

POPULATION REGULATION OF A DOMINANT RAIN FOREST TREE BY A MAJOR SEED PREDATOR

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Abstract. We take advantage of a fortuitous local extinction and recolonization of white-lipped peccaries (WLPs) at the Cocha Cashu Biological Station in southeastern Peru to assess the impact of this high-biomass seed predator on the recruitment of a dominant member of the tree community, the palm *Astrocaryum murumuru*. WLPs were common at Cocha Cashu in the mid-1970s. In 1978, the species vanished from the entire region and did not reappear until 1990. To assess the impacts of the presence–absence of WLPs on *Astrocaryum* recruitment, we conducted transect counts of both the number and spatial distribution of palm seedlings in 1978 (when WLPs were present), in 1990 (after a 12-yr absence of WLPs), and in 1999 (after 10 yr of recovery). Other factors affecting recruitment, such as climate variability, differences in tree fecundity, and fluctuations of vertebrate and invertebrate seed predators were also examined as alternative hypotheses for any changes in seedling spatial distribution and abundance.

In the absence of WLPs, the density of *Astrocaryum* seedlings increased 1.7-fold, and the spatial distribution of seedlings with respect to safe sites was significantly altered. After the return of WLPs to the study area, seedling density dropped to its former level, and the spatial distribution of seedlings with respect to safe sites returned to the same pattern found 21 yr earlier in 1978. None of the other factors investigated varied systematically with the census intervals. These results demonstrate that the absence of a single, albeit important, member of a diverse seed predator guild can have a major impact on the demography of a common tree species. We infer that individual seed predators can play central roles in regulating the demography of tropical trees, as envisioned many years ago by Janzen and Connell, and that their extirpation or extinction can have cascading effects in tropical ecosystems.

Key words: *Astrocaryum murumuru*; Cocha Cashu, Peru; ecosystem experiment; El Niño; extinction; keystone; population regulation; regeneration; seed predation; *Tayassu pecari*; trophic cascade; tropical rain forest.

INTRODUCTION

The role of seed predators in regulating the densities of tropical forest trees is largely known from microcosm studies, even though the process of interest (tree recruitment) can vary over large spatial and temporal scales. Cages designed to exclude seed predators markedly enhance seed survivorship to germination, but cages provide little information on the roles played by individual seed predator species because they indiscriminately exclude much or all of that guild (Terborgh et al. 1993, Silman 1996, Asquith et al. 1997). Numerous studies have documented density- and distance-dependent seed predation around focal trees, but the population-level significance of such measurements has been elusive (Janzen 1972, Clark and Clark 1984, Howe and Schupp 1985, Terborgh et al. 1993, Cintra 1997a). The intensity of seed predation has been shown to vary among islands harboring differing numbers of

mammal species (Asquith et al. 1997), and the pattern of seedling recruitment has been shown to differ dramatically between a “defaunated” site in Mexico and one possessing a complete mammal fauna (Dirzo and Miranda 1991). Although such studies demonstrate that seed predators impact their resources in a general way, the roles of individual mammal species have only rarely been distinguished (e.g., Fragoso 1997a, Asquith et al. 1999, Wright et al. 2000). Additionally, these studies are rarely carried out over large (>1 ha) areas or long time scales, making inferences to effects on natural recruitment difficult. Consequently, these studies fail to provide a clear picture of mammalian impacts on natural populations of trees, or to suggest the effects of local depletion of mammals by hunting on the structure of tropical tree communities (Roldan and Simo-netti 2001).

Here we report on the local extinction and recolonization of the white-lipped peccary (WLP; *Tayassu pecari*), the highest biomass component of Neotropical seed predator communities, over a country-sized region of western Amazonia. We examine its impact on both

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the amount and spatial pattern of recruitment of the palm *Astrocaryum murumuru*, a numerical dominant in the forests of western Amazonia and a keystone resource for mammalian frugivores. The widespread extinction and recolonization event was found to regulate both the number and spatial distribution of *Astrocaryum* seedlings, with patterns changing markedly during the local extinction event and reverting back to the pre-extinction pattern after recolonization. These patterns were not consistent with alternative hypotheses regarding climatic effects, variable recruitment, or population fluctuations of other seed predators.

METHODS

Study system

Astrocaryum murumuru is a dominant tree in western Amazonian rain forest, and a keystone resource for frugivores in these communities (Terborgh 1986, Henderson et al. 1995, Pitman et al. 2001). It is the second most abundant tree species in the Rio Manu floodplain, occurring at densities of ~30 adults/ha (Kiltie 1981a, Terborgh et al. 1996), and is distributed over broad areas of Amazonia at relatively constant densities (Henderson et al. 1995, Pitman et al. 2001). Vertebrate and invertebrate seed predation on *Astrocaryum* is intense, with survival rates of seeds placed in the forest being 0–2%. In contrast, survival rates of *Astrocaryum* seedlings are high, with established (>1-yr-old) seedlings having rates estimated between 69% and 100% survival (Silman 1996, Cintra 1997a, b, Cintra and Horna 1997; M. R. Silman, unpublished data). WLPs are dedicated seed predators, and seeds of *Astrocaryum murumuru* and *Iriartea deltoidea*, another abundant upper-Amazonian canopy palm, are its preferred food resources (61% of stomach contents at site; see Kiltie [1981b] and Kiltie and Terborgh [1983] for detailed observations on diet and foraging at the site, and Bodmer [1991a, b] for diet information in other areas). Traveling in large herds (>100 individuals; Kiltie and Terborgh 1983, Fragoso 1998; M. R. Silman, personal observation), WLPs forage by “bulldozing” leaf litter and are able to substantially reduce the densities of seeds on the forest floor (Kiltie 1981a, Kiltie and Terborgh 1983).

Peccary densities

We compared recruitment of *Astrocaryum murumuru* in the presence and absence of WLP herds by virtue of a fortuitous natural experiment. WLPs were common in the 1970s at the study site, the Cocha Cashu Biological Station in southeastern Peru (11°51' S, 71°19' W). At that time, WLPs contributed 21% of the aggregate biomass of terrestrial granivorous mammals at Cocha Cashu (Terborgh 1983). In 1978, WLP herds appeared within the 2-km² study area weekly during the dry season, and once every 10–14 d in the wet season (Kiltie and Terborgh 1983). Minimum counts

of the number of animals in a herd ranged from 90 to 138. WLPs disappeared from the study area abruptly in 1978, and no herds were seen until 1990, except for isolated sightings of small herds (<50 animals) in 1980 and 1985. We do not know why the species disappeared, although epidemic disease seems the most likely explanation (Emmons 1987, Fragoso 1997b, 1998).

Interviews by Silman with native and colonist communities throughout the Peruvian department of Madre de Dios in the period 1990–1999 indicate that the WLP disappeared from at least 71 000 km² in southeastern Peru, an area greater than that of Costa Rica. This is probably an underestimate, as there is a substantial amount of land where there are no contacted natives, and hence information is unavailable. Herds did not appear again within the study area until 1990, a lapse of 12 yr. Yearly observations by Silman and Terborgh show that WLP numbers built rapidly to former levels, and presently exceed them, with herds of >100 WLPs being on the study area continuously.

Astrocaryum recruitment

In 1978, Kiltie (1981a) censused *Astrocaryum murumuru* seedlings (bifid-leaved, <40 cm tall) along a 2 m wide by 2 km long transect through the central study area at Cocha Cashu. For each *Astrocaryum* seedling encountered, Kiltie recorded the distance to objects ≥ 5 cm in diameter (lianas, roots, fallen trunks) and placed these into six distance classes (0–9, 10–19, 20–29, 30–39, 40–49, ≥ 50 cm). Such objects are used by scatter-hoarding rodents to hide seeds for later consumption, and constitute safe sites from predation by WLPs (sensu Harper et al. 1961, Kiltie 1981a, Forget 1991, 1996). The transect design integrates over large spatial areas and affords good resolution for spatial distributions (Krebs 1999). Growth in *Astrocaryum* seedlings is slow, with seedlings taking at least two and up to six years to reach 20 cm. Long-term measurements at the site show 6-yr-old-*Astrocaryum* seedlings to range from 22 cm to 42 cm tall, depending on light conditions (M. R. Silman, unpublished data). Given their high survival rate and slow growth, the seedlings measured at any census period in the study represent multiple cohorts and integrate patterns found over several years, with larger seedlings being older, on average. Survival rates measured at the site by Cintra (1997a, b) and Silman (1996) suggest that up to 35% of *Astrocaryum* seedlings surviving their first year may survive 10 yr.

We assessed the impact of WLPs on *Astrocaryum* establishment by repeating Kiltie's (1981a) methods within three months of the reappearance of WLPs on the study site in 1990, and then again after a decade of WLP habitation in 1999. The study was performed on the same transect in 1990 and 1999, and in the same area of the forest as Kiltie's 1978 census, although on a slightly different set of trails, because use has

TABLE 1. Seedling counts of the palm *Astrocaryum murumuru* along the 2 × 2000 m transect at the Cocha Cashu Biological Station, Peru, and 95% confidence intervals using Poisson (top) and negative binomial (bottom) distributions.

Distribution and year	Lower 95% CL	Count	Upper 95% CL
Poisson			
1978	103	124	148
1990	182	210	240
1999	126	149	172
Negative binomial†			
1978	95	124	156
1990	171	210	251
1999	117	149	184

† $\sigma^2/\mu = 2$ (observed).

changed over the years. All censuses were performed in the late dry season.

Based on their sheer biomass and observations of WLP behavior at the site, we hypothesized that absence of WLPs would cause an increase in seedling number and a shift in spatial distribution of seedling establishment away from sites shown to be safe from WLP foraging. In the presence of WLPs, we expected *Astrocaryum* seedling numbers to decrease, and spatial distribution to be biased toward safe sites.

Alternative hypotheses

Other factors, such as differences in climate, particularly the El Niño Southern Oscillation (ENSO) cycle, and its effects on *Astrocaryum* reproductive effort between years (e.g., Wright et al. 1999), or variation in other seed predators such as bruchid or scolytid beetles (Janzen 1971a, b, Wright 1990) and rodents (e.g., Forget 1991) could cause changes in seedling abundances and perhaps spatial pattern as well. If such changes are confounded with those of the WLPs, they provide alternative explanations for the patterns observed. In order to test for these alternatives, and to separate WLP effects from other potential effects, we used data from the site to see if the intercensus intervals or census years differed from each other in any of these respects. When data from the site were not available, we used data and observations from the literature.

ANALYSES

Spatial distribution

To test whether WLPs influence the spatial distribution of safe sites for *Astrocaryum* regeneration, we compared the spatial distribution of *Astrocaryum* seedlings found in the presence of WLPs in 1978 with those found after 12 yr of absence (1990) and again after a decade of their presence (1999). Also, to control for possible differences among years in the distribution of “objects” on the forest floor, a null model was generated by randomly locating 200 points along the transect at random distances from the trail and measuring

the distance of these points to cover objects as was done for the seedlings. This was performed in both 1990 and 1999. Frequencies from the null models were used to test for deviations from “random” dispersal of seedlings with respect to safe sites. It is important to note that the distribution of seedlings in all cases is determined by both primary and secondary dispersal and subsequent seed predation (e.g., Forget 1996, Brewer and Webb 2001); a “random” result simply implies that seeds are dispersed to, and survive in, sites that do not correspond with large, protective cover objects.

Seedling counts

Differences in total number of seedlings among censuses were tested by modeling the data as counts, using both Poisson and a negative binomial model. The negative binomial model accounts for clumping in seedling spatial distributions, allowing appropriate confidence intervals to be drawn for the counts. The mean and variance from 100-m subsets of the transect were used to parameterize the negative binomial distribution for seedling counts. The variance to mean ratio in all censuses was indistinguishable from two (2.03, 2.02, and 1.98 in the respective censuses). To be conservative, we also turned the question around and asked how large the variance to mean ratio needed to be to make the differences among years nonsignificant at the $P < 0.05$ level.

RESULTS

Seedling counts

The number of seedlings found along the transect was significantly higher in 1990 than in either 1978 or 1999 (Tables 1 and 2). Between 1978 and 1990, seedling numbers increased by 70%, and between 1990 and 1999, seedling numbers fell 71%. Seedling counts in 1978 were indistinguishable from those in 1999 (Table 2).

Spatial distribution: differences among years

The spatial distribution of *Astrocaryum* seedlings was markedly different among years ($\chi^2_{10} = 56.44$, $P = 1.7 \times 10^{-8}$; Fig. 1), with more seedlings establishing near cover objects when WLPs were present at the

TABLE 2. Hypothesis tests of no difference in palm seedling counts at the Cocha Cashu transect between years based on a negative binomial distribution with $\sigma^2/\mu = 2$.

Test	Probability†	Required σ^2/μ ‡
1990 vs. 1999	6.1×10^{-4}	8
1990 vs. 1978	1.1×10^{-6}	15
1978 vs. 1999	0.064	

† The probability that the 1990 count equals the 1999 count ($\Pr(\mu_{1990} \leq 149)$), etc.

‡ The variance to mean ratio required to generate a negative binomial distribution where the counts between years were not significantly different ($P < 0.05$).

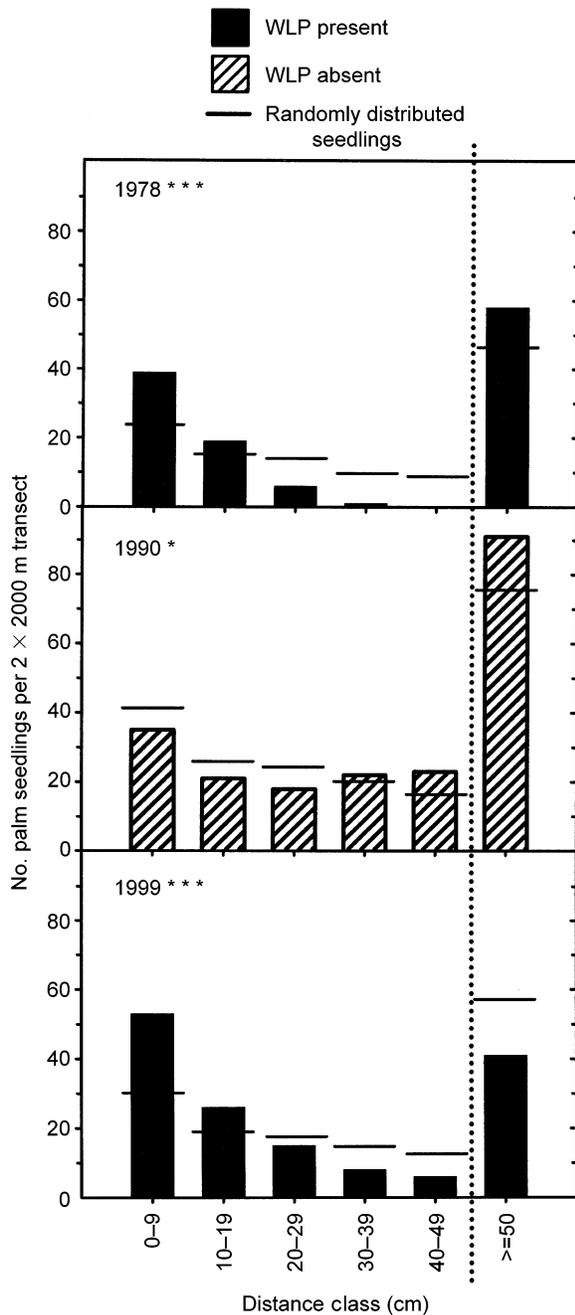


FIG. 1. Palm (*Astrocaryum murumuru*) seedling counts vs. distance from cover objects along the transect in the presence (1978, 1999) and absence (1990) of white-lipped peccaries (WLP). Yearly comparisons are among panels. Horizontal lines indicate frequencies expected from random seedling distribution at each census. Asterisks indicate significant departure of counts from random expectations in that year. The dashed line denotes the fact that the ≥ 50 cm class covers 15 times the area of any of the other classes (51–200 cm vs. 10 cm for all other classes).

* $P < 0.05$; *** $P < 0.001$.

study site, and an excess of seedlings establishing away from cover objects when peccaries were absent. Pairwise comparisons among years show that all years were significantly different from each other (1978 vs. 1990, $\chi^2_3 = 35.49$, $P = 1.2 \times 10^{-6}$; 1999 vs. 1990, $\chi^2_3 = 30.59$, $P = 1.1 \times 10^{-5}$; 1978 vs. 1999, $\chi^2_3 = 18.70$, $P = 0.002$). However, the difference between the two years when peccaries were present (1978 and 1999) was predominantly due to differences in the number of seedlings in the ≥ 50 cm distance class, which has more than five times the area of the other distance classes (51 cm to >100 cm). Excluding the ≥ 50 cm class caused the difference in spatial pattern between 1978 and 1999 to disappear ($\chi^2_4 = 8.21$, $P = 0.08$).

Because of the extreme shade tolerance and slow growth rates of *Astrocaryum* seedlings, the 1999 census probably included individuals that established while WLPs were absent from the area, or in the early 1990s when WLP numbers were recovering. In order to control for this, we analyzed seedlings ≤ 20 cm tall in 1999. This increased the similarity to the pattern found in 1978 ($\chi^2_3 = 14.59$, $P = 0.01$). Again, the distributions were indistinguishable when the ≥ 50 cm distance class was excluded (1978 vs. 1999, with ≤ 20 cm seedlings and excluding the ≥ 50 cm distance class, $\chi^2_4 = 5.16$, $P = 0.27$).

Spatial distribution: safe sites

Comparisons of *Astrocaryum* seedling distributions with the null model of random establishment with respect to safe sites showed highly nonrandom distributions in 1978 and 1999 (1978 $\chi^2_4 = 40.1$, $P = 1.4 \times 10^{-7}$; 1999 $\chi^2_4 = 29.5$, $P = 1.8 \times 10^{-5}$; Fig. 1), with deficits of seedlings occurring away from cover objects and the pattern of deviation being nearly identical (Table 3). The distribution of *Astrocaryum* seedlings in the absence of WLPs (1990 census) was nearly random with respect to safe sites, even though the chance of detecting differences from the null model was highest in this year because of the larger sample sizes ($\chi^2_4 = 11.3$, $P = 0.04$). Deviations of seedling counts in 1990 from the null model are in the opposite direction from those of 1978 and 1999 (Table 3). Again, differences between 1978 and 1999 lay in the ≥ 50 cm distance class, and removal of only two seedlings from this class

TABLE 3. Deviations of numbers of palm seedlings in each distance class from the null model of random dispersal in goodness-of-fit tests. Signs indicate the direction of deviation.

Distance class (cm)	1978	1990	1999
0–9	+	–	+
10–19	+	–	+
20–29	–	–	–
30–39	–	+	–
40–49	–	+	–
≥ 50	+	+	–

makes the difference nonsignificant at the $P < 0.05$ level.

DISCUSSION

White-lipped peccaries apparently had large impacts on both the quantity and spatial distribution of recruitment of the palm *Astrocaryum murumuru*, a dominant tree and keystone resource in the forests of southeastern Peru. After the disappearance of WLPs, the density of *Astrocaryum* seedlings increased 1.7-fold. In 1999, 10 yr after the reappearance of WLPs on the study site, counts of *Astrocaryum* seedlings had fallen 71% and were indistinguishable from counts taken in 1978. The spatial pattern of palm regeneration also changed markedly with the abundance of WLPs, with regeneration of seedlings in the presence of WLPs being concentrated near cover objects, and becoming essentially random in their absence. After the return of the WLPs, the pattern changed significantly from that found in their absence, and, importantly, returned nearly exactly to that found 20 yr earlier when WLPs were present.

These results are consistent with the hypothesized effects of WLPs, and, in the absence of confounding changes in either climate or other seed predators, support a causal interpretation. That both the spatial pattern and the number of regenerating *Astrocaryum* seedlings could change so markedly with the disappearance of WLPs and then revert to both the earlier abundance and pattern of spatial distribution, in the absence of confounding factors, exposes a major control of this seed predator on *Astrocaryum* reproduction. We suggest that the abundance of *Astrocaryum* is regulated through a dynamic interaction involving populations of seed predators, as long ago envisioned by Janzen (1970) and Connell (1971). In such a case, *Astrocaryum* densities would be determined primarily by biotic interactions, not simply stochastic drift (Hubbell 1979, 2001, Bell 2001).

Alternative hypotheses

Although unplanned natural experiments often afford the only insight into large-scale ecological patterns (Carpenter 1990), causal inference requires examination of alternative explanations (e.g., Beyers 1998, Carpenter et al. 1998). In order to exclude alternative explanations, we looked at climate, and its effects on tree reproduction (Wright et al. 1999), and at the abundances of other seed predators on *Astrocaryum*, particularly rodents and beetles.

Climate.—To examine the effects of climate, we asked the following questions. (1) What are the effects of ENSO on the southwestern Amazon basin? (2) Were there any differences between the actual censuses dates and intercensus intervals in ENSO dynamics? Although the El Niño/La Niña cycle has a strong effect on precipitation (and plant reproduction; see Wright et al. [1999]) in Central America, Northern South America, and northeastern Brazil, its effects on the southwestern

Amazon basin are small (Marengo et al. 1993, Marengo and Hastenrath 1993, Pezzi and Cavalcanti 2001, Coehlo et al. 2002). In particular, southeastern Peru is affected minimally, being just south of the transition node from the wetter than normal conditions of northern South America and the drier than normal conditions of Bolivia and southwestern Brazil (Marengo 1992, Pezzi and Cavalcanti 2001, Coehlo et al. 2002). Evidence of the lack of strong effect on fruit production in southeastern Peru is also shown by the lack of any record of mass frugivore mortality at Cocha Cashu Biological Station for the period 1974 to the present, in contrast with that found by Wright et al. (1999) on Barro Colorado Island, Panama.

Climatic conditions at the time of the censuses and during the intercensus intervals showed few differences. None of the censuses was performed during a strong El Niño/La Niña event (as defined by Wright et al. [1999]). In terms of the prevailing temperature anomaly, the 1978 and 1990 censuses were conducted during periods of neutral or slightly warm anomalies, preceded by the same. The 1999 census was conducted during a period of relatively cool surface waters, preceded by the same. That the 1999 census was most similar to 1978 in terms of seedling number and distribution, even though 1990 and 1978 were most similar climatically, bolsters the argument that the patterns are not climate driven.

The occurrence of El Niño events in the intercensus interval might be considered more important because seedlings have high survival rates and overlapping cohorts. High cohort variation could lead to “pulses” of seedlings; if these were to interact with other mortality agents in a distant-dependent manner that related to our definition of a safe site, it could influence the results. However, according to the Southern Oscillation Index, SOI (ABM 1999), and the analysis of Yue (2001), there were four El Niño cycles of comparable severity in the two intercensus intervals, and also during the decade preceding the start of the study in 1978.

In summary, climatic variation or extreme climatic events and their effects on tree reproduction are unlikely to have caused the observed patterns. Analysis shows that ENSO effects on the study area are weaker than those of other areas of the Neotropics, and that the ENSO dynamics over the duration of the study did not vary in a way that would confound the results of this study. Year-to-year variation in rainfall, although present at the site, is not likely to confound the results of this study because the standing seedling crop at any time is a mixture of cohorts varying broadly in age, and there is no evidence that the patterns of wet and dry years coincide in any way with the census intervals (Terborgh 1983; *unpublished climatic data* from Cocha Cashu Biological Station).

Seed predation

Variation in the densities of seed predators other than WLPs could also change seedling density and spatial

distribution. Here we look at variability in other vertebrate and invertebrate seed predators, particularly large spiny rats of the genus *Proechimys*, which are both secondary dispersers and seed predators, and bruchid and scolytid beetles. All are known to be important seed predators on *Astrocaryum* and other palms, both at the study site and elsewhere in the Neotropics.

Vertebrates.—If *Proechimys* abundance followed the same trends as WLP abundance, it would be difficult to ascribe the observed effects on spatial pattern and distribution solely to WLPs. We used rodent census data from Emmons (1984: Tables 2 and 5) available at the site for both visual transects (1978 vs. 1982) and trapping (1979 vs. 1982), to ask if vertebrate seed predator abundance varied at the site. The census interval is particularly fortuitous because it coincides with the disappearance of WLPs at the site. Census data for rodent seed predators showed no significant difference either in trap-based or visual-transect-based density estimates. For trap estimates, $N = 29$ *Proechimys* and 1507 trap-nights in 1979, and $N = 16$ *Proechimys* and 900 trap-nights in 1982 (Fisher's exact test two-tailed $P = 0.88$). For transect estimates, $N = 69$ *Proechimys* and $N = 82$ total rodents in 1978, and $N = 82$ *Proechimys* and $N = 87$ total rodents in 1982 (Fisher's exact test two-tailed $P = 0.65$). In general, although rodent densities are known to vary with time at other sites (e.g., Emmons 1984), they do not vary with anywhere near the magnitude of the WLP fluctuation reported here. Data for collared peccaries (*Tayassu tajacu*) are not available from the site, but any large-scale changes in this frequently encountered mammal would have been obvious to observers at the site.

Invertebrates.—Bruchid and scolytid beetles are important seed predators on palms (e.g., Janzen 1971a, b) and have been shown at Central American sites to undergo large fluctuations in abundance (Wright 1990). We tested for this by using estimates of invertebrate predation from 1989, when peccaries had been absent for 11 yr, and from 2001, when they had been back for 11 yr (Terborgh et al. 1993, Wyatt 2002). The percentage of *Astrocaryum* seeds failing to germinate in rodent exclusion cages (taken to be an estimate of invertebrate predation) was 75% at 5 m and 33% at 25 m from parent trees in 1989, giving a rough overall estimate of 54% predation by invertebrates. In 2001, a forest-wide census showed that 55% of *Astrocaryum* seeds were preyed upon by beetles (Wyatt 2002). The lack of variation found at Cocha Cashu in this study compared to that known from Central America, particularly Barro Colorado Island, Panama (Wright 1990) is probably due to two factors. First, at Barro Colorado Island, bruchid beetles have discrete generation on a single palm host that is alternate bearing, leading to fluctuations in resource abundance in time and space (Wright 1990, Delobel et al. 1995). At Cocha Cashu, bruchids have 2–8 host species that have asynchronous fruiting periods, leading to less fluctuation in resources,

with alternate host species always available. Second, the diversity of invertebrate seed predators in the Amazon is higher, with a broader range of hosts. This makes it likely that population fluctuations in a single invertebrate species or host tree will have less effect on the percentage of seeds preyed upon, and ensures that predator generations overlap (Delobel et al. 1995).

In summary, we found no evidence of variation in climate or seed predators that would account for the observed patterns of seedling abundance shifts, supporting the interpretation that WLPs alone are responsible for the observed shifts in *Astrocaryum* recruitment at the site.

Compensatory predation

The absence of WLPs caused recruitment fluctuations in *Astrocaryum* that were not related to climate or the recruitment of other, nonpreferred species in the forest (Kiltie 1981b). This lack of compensatory predation of *Astrocaryum* by other members of the seed predator community was probably due to predatory (top-down) control of smaller seed predators. In her study of feline diets, Emmons (1987) suggested that predation regulated the abundance of rodent seed predators at the study site, and predator removal experiments in other tropical systems have shown this regulation to be important (Terborgh et al. 2001). Invertebrate seed predators are susceptible to a host of parasitoids at the site, and their consistent numbers may also be due, in part, to top-down regulation, as well as having multiple host species (Delobel et al. 1995).

The relative meaning of safe sites

Results from this study show that the meaning of safe sites is relative. Kiltie (1981a) originally studied the spatial distribution of *Astrocaryum* seedlings to gain insight into the foraging habits of WLPs. Given the severe attenuation of *Astrocaryum* recruitment >20 cm from cover objects (Fig. 1), Kiltie concluded that peccaries foraged near cover objects because scatterhoarding rodents cached seeds there. In 1990, however, *Astrocaryum* recruitment was significantly higher in the >20 cm distance classes, and not significantly different from that expected if rodents cached seeds at random in the forest. This demonstrated that peccaries were causing the 1979 pattern by eating seeds cached away from objects, rather than responding to it. These results are consistent with the results of Forget (1991), who found that rodents cache seeds throughout the forest. Trampling and uprooting of seedlings by large herds searching through leaf litter may account for additional mortality, and probably would be biased away from cover objects.

The small differences detected between the numbers and distribution of *Astrocaryum* seedlings found 1978 and 1999 can be attributed to (1) confounding of the 1999 counts by seedlings established years earlier, when peccaries were absent; and (2) an excess of seed-

lings in the far (≥ 50 cm) distance class of Kiltie (1981a). As the far class contains a disproportionate number of seedlings, it is more sensitive to both real differences in the data and those caused by any differences in the methodologies employed in the two studies.

Conservation implications

Although WLP populations recovered in this area of western Amazonia, prospects for their continued survival in other areas are less sanguine. What little we know of WLPs suggest that they require large areas of intact habitat for survival. Home ranges at one site in eastern Amazonia encompass ~ 100 km², with animals requiring a mosaic of several habitat types (Fragoso 1998, 1999). In other areas of the Neotropics, WLP habitat requirements remain pure speculation. WLPs are quickly extirpated by even moderate hunting pressures (Peres 1996), and their reliance on large-scale habitat mosaics makes them particularly sensitive to anthropogenic fragmentation (Fragoso 1999). These findings indicate that WLPs, functionally extinct in Central America and disappearing from the Amazon Basin (Fragoso 1999), may only be maintained in large tracts of tropical wilderness. That they demonstrably limit the recruitment of one of the dominant Amazonian tree species and are known to be a principal predator of another (Kiltie 1981b) suggests that Amazonian forests may undergo revolutionary changes in species composition in their absence.

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