DO FRUGIVORES RESPOND TO FRUIT HARVEST? AN EXPERIMENTAL STUDY OF SHORT-TERM RESPONSES

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Abstract. Many nonexperimental studies have shown positive correlations between resource abundance and vertebrate abundance. These relationships, however, are difficult to interpret because of confounding factors that may independently determine the abundance of vertebrates and their resources. Moreover, verifying links between vertebrate and resource abundance is complex because human perception of resource abundance may differ from that of nonhuman vertebrates and because manipulating resource abundance on an ecologically meaningful scale is difficult.

We studied the dependency of frugivores on fruit abundance in eastern Amazonian floodplain forests dominated by one species of palm tree (*Euterpe oleracea*) from which people harvest fruit. We first compared spatial and temporal use by frugivorous parrots of four sites dominated by *E. oleracea* and four sites with no *E. oleracea*. Parrots spent 48–92% more time in the former, where their activity over the fruiting season mirrored the abundance of fruits. To test whether fruit abundance was the mechanism underlying these patterns, we removed fruit at two intensities in replicated 1.8-ha plots, and then monitored responses of frugivorous birds and mammals. High-intensity removal (75% of ripe fruit harvested) significantly reduced the number of frugivorous bird individuals by 29% and the length of frugivorous bird visits by 68%, relative to controls. In contrast, low-intensity removal (41% of ripe fruit removed) had no impact on these metrics. Frugivore species richness did not differ among treatments and controls, but the composition of the frugivore community was altered by harvest, with the presence of 11 species being linked to fruit abundance. Nonfrugivorous birds did not respond to either intensity of fruit harvest. The number of fruit-eating mammal species was 58% lower in both the low- and high-removal treatments, relative to control plots.

These results verify that fruit abundance influences the species composition of frugivore communities and the abundance and foraging behavior of individual species. They also document short-term dependency of fruit-eating mammals on fruit abundance. Harvest of fruit from forest systems, a common practice in tropical forests, therefore can affect populations of fruit-eating animals.

Key words: Amazonia; Brazil; Euterpe oleracea; *extractive reserves; fruit–frugivore interactions; fruit harvest; fruit tracking; non-timber forest products; palm trees; parrots; vertebrate population ecology.*

INTRODUCTION

A central theme in ecology is how animals respond to variation in food abundance and distribution. For some species, resource fluctuation may drive seasonal movements or regulate populations (Wiens 1976, Foster 1982, Loiselle and Blake 1991, Fleming 1992, Rodenhouse and Holmes 1992, van Schaik et al. 1993, Adler 1998, Wright et al. 1999, Johnson and Sherry 2001). Other species may simply switch their diet in response to scarcity of a given prey type (Martin et al. 1951, Whelan et al. 2000). However, clear examples of such responses of vertebrates to variation in food abundance are rare. A principal reason is the difficulty

of accurately quantifying food abundance: human perception of resources is typically different from that of their study organisms. Fruit-eating animals offer a solution to this problem because from an evolutionary perspective, their food is ''made to be eaten'' (Snow and Snow 1980). Fruits are found on a predictable subset of plants and are presented in a conspicuous way because their consumption increases plant fitness. Thus, they are relatively easy to find and accurately count.

Studies that have quantified fruit production have generally shown that frugivorous birds (i.e., species that include >50% fruit in their diet) are most abundant when and where fruits are most abundant (Wheelwright 1983, 1991, Levey 1988, Loiselle and Blake 1991, 1993, Jordano 1994, Powell and Bjork 1995, Rey 1995, Kinnaird et al. 1996, Malizia 2001, Renton 2001; but see Herrera 1998). A major design constraint of these studies is that they are based on correlations. Conse-

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quently, their most basic conclusion, that frugivores track fruit supplies over space and time (Levey and Stiles 1992), may be misguided. Moreover, alternative explanations are rarely considered. For example, fruiting phenology may be tied to seasonal shifts in the abundance of fruit-eating birds, not vice versa (Fuentes 1992, Noma and Yumoto 1997). Alternatively, abundances of frugivores and fruits may both respond to the same external cues, such as weather or habitat change, rather than to each other (Davis 1945, Karr and Freemark 1983, Herrera 1998, Restrepo et al. 1999). The only way to determine conclusively the response of frugivores to variation in fruit abundance is via experimentation (Rey 1995, Adler 1998, Sherman and Eason 1998).

For several reasons, palms are unusually amenable to experiments that explore the relationship between fruit and frugivore abundance. First, palm fruits are eaten by a wide diversity of birds and mammals (Terborgh 1986, Bodmer 1990, Allen 1997, Adler 1998, Galetti et al. 1999) and in many regions are considered "keystone" resources that maintain frugivore populations during periods of food scarcity (Terborgh 1986, Snyder et al. 1987, Peres 2000). Second, palms often form dense, monodominant stands (Peters et al. 1989, Kahn 1991). In such forests, fruit production by other species is minimal. Third, palm fruits are produced on discrete infructescences that are relatively easy to remove (Henderson 1995). Finally, many species of palm fruits are harvested by humans and are used as food or as a source of income (Kahn 1991). This human harvest of fruits provides an opportunity to extract large quantities of fruit with relative ease. All of these advantages applied to our study species, *Euterpe oleracea*, along the Amazon River in eastern Brazil.

We first monitored abundances of palm fruits, parrots, parakeets, and macaws (hereafter "parrots"), the most frequent visitors to fruiting *E. oleracea* trees, in four *E. oleracea*-dominated forest stands and in four nearby forest stands that lacked *E. oleracea*. Because we found that parrot activity was closely associated with times and places of ripe palm fruit abundance, we then attempted to confirm, on a smaller scale and with a broader set of frugivores, that palm fruit abundance directly impacts frugivore abundance. In replicated 1.8-ha plots, we experimentally tested the sensitivity of frugivorous birds and mammals to two levels of reduced fruit availability, each of which mimicked a different type of harvest regime by humans. In addition to abundance and species richness, we monitored and compared frugivore foraging behavior in plots. We included both seed-dispersing frugivores and seed-consuming frugivores in our analyses.

Although our study was framed ecologically, it has direct relevance to conservation of Amazonian forests, which are under increasing pressure on several fronts (Anderson 1990*a*, Laurance 2000). Brazil has implemented a strategy to conserve Amazonian forests through a system of extractive reserves, areas designated for the long-term sustainable harvest of forest products, including fruit (Fearnside 1989). The success of this conservation strategy hinges on the effective merger of profitable resource utilization with conservation of biodiversity. However, the effects of harvesting non-timber resources on species diversity are largely unexplored (Hall and Bawa 1993). Thus, another goal of our study was to determine at what level of fruit harvest frugivores abandon harvested areas, an essential ingredient in the formulation of sustainable harvest guidelines.

MATERIALS AND METHODS

Study species

Euterpe oleracea occurs throughout eastern Amazonian Brazil, along the Pacific coast of Colombia and northern Ecuador, and in Trinidad, Venezuela, and the Guianas (Henderson 1995). Across ~10 000 km² of floodplain forests in the Amazon River estuary, it forms monodominant stands, some of which are the result of its management (Calzavara 1972, Peters et al. 1989, Kahn 1991). Individual genets (hereafter "trees") contain up to 25 slender stems that reach heights of 30 m (Henderson 1995). Reproductive stems produce infructescences bearing several thousand purple-black globose drupes (hereafter "fruits") ~1 cm in diameter (van Roosmalen 1985). The fruits are among the most commonly harvested and highly valued native fruits in eastern Amazonia (Anderson 1988, 1990*b*, Muñiz-Mirit et al. 1996). Fruits, colloquially called "açaí", are harvested by climbing stems and severing infructescences (Anderson 1988).

Study sites and plots

We worked at the 33 000-ha Ferreira Penna Scientific Station (1°42′30″ S, 51°31′45″ W), operated by the Emílio Goeldi Museum of Belém and located within Caxiuanã National Forest in the municipality of Melgaço, Pará State, Brazil (Fig. 1). Annual rainfall totals 2500–3000 mm, mean annual temperature and relative humidity are 26°C and 85%, respectively, and the vegetation is evergreen humid rain forest (Lisboa 1997). The majority of the site is nonflooded, terra firme forest. However, ~3300 ha along the Bay of Caxiuanã are flooded during the rainy season (December–May) and high tides. Water depths reach their maxima (~1 m) in May. Much of this floodplain forest is dominated by *E. oleracea*, with *Virola surinamensis* (Myristicaceae) and *Pterocarpus santalinoides* (Fabaceae) also common (Ferreira et al. 1997). *E. oleracea* fruit begin to appear in May and persist until September. There are currently no homes in, nor management of, this forest (Moegenburg 2000).

Data collection took place in two types of study plots: monitoring plots and experimental plots (Fig. 1). The monitoring plots were established in 1997. Four
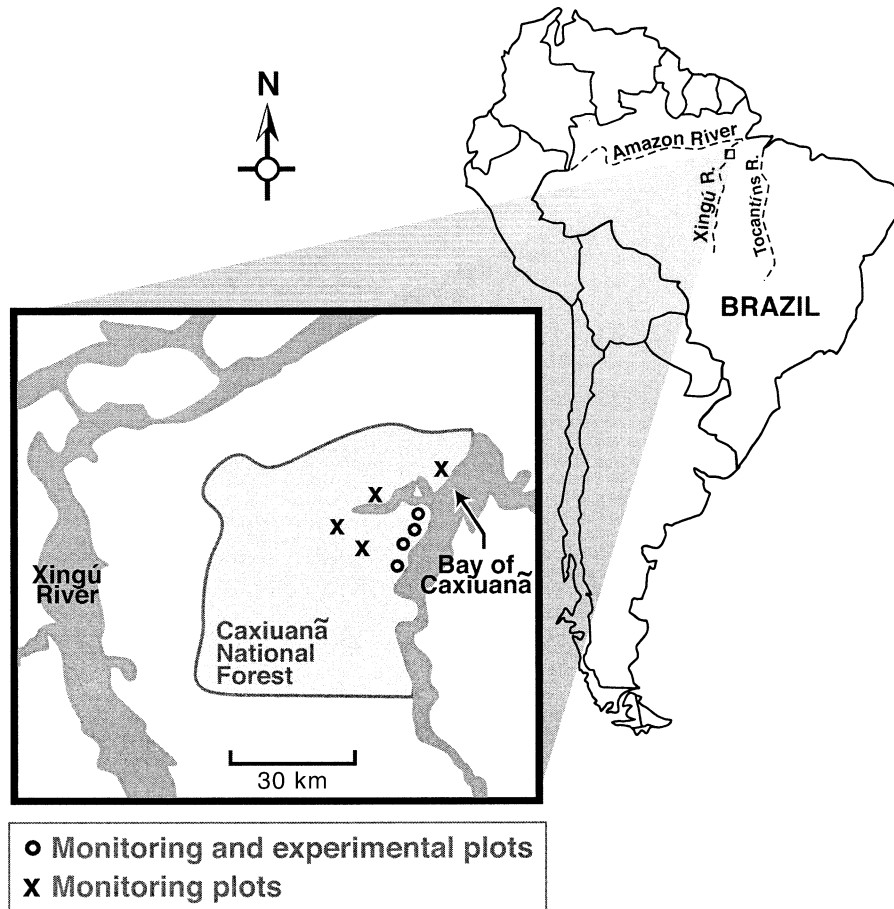
FIG. 1. Map of study sites showing four monitoring and experimental plots and four monitoring plots.

(Plaquinha, Fazenda, Miriti, and Moreira) were in floodplain palm forest (hereafter ''palm forest'') and were located ~1 km apart along the Bay of Caxiuanã. The remaining four (Estação Sur, Estação Norte, Heliporto, and Inventório) were in nearby terra firme forest (hereafter ''non-palm forest''). Monitoring plots were 1-ha squares bisected by a 100-m transect and were used for monitoring fruit availability and parrot abundance. The experimental plots were established in 1998 in the same palm forest sites and were used for monitoring fruit availability and frugivore abundance. These experimental plots were 1.8-ha circles that were divided into three equal, pie-shaped subplots, which were further divided by transects extending from the center of the plot to the midway point of each subplot's perimeter (Fig. 2).

Fruit availability

Fruit availability was estimated by recording the number and sizes (small, medium, large) of infructescences bearing ripe fruit. In the monitoring plots, this was done twice monthly during the peak of the fruiting season (July–August) for 50 trees along the 100-m transect ($n = 200$ trees, total). In the experi-

mental plots, this was done twice monthly for the entire fruiting season (May–August) for 20 trees along each of the three subplot transects ($n = 240$ trees, total).

To convert infructescence size to fruit mass, we collected and weighed fruits from five infructescences of each size class. The average mass for each class was multiplied by the total number of infructescences of that class. This total fruit mass was then divided by the number of trees sampled to yield kilograms of fruit per tree. To determine fruit abundance per hectare, per tree fruit biomass was multiplied by the number of trees per hectare.

Parrot use of palm vs. non-palm forest

In 1997, we conducted four parrot surveys in each of the monitoring plots in palm forest stands and three in each of the monitoring plots in non-palm forest stands. A survey consisted of slowly walking back and forth along the 100-m transect for 3 h (0700–1000 hours), recording for all parrots within the plot the species, size of group (when possible), and time spent in plot. The observer sometimes left the transect or stopped for several minutes to identify species, count individuals, or record data. Otherwise, a continuous
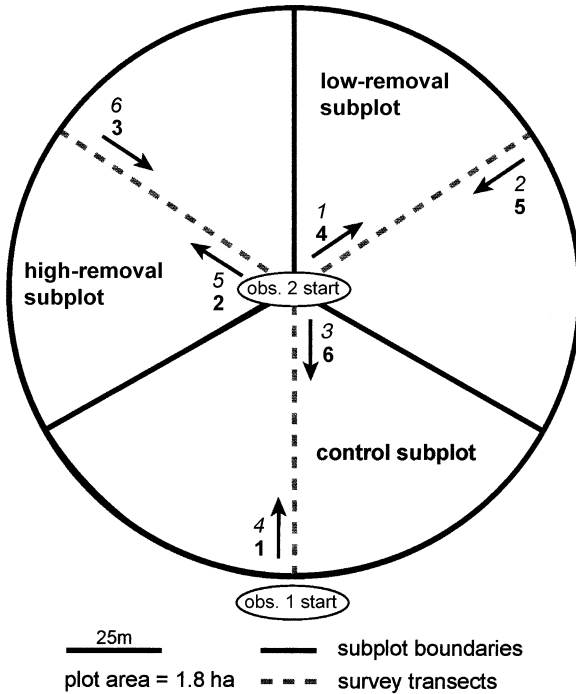
FIG. 2.   Schematic map of an experimental plot, divided into three subplots, each with a 75-m transect down the middle. One subplot was randomly designated high fruit removal, another low fruit removal, and the third control. During surveys, observer 1 (obs. 1) began near the edge of the control subplot, while observer 2 (obs. 2) started at the plot center. Boldface and italicized numbers next to arrows indicate paths and directions walked by observers 1 and 2, respectively.

slow walk was maintained to increase the likelihood of observing the arrival of parrots that entered the plot. Most parrot groups were quite conspicuous because of vocalizations, which we quickly learned. Particular attention was paid to the location of parrots, so that groups could be distinguished and visit lengths could be calculated.

We estimated the number of minutes that parrots spent in plots as the longest interval between observations of a particular group. At the end of the season, average group size for each species was calculated from all observations in which group size could be ascertained. (We detected no change in parrot group sizes over the season.) For each group, we multiplied the number of minutes that it spent in the plot by the average group size for that species. The sum of this value for all groups observed during a survey, termed ''visit length,'' was used in analyses.

Frugivore responses to experimental fruit harvest

In each experimental plot, one subplot was randomly selected for the high-removal treatment (~75% of ripe fruit removed) and one for the low-removal treatment (~40% of ripe fruit removed). These harvest intensities mimic extraction for both consumption and marketing of fruit (high-removal treatment) and for household

consumption only (low-removal treatment). The remaining subplot in each plot was left as a control (no fruit removal).

We began monitoring frugivores in all subplots at the beginning of the 1998 fruiting season (May) and continued at biweekly intervals (i.e., every two weeks) until the end of the fruiting season (August). Fruit harvest commenced halfway through this period, allowing comparisons of frugivores within individual subplots pre- and post-harvest, and among subplots assigned to the different treatments, a statistically powerful design for experiments with limited replication ($n =$ four experimental units; James and McCulloch 1995).

Harvests were done on a biweekly schedule, one day prior to frugivore surveys in a given plot. Harvesters, who lived nearby and were skilled at collecting fruit, were instructed where to harvest, but not which infructescences to harvest. Thus, harvested infructescences were those that would actually be selected by local people. Harvest from some trees (<5% of those in fruit) was impossible, as they were too thin and fragile to allow climbers to safely reach the infructescence.

Animal surveys in the experimental plots included all fruit-eating birds and diurnal mammals. Moreover, although their abundance was not expected to change in response to fruit harvest, we sampled nonfrugivorous birds as a general gauge of seasonal fluctuations in bird abundance and as a control against response to harvest activity not related to fruit abundance. Animals were classified as frugivores, partial frugivores, granivore/frugivores, insectivores, or carnivores based on personal observations of fruit eating and on reports in the literature (see the Appendix; Hilty and Brown 1986, Levey 1988, Levey and Stiles 1992, 1994, Remsen et al. 1993, Ridgely and Tudor 1994, Emmons 1997). Note that we consider ''frugivores'' to be those animals that consume ripe or unripe fruit, regardless of whether they disperse seeds (many parrots destroy seeds).

Fruit and frugivore surveys were conducted on the same days in each experimental plot. Fruit surveys followed the previously established protocol. To survey fruit-eating birds and mammals, two observers simultaneously walked transects from 0700 to 1300 hours, one starting at the plot edge and the other at the plot center. They walked slowly toward the center or edge, respectively, allowing 30 min to complete a 75-m transect (Fig. 2). Observers were always in different subplots and walked each transect twice during a survey. Because surveys were conducted at about two-week intervals, with few intervening visits to plots, it is unlikely that animals became habituated to our presence or modified their behavior. Each observer recorded on a map the time and location of vertebrates seen or heard, paying particular attention to subplot boundaries. Multiple and often simultaneous observations by the two observers were compiled to provide detailed data on animal location and behavior. We followed sev-

eral rules when estimating the number of animals and their visitation times. First, the number of individuals in a group, if not readily countable, was assumed to be the average number of that species in groups. Second, when an animal was first detected in one subplot and later in another, it was assumed to have spent equal amounts of time in the two subplots. Four pre-harvest and four post-harvest surveys were conducted in each plot.

Statistical analyses

Parrot use of palm vs. non-palm forest.—We used a least squares regression between ripe *E. oleracea* fruit and the number of minutes (''visit length'') that parrots spent in monitoring plots (SAS Institute 1996). Because the samples at each site were not independent, they were first averaged.

Frugivore response to experimental fruit harvest.— Data from the fruit harvest experiment were analyzed using a repeated-measures factorial ANOVA (SAS Institute 1989). When necessary, data were log- or square-root transformed to achieve normality and reduce heteroscedasticity. The four pre-harvest and four post-harvest surveys were first averaged to control for lack of independence. The between-model factor was ''treatment'' (control, low-removal, and high-removal), and the within-model factor was ''time'' (pre-harvest vs. post-harvest). Response to fruit harvest is indicated by a significant ''treatment × time'' interaction term. Response variables were fruit abundance, number of frugivore species, number of individuals, and visit lengths. The latter three were analyzed separately for frugivorous birds, nonfrugivorous birds, and mammals, for a grand total of 10 response variables. Because we had only four replicates, our ability to detect true differences between treatments was low. To increase statistical power and reduce Type II error, we used an alpha level of 0.1. However, because we made multiple comparisons for each group of organisms, we adjusted alpha values accordingly (Bonferroni sequential technique; Rice 1989).

We used data from the 1998 fruit removal experiment to identify ''fruit-sensitive species,'' those whose presence was affected by fruit abundance. We included only ''regular'' visitors (i.e., species that occurred in >75% of the samples) and included only visits >5 min. Fruit-sensitive species were identified by two methods. First, we simply identified the species that were absent from high-removal and low-removal subplots, once fruit harvest began. Second, we used logistic regression to determine: (1) which species' presence/absence was predicted by fruit abundance, and, for each of those species, (2) how much fruit would be required for 25%, 50%, 75%, and 99% probabilities of that species visiting a plot.

Results

Parrot use of palm vs. non-palm forest

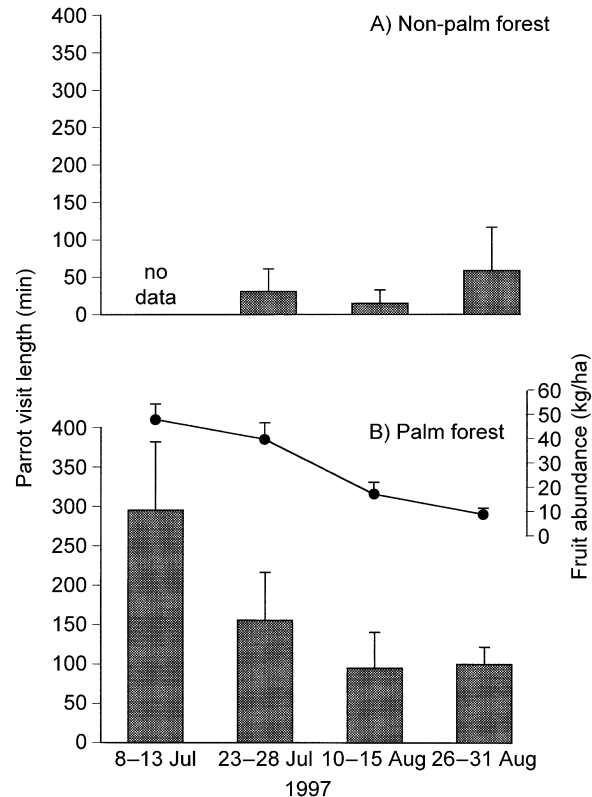Average sizes of the parrot groups that visited the monitoring plots were: *Pyrrhura perlata*, Pearly Parrot,

FIG. 3. Parrot visit lengths during 3-h surveys in 1-ha monitoring plots in (A) four non-palm forest stands and (B) four *Euterpe oleracea*-dominated forest stands. Visit lengths in palm forest stands were significantly correlated with the *E. oleracea* fruit abundance (line). All values are mean + 1 SE.

(12), *Pionites leucogaster*, White-bellied Parakeet (4), *Deroptyus accipitrinus*, Red-fan parrot (3), *Amazona amazonicus*, Orange-winged parrot (2), and *Ara* spp., *Macaw* spp. (2). In the non-palm forest plots, visit lengths of parrots showed no temporal trend (Fig. 3A). In contrast, parrot visit lengths in the palm forest plots were greatest at the initial survey and declined steadily through late August (Fig. 3B). These visits were 48–92% longer than those in the non-palm forest (paired *t* test; $t = 3.69$, df = 22, $P < 0.001$) and were positively correlated with ripe fruit abundance ($r^2 = 0.41$, $F_{1,12} = 8.45$, $P < 0.02$).

Frugivore responses to experimental fruit harvest

Fruit availability.—Fruit production in experimental plots in 1998 peaked in July and declined through August (Fig. 4A). Ripe fruit availability did not differ among treatments in the pre-harvest phase ($F_{2,18} = 0.95$, $P = 0.44$; Fig. 4) and, as expected, harvest significantly reduced fruit abundance in the post-harvest phase ($F_{2,18} = 4.02$, $P = 0.07$; Fig. 4A–C). Low-removal treatments averaged 41% less fruit than controls ($F_{1,18} = 4.15$, $P = 0.09$), whereas high-removal treatments averaged 75% less fruit ($F_{1,18} = 10.52$, $P = 0.02$). However, low-

Pre-harvest　　Post-harvest

A) control

B) low removal

C) high removal

Fruit abundance (kg/ha)

Early May　Late May　Early Jun　Late Jun　Early Jul　Late Jul　Early Aug　Late Aug
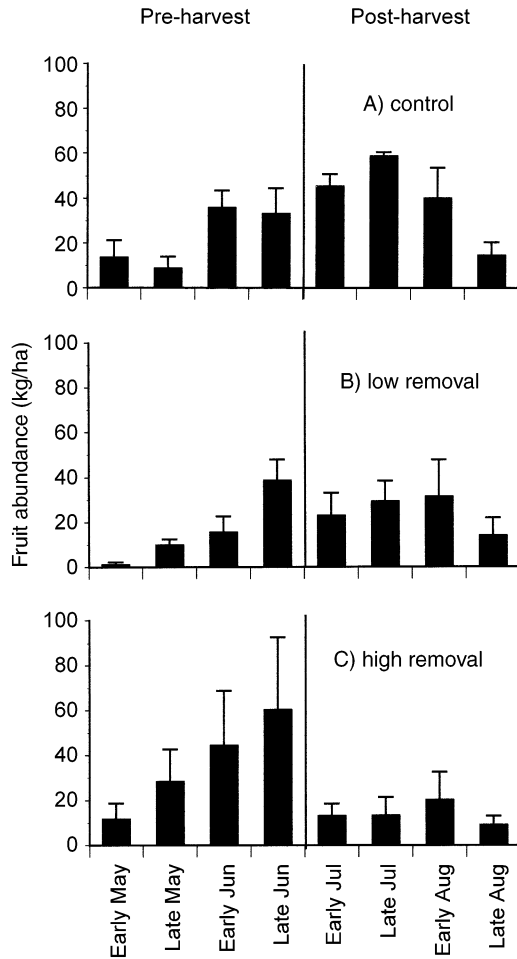
FIG. 4. Average *Euterpe oleracea* fruit abundance in four sites over time, in (A) control, (B) low-removal, and (C) high-removal experimental treatments. Surveys in May and June are pre-harvest; those in July and August are post-harvest. Both low-removal and high-removal treatments had significantly lower fruit abundance than controls. Values are means + 1 SE.

removal and high-removal treatments did not differ significantly in fruit abundance ($F_{1,18} = 1.46$, $P = 0.27$).

Birds: community-level responses.—Frugivorous and nonfrugivorous birds differed in their responses to reductions in fruit abundance. The "treatment × time" interaction was significant for the number of frugivorous individuals and their visit lengths, but not for the number of frugivorous species. The "treatment × time" interaction was not significant for any measure of nonfrugivores (Table 1).

Forty-one species of frugivorous birds visited the experimental plots (Appendix). We found no differences among treatments in the number of frugivorous species ($F_{2,18} = 0.34$, $P = 0.72$), individuals ($F_{2,18} = 0.13$, $P = 0.88$), or their visit lengths ($F_{2,18} = 0.04$, $P = 0.96$) in the pre-harvest phase (Fig. 5). In the post-harvest phase, however, the number of individuals declined by 29% ($F_{2,9} = 4.83$, $P = 0.04$), and visit lengths

declined by 68% ($F_{2,9} = 3.98$, $P = 0.06$) in the high-removal subplots compared with the controls (Fig. 5). The number of species did not differ among treatments ($F_{2,9} = 2.63$, $P = 0.13$). Moreover, high-removal treatments had significantly fewer individuals ($F_{1,9} = 10.62$, $P = 0.01$) and shorter visit lengths ($F_{1,9} = 10.48$, $P = 0.01$) than the low-removal treatments (Fig. 5). In contrast, low-removal subplots showed no significant differences from controls in the number of individuals ($F_{1,9} = 0.93$, $P = 0.36$) or visit lengths ($F_{1,9} = 0.01$, $P = 0.99$).

Forty species of nonfrugivorous birds visited the plots (Appendix). No "treatment × time" interaction terms were significant for these species (Table 1). In particular, nonfrugivores showed no differences in number of species, number of individuals, or visit lengths among treatments (all P's > 0.83). Variances of these parameters were similar to those for frugivorous birds (Fig. 5).

"Time" was a significant effect in all six bird analyses (Table 1). This factor compares the responses of birds in May and June (the pre-harvest phase) with those in July and August (the post-harvest phase), independent of treatment. For both frugivorous and nonfrugivorous birds, the number of species, number of individuals, and visit lengths were generally higher later in the season than earlier (Fig. 5).

Birds: species-level responses.—Although overall species richness of frugivorous birds did not decline after fruit harvest, a number of species showed sensitivity to harvest. Twenty species of frugivorous birds were regular visitors to the pre-harvest experimental plots. Of these 20, 11 species were fruit sensitive (Appendix), meaning that their visits to plots changed once harvest began. Six of the 11 fruit-sensitive species totally ceased their visits to the high-removal sites. This group consisted of the Palm Tanager (*Thraupis palmarum*), the Collared Trogon (*Trogon collaris*), the Red-fan Parrot (*Deroptyus accipitrinus*), two parakeets (White-bellied, *Pionites leucogaster*, and Canary-winged, *Brotogeris versicolorous*), and the Scarlet Macaw (*Ara macao*). Only one species, the White-tailed Trogon (*Trogon viridis*), stopped visiting low-removal sites. No species stopped visiting control sites.

Logistic regression revealed four additional fruit-sensitive species (Table 2). The probability of these species occurring in plots increased as fruit abundance increased. The most sensitive to fruit availability was *Rhitipterna simplex* (Grayish Mourner), requiring 103 kg/ha (24 medium infructescences, which hold ~2900 fruits) and 1448 kg/ha (339 medium infructescences) of fruit for a 25% and 99% chance of occurring, respectively. The least sensitive was *Vireo olivaceus* (Red-eyed Vireo), requiring 32 kg/ha (seven medium infructescences) and 583 kg/ha (137 medium infructescences) of fruit for a 25% and 99% chance of occurring, respectively.

TABLE 1. Results of repeated-measures ANOVAs examining responses in number of species, number of individuals, and visit lengths of (A) frugivorous birds, (B) nonfrugivorous birds, and (C) mammals to experimental fruit harvest.

Source of variation	No. species				No. individuals				Visit lengths			
	df	F	P	Adj. sig.	df	F	P	Adj. sig.	df	F	P	Adj. sig.
A) Frugivorous birds												
Time	1	5.07	0.05	†	1	18.95	0.002	‡	1	18.30	0.002	*
Treatment	2	2.87	0.13		2	5.19	0.05		2	3.41	0.10	
Treatment × time	**2**	**2.63**	**0.13**		**2**	**4.83**	**0.04**	‡	**2**	**3.98**	**0.06**	*
B) Nonfrugivorous birds												
Time	1	9.70	0.01	*	1	12.33	0.007	‡	1	8.18	0.02	†
Treatment	2	0.51	0.63		2	0.87	0.47		2	0.23	0.80	
Treatment × time	2	0.18	0.84		2	0.17	0.84		2	0.15	0.86	
C) Mammals												
Time	1	18.79	0.005	‡	1	6.548	0.043	*	1	0.693	0.430	
Treatment	3	33.74	0.004	‡	3	23.29	0.001	*	3	12.07	0.0059	†
Treatment × time	**2**	**7.435**	**0.024**	‡	**2**	**3.723**	**0.089**		**2**	**2.883**	**0.133**	

Notes: Adjusted significance levels are as follows: † $P < 0.01$; * $P < 0.05$; ‡ $P < 0.033$. Boldface indicates a significant response to the experimental treatment in the treatment × time interaction.
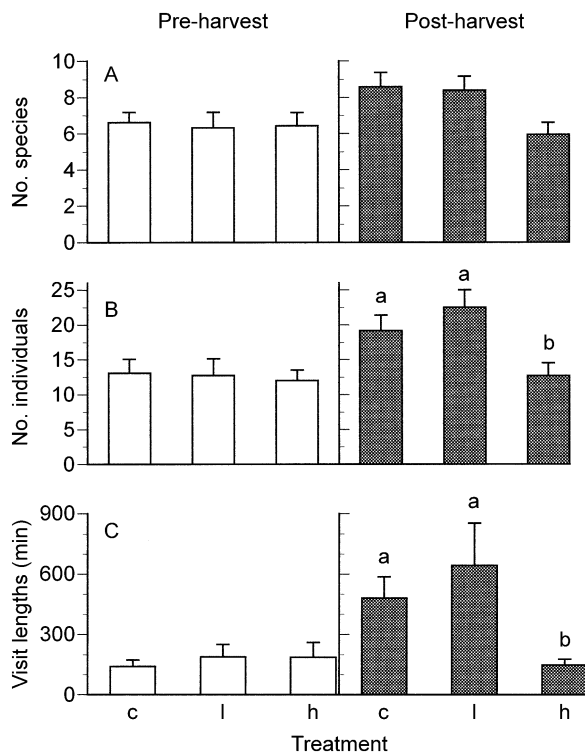

FIG. 5. Effects of *E. oleracea* fruit harvest on the number of (A) frugivorous bird species, (B) number of individuals, and (C) their visit lengths in control (c), low-removal (l), and high-removal (h) treatments. Different letters above columns indicate significant differences among them in that harvest phase. No differences existed pre-harvest (open columns). Post-harvest (gray columns), high-removal treatments had significantly fewer individuals that spent less time than did the controls and low-removal treatments. Values are mean + 1 SE.

Mammals.—Five species of mammals known to eat *E. oleracea* fruit were observed in the plots: Guianan squirrel (*Sciurus aestuans*), South American coati (*Nasua nasua*), brown capuchin monkey (*Cebus apella*), red-handed howler monkey (*Alouatta belzebul*), and golden-handed tamarin (*Saquinus midas*).

The "treatment × time" term was significant for number of species, but not for number of individuals or visit lengths (Table 1). As with birds, mammals showed no differences in the number of species, individuals, or visit lengths among treatments in the pre-harvest phase (Fig. 6, Table 1). Post-harvest, however, the number of mammal species was 58% lower in both the high-removal ($F_{1,18} = 9.59$, $P = 0.02$) and the low-removal ($F_{1,18} = 9.59$, $P = 0.02$) treatments compared with the controls; the low- and high-removal treatments did not differ ($F_{1,18} = 0.01$, $P = 0.99$). The lower species richness in high-removal subplots reflects the total lack of visits by howler monkeys and tamarins once fruit harvest began. Howler monkeys, but not tamarins, also stopped visits to low-removal treatments after fruit harvest; squirrels and capuchin monkeys made less frequent visits post-harvest to low-removal treatments, resulting in the lower species richness. Too few observations of coatis were made to detect a pattern for that species. Unlike species richness, the number of individuals and their visit lengths did not differ among the treatments after fruit harvest (Fig. 6; all *P*'s > 0.09).

As with birds, the number of mammal species ($F_{1,18} = 18.78$, $P = 0.005$) and number of individuals ($F_{1,18} = 29.26$, $P = 0.043$) showed an overall significant response to "time," independent of the level of harvest (Table 1). More species and individuals occurred in all three treatments post-harvest (Fig. 6).

DISCUSSION

Frugivores responded strongly to both natural and experimental variation in palm fruit abundance. When

TABLE 2. Significant results of logistic regression between *Euterpe oleracea* fruit abundance (independent variable) and the probability (25–99%) of the presence of six frugivorous bird species (dependent variable).

Species	χ^2	P	Amount of fruit needed (kg/ha) to attract birds, by occurrence probability			
			25%	50%	75%	99%
Ara macao	2.87	0.090	73	197	238	718
Pionites leucogaster	5.02	0.020	47	140	233	528
Pyrrhura perlata	8.82	0.003	13	87	160	395
Attila cinnamomeus	3.66	0.050	100	203	307	635
Rhitipterna simplex	2.90	0.080	103	363	622	1448
Vireo olivaceus	3.16	0.080	32	42	172	583

Notes: The presence of the other 35 frugivorous bird species was not predicted by fruit abundance. All df = 1.

intensive fruit extraction by people was mimicked (75% removal of ripe fruit; high-removal treatment), frugivorous bird abundance and visit lengths and frugivorous mammal species richness were significantly reduced. Moreover, the species composition of the frugivorous bird community changed in harvested sites. Removing 41% of the ripe fruit (low-removal treatment) had no such effects. That nonfrugivorous birds showed no differences among treatments implies that
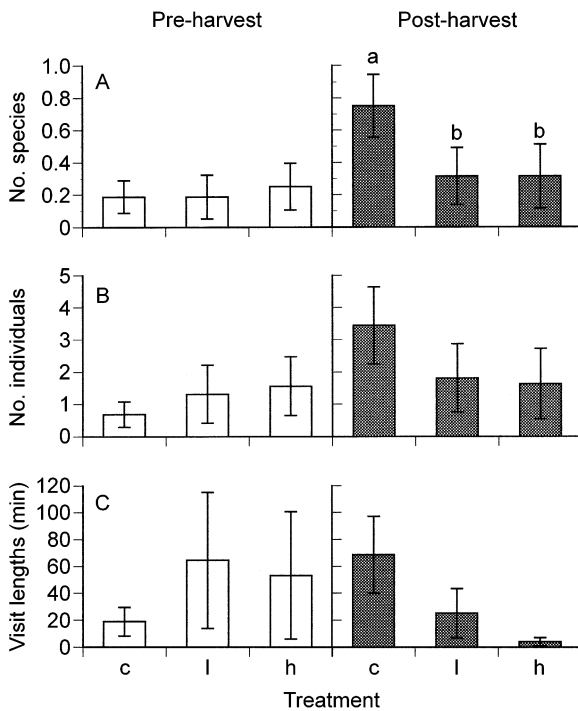

FIG. 6. Effects of *E. oleracea* fruit harvest on (A) the number of frugivorous mammal species, (B) the number of individuals, and (C) their visit lengths in control (c), low-removal (l), and high-removal (h) subplots. Different letters above columns indicate significant differences among them in that harvest phase. No differences existed pre-harvest (open columns). Post-harvest (gray columns), both high-removal and low-removal treatments had significantly fewer species, but the number of individuals and the time they spent did not differ. Shown are mean ± 1 SE.

factors other than fruit abundance were not responsible for the observed patterns in frugivore abundances. Although fruit abundance was manipulated on a small scale relative to the home ranges of most frugivores, we argue that the same responses may occur at larger scales because: (1) fruit harvest is both extensive and intensive throughout the region; (2) frugivores are more abundant in large tracts of managed forest stands that have higher production of *Euterpe oleracea* fruit than in nonmanaged stands (Moegenburg and Levey 2002), and (3) region-wide, *E. oleracea* fruit production occurs during a period of community-wide fruit scarcity.

Frugivore responses to fruit harvest

Birds: community-level responses.—Spatial and temporal fluctuations in tropical frugivore abundance can be affected by many factors, including weather, breeding cycles, anthropogenic edges, and resource abundance (Karr 1976, Herrera 1998, Restrepo et al. 1999). Of these, food abundance has been most often correlated with frugivore abundance across many scales (Snow 1962*a, b*, Levey 1988, Loiselle and Blake 1993, Stouffer and Bierregaard 1993, Wright et al. 1999), implying that frugivores track fruit abundance across space and time (Loiselle and Blake 1991, Powell and Bjork 1995, Rey 1995, Kinnaird et al. 1996; but see Herrera 1998). However, most previous studies are not experimental, raising doubts about (1) whether fruit abundance or other factors not measured cause changes in frugivore abundance, and (2) whether frugivores respond to fruit abundance or whether plants fruit at times when fruit removal is likely to be highest (e.g., during migration; Thompson and Willson 1979, French 1992, Fuentes 1992).

Several previous studies have experimentally explored the link between fruit abundance and frugivore ecology. Removal of fruit from Trumpeter (*Psophia leucoptera*) territories in Peruvian rain forest demonstrated that fruit abundance determined minimum territory size, at least during periods of general fruit scarcity (Sherman and Eason 1998). Addition of fruit to isolated populations of spiny rats (*Proechimys semispinosus*) in Panama increased rat reproductive success

(Adler 1998). In Spanish olive orchards, Rey (1995) found that the two most common species of frugivorous birds (Blackcap, *Sylvia atricapilla*, and Song Thrush, *Turdus philomelos*) responded to harvest of olives by tracking olive abundance on local and regional scales. If the strong influence of fruit abundance found in these experimental studies represents a general pattern, then fruit abundance may explain frugivore abundance and behavior in foraging flocks (Chapman et al. 1989, Develey and Peres 2000), in individual fruiting trees (Howe and Vande Kerckhove 1980), within and among habitats (Levey 1988, Loiselle and Blake 1993, Malizia 2001, Renton 2001), across regions and elevations (Levey and Stiles 1992, Stouffer and Bierregaard 1993, Rey 1995, Blake and Loiselle 2000), and through time (Martin and Karr 1986, Bronstein and Hoffmann 1987, Kinnaird et al. 1996, Wright et al. 1999).

Our results differ from those of Galetti and Aleixo (1998), who studied responses of birds to reduced *Euterpe edulis* palm fruit abundance resulting from harvest for heart-of-palm in the Atlantic forest of Brazil. They found no difference in the abundance of frugivorous birds in unharvested and harvested forests, despite 96% lower palm density in the latter. Clearly, such a large reduction in palm abundance would have induced a large response from frugivores in our Amazonian site.

We propose three explanations for the different outcomes of these studies. First, as Galetti and Aleixo (1998) suggest, the 96% reduction of palm density may have represented a small overall loss of fruit in the community, because *E. edulis* produces fruit concurrent with many other species of trees. In contrast, *E. oleracea* at our site produces fruit at a time when few other species are in fruit (Lisboa 1997). Second, because Galetti and Aleixo measured fruit fall rather than fruit production, they may have miscalculated the amount of fruit actually available to frugivores. Third, the studies were done on different spatial and temporal scales. Galetti and Aleixo sampled birds in a much larger area from which palms had been harvested 5–10 years previously. The long lag time between harvests and the commencement of their study probably reduced differences between their control and treatment sites, relative to differences between our control and treatment sites, which were sampled the day after harvest. Alternatively, the different spatial scales of the two studies may indicate that the small-scale differences we measured do not hold at larger scales (but see Rey 1995).

Birds: Species-level responses.—Although the number of species did not differ among treatments after fruit was harvested, the identity of the species that continued to visit differed in two ways. First, 11 species were found to be ''fruit-sensitive'': they either discontinued visits to high-removal sites (six species) or low-removal sites (one species), or their visits depended, according to logistical regression, on fruit abundance

(four additional species). In practical terms, managers could use these data to establish the minimum amount of fruit that should remain in harvested areas to ensure, within a chosen probability, the persistence of a certain species. These ''fruit-sensitive species'' account for the reduction in species richness in high-removal plots (Fig. 5). The second component of the change in species composition after harvest was less consistent visits to plots by other species (e.g., White-necked Thrush, *Turdus albicollis*, and Red-headed Manakin, *Pipra rubrocapilla*), presumably because reduced fruit availability caused by harvest forced them to search a wider area for food (Chapman et al. 1989, Fleming 1992). These results underscore the need to dissect overall species richness into the responses of individual species.

Our results parallel other studies of fruit–frugivore relationships that show no response of species richness to fruit abundance at the community level, but show responses of individual species. In some studies, the abundances of the most highly frugivorous species seem especially linked to fruit availability (Pratt and Stiles 1983, Levey 1988, Loiselle and Blake 1993). For example, Levey (1988) found a positive relationship, in Costa Rica, between abundance of fruit and two highly frugivorous species (Red-capped Manakin, *Pipra mentalis*, and White-collared Manakin, *Manacus candei*), but not between fruit abundance and community-wide abundance of frugivores. Similarly, Rey (1995) found positive correlations between olive abundance and some frugivores in some plots, some of the time. Further study is needed to identify which traits of frugivores more or less tie their occurrence to fruit abundance.

Our findings of community- and species-level responses to *E. oleracea* fruit abundance differ from the results of Herrera (1998), who found virtually no evidence of fruit tracking by frugivores across 12 years in a 4-ha plot in montane Spain. Despite strong preferences for certain species of fruit by the two major frugivores (*Sylvia atricapilla* and *Erithracus rubecula*, European Robin), Herrera found that abiotic factors, not fruit abundance, were correlated with frugivore abundance across years. This decoupling of interannual abundance of fruit and frugivores, and the apparent ''indifference'' of frugivores to variation in fruit abundance, has led to reconsideration of the evolutionary significance of fruit–frugivore mutualisms (e.g., Herrera 1998, Levey and Benkman 1999, Restrepo et al. 1999).

Our study provides an alternative interpretation of Herrera's (1998) results. The most important determinant of frugivore abundance may not be *absolute* fruit abundance at one particular site, but rather fruit abundance at that site *relative* to fruit abundance at other sites within the frugivores' ranges, information not given in Herrera's study. This point is exemplified when two results of our experiment are considered to-

gether. First, frugivore abundance and visit lengths were always lowest in the high-removal experimental subplot, suggesting that frugivores chose sites in which to forage by ''comparing'' among the available sites. Second, the presence or absence of most species of frugivores could not be predicted in logistic regression solely by fruit abundance, suggesting that relative fruit abundance, not absolute abundance, affects frugivore foraging choices (Levey 1988). The highly mobile nature of avian frugivores implies the need to study their fruit-tracking behavior in response to conditions across their entire ranges (Loiselle and Blake 1991, Kinnaird et al. 1996).

Mammals

Both low and high intensities of fruit removal reduced the species richness of fruit-eating mammals. The number of individuals and visit lengths, however, were unaffected by intensity of fruit harvest. Howler monkeys, tamarins, and squirrels showed the most significant responses to fruit harvest, apparently avoiding the areas from which fruit had been harvested. Of the three primate species observed in plots, howler monkeys are the most frugivorous ($>71\%$ of the diet consists of fruit; Jardim and Oliveira 1997, Pina 1999). The other two primates, tamarins and capuchin monkeys, consume a more balanced diet of insects and fruit (Chapman and Fedigan 1990, Peck et al. 1999). That these large-bodied mammals responded to fruit harvest treatments on a scale of 0.6 ha demonstrates their sensitivity to small-scale differences in food availability within their much larger home ranges. A similar response of mammals was reported by Allen (1997), who found that agouti and tayra responded to differences in availability of *Mauritia flexuosa* (Palmae) fruit by removing a significantly greater proportion of fruit from areas with low fruit availability. Fruit abundance not only affects the behavior of fruit-eating mammals, but also can regulate their populations (Foster 1982, Terborgh 1986, Bodmer 1990, Adler 1998, Wright et al. 1999). Intensive harvest of *E. oleracea* fruit over a large area could therefore have population-level impacts.

Further explanation is necessary for three methodological issues affecting both birds and mammals. First, because trees were not climbed in control plots during harvests, the differences that we detected in frugivore activity among treatments may have been due to human activity associated with fruit harvest rather than to the reduction of fruit. Because fruit harvest occurred a full day prior to the frugivore surveys, and because non-frugivorous birds showed no sensitivity to harvesting activities, however, we believe that the responses of frugivores were directly due to the reduction in fruit availability. Second, despite the difference in mean fruit removal between the two treatments (75% and 41%), fruit abundance did not differ statistically between them. This may be because the difference was

not great enough, or because of the high variance-to-mean ratios within treatments. That we found differences between the number of individuals and visit lengths of frugivorous birds between these two treatments suggests that the difference in fruit availability was biologically significant. Nevertheless, this result must be interpreted with caution.

Finally, for mammals, frugivorous birds, and non-frugivorous birds, both species richness and abundance were consistently higher in the post-harvest phase than the pre-harvest phase, irrespective of treatment. This pattern was likely to be due to several factors. First, total fruit availability was higher in July and August than in May and June (Fig. 4), which probably attracted more individuals of more fruit-eating species to the plots. Second, the post-harvest phase followed the breeding season for most bird species, which are thought to breed soon after the end of the rainy season, i.e., May (J. Cardoso da Silva, *personal communication*). This may have allowed species that do not breed in the flooded forest to spend time there later in the season. Finally, the post-harvest phase also coincided with the complete dry-down of the forest floor, which is periodically inundated at other times from tidal and seasonal floods. This may have increased habitat suitability for terrestrial or understory species, such as the Silvered Antbird (*Sclateria naevia*) and Euler's Flycatcher (*Empidonax euleri*).

Conservation implications

Euterpe oleracea is only one of hundreds of species of fruit that are harvested from tropical forests (Vasquez and Gentry 1989, Moegenburg 2002). Some, like *E. oleracea*, are harvested for subsistence and regional markets only. Others are intensively harvested to meet national or international demands. In Brazil, for example, ~50 000 tons (=50 000 Mg) of Brazil nuts (*Bertholettia excelsa*, Lecythidaceae) are collected annually from wild trees, and in India, ~1251 tons (=1251 Mg) of amla fruit (*Phyllanthus emblica*, Euphorbiaceae) are harvested each year (Panayotou and Ashton 1992, Shankar et al. 1996). As our data suggest, extraction of fruit from forests may negatively impact fruit- and seed-eating animal populations. Of the birds most sensitive to *E. oleracea* fruit harvest, at least one (Scarlet Macaw, *Ara macao*) is considered vulnerable to extinction (Parker et al. 1996). Several other rare species also rely on *E. oleracea* fruit. The Golden Parakeet (*Guarouba guarouba*), for example, favors the fruits from *E. oleracea* (Sick 1993) and is one of the most threatened psittacids in the Brazilian Amazon (Oren and Novaes 1986).

If the frugivores impacted by fruit harvest are seed dispersers, then their reduced abundance and activity may also affect dispersal of seeds (DeSteven and Putz 1984, Strahl and Grajal 1991, Hamann and Curio 1999, Loiselle and Blake 2002). Less time spent in fruiting patches may increase the dispersal of ingested seeds if

frugivores are forced to move farther and more frequently in search of food (Pratt and Stiles 1983). On the other hand, less frequent and shorter visits can mean that fewer total seeds are ingested and dispersed (Davidar and Morton 1986, Sargent 1990). In the case of *E. oleracea*, legitimate seed dispersers (e.g., *Ramphastos* spp.) remove fruit pulp, a requirement for germination, whereas seed predators (e.g., *Amazona* parrots) usually consume both pulp and seed (S. Moegenburg, *unpublished data*). Thus, a change in the relative abundance of seed dispersers and seed predators may alter patterns of seed deposition and regeneration. Ingestion of fruit by dispersers is also important for *E. oleracea* because lack of dispersal results in high mortality from insect seed consumers near parent plants (S. Moegenburg, *unpublished data*).

Our data also suggest that moderate levels of fruit harvest may not substantially impact frugivore abundance and behavior. We stress that our conclusions are based on our 1.8-ha plot sizes, and that our study has limited power to determine frugivore responses to harvest on the larger scale at which extraction takes place. In response to ''real-world'' harvest, frugivores may migrate in search of food (Loiselle and Blake 1991), switch diets (Rey et al. 1996), or have lowered reproduction (Adler 1998) or survival (Wright et al. 1999). Frugivore responses may depend, in part, on the availability of alternative food sources, which we did not measure.

The harvest of marketable species from tropical forests, especially fruits and seeds, forms the basis of extractive reserves (Fearnside 1989) in Brazil and elsewhere. For extractive reserves to meet their dual goals (resource utilization and biodiversity conservation), the effects of resource use on other plants and animals must be understood through further research (Hall and Bawa 1993). Our study can inform the development of sustainable fruit harvest policies in two ways. First, it suggests that intensive fruit harvest may not be ''benign'' (Anderson 1988, Peters et al. 1989, Peters 1996). Second, it suggests that moderate levels of harvest may be compatible with the conservation of frugivore abundance. We conclude that forests dedicated to fruit harvest should be considered as complements to, not substitutes for, more fully protected areas.

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APPENDIX A

A table providing the diet classification of birds species observed in *E. oleracea* experimental plots is available in ESA's Electronic Data Archive: *Ecological Archives* E084-067-A1.