispersed seeds to some latrines may end. A new resident tapir may begin the cycle anew by defecating around the base of previously unused tauris (tapir latrines in terra firme forests), creating new high density aggregations of *M.*

maripa. Eventually the tauri dies and tapirs no longer have the tree to defecate around. However, the seedlings and saplings at the site will grow into adults and eventually form new clumps or perhaps the tauri may have already been in the midst of an adult clump when it died.

High density adult clumps may also originate from parent sites, but this is less likely because they generally hold only low density lumps of older saplings. More likely these sites eventually disappear as the adults die or they support single adults or low density clumps, because adult aggregations attract seed and seedling predators, that reduce recruitment rates into adult age classes. Hence succession at this site results in a mixed forest with perhaps one, a few or no M. maripa adults. Current adult dispersion patterns may thus be the result of past interactions that we no longer see, either recent or less recent extinction, given the longevity of palms and other rainforest trees.

At a smaller scale, seed predators and dispersers can also affect seed characteristics. For example, I found that all predators in the study area attacked all palm seeds regardless of physical differences; however, seeds that lost all endosperms differed in their physical characteristics from those in which at least one endosperm survived. White-lips killed all endosperms in two and three endosperm seeds, because they could easily crush the thin endocarps. A seed population responding only to the selective pressure exerted by white-lips should be dominated by thick-endocarp single endosperm seeds. On the other hand, the direction of selection exerted by beetle larvae and rodents is towards multi-endosperm seeds, regardless of endocarp thickness, because they kill all single endosperm seeds they penetrate. Therefore if seed traits were a response to predation by beetle larvae or rodents the population should be dominated by two or three endosperm seeds. The Maraca Island _Maximiliana_ seed population as a whole was dominated by single endosperm seeds, suggesting that past selective pressures favored the development of single over multi-endosperm seeds, and therefore that white-lips, or white-lip-like seed predators may have been the dominant force influencing seed traits.

The ecology of each species of seed predator influences the selective pressure it exerts on plants. White-lips move through forests as units of tens to hundreds of individuals, they have overlapping home ranges, each of which can be tens to hundreds of square kilometers. One herd's home range would encompass many clumps of _Maximiliana_. The large numbers of individuals per herd and the many clumps of _Maximiliana_ per home range would result in white-lips spending little time within a clump before moving on. In contrast, agoutis are territorial and tend to locate their territories in and around rich food sources. This is probably true of many other rodents as well. An agouti's home range may be smaller than a single _Maximiliana_ clump. These animals visit trees within their clump on a daily if not hourly basis in search of fruits and seeds. During peak fruit-fall within a clump these animals would be overwhelmed by fruit availability, because each tree drops hundreds to thousands of fruits. Thus many seeds would escape predation by territorial as well as smaller non-territorial rodents, which cannot reproduce quickly enough to take advantage of the crop, and cannot aggregate to any great degree because of their solitary-territorial social structure.

On the other hand, although beetle larvae can take advantage of large seed crops due to their high reproductive rates and population densities, their impact on seed traits is probably reduced by predation by white-lips. My experimental data with a caged white-lip indicates that beetle larvae are readily eaten by white-lips. For a larva to escape consumption by white-lips it would have to inhabit a seed unbreakable by white-lips (i.e., single endosperm seeds with thick endocarps). Therefore, even if multi-endosperm seeds are more likely to survive a beetle attack, these are the seeds most likely to be eaten by white-lips, and a white-lip will eat larvae within seeds. This reasoning suggests that most larvae that survive to adulthood do so in single endosperm seeds with thick endocarps. The interaction between these two species of seed predators can alter the selective outcome of predation. White-lips provide additive selective pressure for thick, single endosperm seeds through their consumption of larvae, not only by effectively neutralizing the effect of larvae, but also by exerting selective pressure on beetles to oviposit on the thick endocarp, single endosperm seeds that are most likely to escape consumption by white-lips. White-lips and beetles then both exert selection in the same direction.

My hypotheses suggest that large-seeded trees should exhibit a mixed evolutionary strategy. Most trees should respond to white-lips, but some should also respond to beetle larvae or rodents. The mixed strategy would be stable, because complete synchrony could result in high mortality by peccaries, while complete asynchrony could result in high mortality by rodents. A population composed solely of single endosperm seeds could also be destroyed by rodents and larvae, while one containing only multiple endosperm seeds would be destroyed by peccaries. This mixed strategy is even more critical when we consider that white-lip, rodent and beetle populations may fluctuate asynchronously in size over time. Given the variation in seed traits already present in the population, the response to a change in selection direction could occur quickly.

When possible studies of ecological interactions in tropical forests should be conducted in the most intact communities available, otherwise we risk building theory and concepts from biological artifacts resulting from habitat fragmentation and disturbance.

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BIOGRAPHICAL SKETCH

Jose Manuel Vieira Fragoso was born to fisherfolk on the island of Sao Miguel, Azores, 900 miles from northern Africa and southern Europe, near the middle of the Atlantic Ocean. As a child he frequented the tidal pools along the coast of this remote, volcanic island. The beauty of the tidal inhabitants and the ruggedness of the coast sparked a lifelong interest in nature and wilderness. At the age of six, he moved with his family to downtown Toronto, Canada. For the longest time he thought Canada consisted of concrete sidewalks, tall buildings and people. Eventually, he discovered the great Canadian wilderness and spent years exploring it by canoe and on foot. A scuba diving trip to Jamaica led to the personal discovery of the tropical forests of Belize, Central America, and then to the ultimate challenge of the Amazon. He remains trapped by the allure of tropical wilderness and will probably remain penniless, parasite-ridden and unrecognized for the remainder of his very happy jungle life.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Eisenberg

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