

Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil

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Summary

1. It has been suggested that palm fruits are keystone resources for frugivores in tropical rain forests, but no study has addressed this hypothesis. The effects of the harvesting of a dominant palm tree *Euterpe edulis* were studied over 2 years in the Atlantic forest of Brazil.

2. The abundance of 15 large frugivorous birds from five families (Ramphastidae, Cracidae, Cotingidae, Trogonidae and Psittacidae) was estimated using unlimited distance point counts (IPA) and encounter rate.

3. Although all species studied are known to eat *Euterpe* fruits, only one Cotingidae (*Carpornis melanocephalus*) and one Ramphastidae (*Ramphastos vitellinus*) were negatively affected by the removal of this palm from the forest.

4. This result indicates that *Euterpe* palms in the lowland forests do not fulfil the role of keystone species, because they bear ripe fruits during the period of peak overall fruit availability and because birds may switch their diets to other food sources when palms are removed.

5. Palm-heart exploitation is not recommended in small forest areas, nor in areas where *E. edulis* bears fruit during the period of overall fruit scarcity. Only long-term monitoring can evaluate the responses of the bird and mammal communities to the harvesting process.

Key-words: census, Cotingidae, *Euterpe*, keystone species, Ramphastidae.

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Introduction

Since the seminal paper of Paine (1969) on inter-tidal rock communities, the term 'keystone species' has been widely used. The idea that regulation of communities resembles a puzzle and that the removal of a single piece can cause the collapse of the entire community has been well accepted among researchers, policy makers and conservationists.

In the last few years an avalanche of studies has attempted to detect keystone species, including plants (White 1994; Ratsirarson, Silander & Richard 1996), soil biota (Whitford 1996), parasites (McCallum & Dobson 1995), insect and vertebrate pollinators (Fujita & Tuttle 1991; Manning & Goldblatt 1996), seed dispersers (Howe 1984, 1993), anadromous fish (Willson & Halupka 1995), woodpeckers (Daily, Ehrlich & Haddad 1993), kangaroo rats (Heske,

Brown & Guo 1993), prairie dogs (Miller, Ceballos & Reading 1994) and large predators (Terborgh 1992a). Evidence for the keystone species hypothesis derives mainly from controlled experiments (e.g. Menge *et al.* 1994; see also Bond 1993 and Mills, Soulé & Doak 1993 for reviews), but experiments are impractical on a large scale and for many organisms, such as large vertebrates. In these cases, studies that compared areas with and without possible keystone species produced suggestive results (Wright, Gompper & De Leon 1994).

It has been widely accepted that palms and figs are keystone resources for frugivores in tropical forests, because they bear large fruit crops during periods of fruit scarcity and are consumed by large assemblages of frugivores; from small birds to bats, monkeys and ungulates (Leighton & Leighton 1983; Terborgh 1986a,b; Bodmer 1990; Lambert 1991; Lambert & Marshall 1991; Peres 1994; Ratsirarson, Silander & Richard 1996). In regions where figs and palms are rare, other species have been identified as keystone species (Gautier-Hion & Michaloud 1989).

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This deep-rooted concept has been publicised in several books for the general public and in scientific text books (Terborgh 1992b; Moffett 1993; Primack 1993; Eblen & Eblen 1994; Whitmore 1995; Hunter 1996), but the hypothesis has never been really tested for tropical frugivores and much of what we consider as keystone species is based on weak evidence (Gautier-Hion & Michaloud 1989).

The impact of harvesting a so-called keystone palm tree species on the population density of vertebrate frugivores in a Neotropical rain forest is assessed in this study. The palm *Euterpe edulis* Martius is a dominant palm species and the population decline of some bird species in the Brazilian Atlantic forest has been attributed to the over-harvesting of *E. edulis* (Collar *et al.* 1992; Collar, Crosby & Stattersfield 1994). At least 30 birds and 13 mammal species, including toucans (*Ramphastos* spp., *Selenidera maculirostris* and *Baillonius bailloni*), guans (*Penelope obscura* and *Pipile jacutinga*), parrots (*Pyrrhura frontalis* and *Brotogeris tirica*), rodents (*Agouti paca*, *Dasyprocta agouti* and *Proechymis* spp.), tapirs (*Tapirus terrestris*), deers (*Mazama* spp.) and bats (*Artibeus lituratus*) consume the fat and sugar rich palm fruits during winter, which is considered to be a period of general fruit scarcity (Laps 1996; Reis 1996).

Euterpe edulis has been over-harvested for palm-heart extraction throughout its distribution in the Atlantic forest (Hodge 1965; Henderson, Galeano & Bernal 1995) and large palm populations only remain in a few well-protected reserves (Galetti & Chivers 1995). *Euterpe edulis* is a single-stemmed palm and it is necessary to sacrifice the plant for the extraction of the heart (apical meristem or cabbage). Palm-heart harvesting is not ecologically and economically sustainable unless strictly managed (Pereira 1993; Ribeiro *et al.* 1993). The structure of canopy trees in a harvested forest remains unaltered, but the understorey vegetation surrounding the harvested palm is drastically disturbed during the harvesting process.

Study sites

This study was carried out from October 1993 to December 1995 at the Parque Estadual Intervales, a 490-km² reserve of Atlantic forest in the Paranaípiacaba mountains in southern São Paulo, Brazil. The abundance of frugivorous birds was studied in the Base do Saibadela (24°14'08"S, 48°04'42"W), Sete Barras, São Paulo. Elevation varied from 70 to 300 m above sea level. The annual rainfall in 1994 was 4244 mm and in 1995 was 3958 mm. In 1994, the maximum temperature was 41°C and the minimum was 3°C, in 1995 the maximum temperature was 42°C and the minimum was 11°C.

Two areas were chosen to compare the abundance of birds: the Saibadela area within the Parque Estadual Intervales (hereafter referred to as unharvested forest) and a private area, located 1 km from the

reserve, that was largely harvested for *E. edulis* (harvested forest) about 5–10 years ago. The climate and topography of both areas are similar.

The unharvested forest consists mainly of primary forest with the canopy reaching up to 35 m in height. The most common plant families are Myrtaceae, Lauraceae and Rubiaceae (Almeida-Scabbia 1996). There are at least 355 bird species in the whole reserve and 233 in the lowland area (Aleixo & Galetti 1997). Palm heart harvesting of *E. edulis* was not known to have taken place in Saibadela forest until we started this study.

The harvested area studied has a similar vegetation to the Saibadela forest, but with a much reduced density of *E. edulis*. In fact, palm-heart harvesting has eliminated a large part of the population of *E. edulis* in the area and the density of adult *Euterpe* trees is now less than 10 individuals per hectare, where in the unharvested forest the density is 255 individuals per hectare. Small-scale selective logging occurred in the harvested area more than 10–15 years ago, but was restricted mainly to edge vegetation and flat areas (Aleixo 1997). In flat areas the natural forest was replaced by banana plantation. The harvested area is affected by occasional hunting and the density of some game species such as solitary tinamous *Tinamous solitarius* is lower than in the reserve (Aleixo 1997).

For the purposes of this paper, we make the assumption that the only thing that differs between the harvested and unharvested areas is the harvest.

Methods

The frugivore assemblage that uses *E. edulis* fruits was well known from previous studies (Laps 1996; M. Galetti unpublished data), but only 15 species of large frugivorous birds from five families (Cracidae, Trogonidae, Cotingidae, Ramphastidae and Psittacidae) that include *Euterpe* fruits in their diet were recorded during this study. Nomenclature and English names of the birds follow Sick (1993).

BIRD CENSUSES

Various methods have been used to estimate bird density (or abundance) in tropical forests, but it remains extremely difficult to obtain a precise value of the bird density for the majority of species (see Terborgh *et al.* 1990). In this study, bird abundance was estimated by two methods: unlimited distance point counts (IPA; Blondel, Ferry & Frochot 1970, 1981) and transect counts (encounter rates) (Willis 1979). Censuses were carried out on dry days, slowly (1 km h⁻¹), and in the morning (from sunrise to 11.00 h) when most birds are active. The sampling effort was similar for all months.

The point counts (IPA or 'stations d'écoute') were placed along eight trails (six in unharvested and two in harvested forest) measuring at least 1 km in length.

Along each trail, 5 'point counts' were spaced 200 m apart. At these points all birds heard or seen during a 20-min period were recorded. At least three trails (or 15 points), randomly chosen, were sampled each month in the unharvested forest and 10 points in the harvested forest. The index of point abundance (IPA) was calculated by dividing the number of contacts by the total number of points sampled. A contact is defined as a record of one individual or a flock of birds in the vicinity of the point. The radius of detection, in this method, is not taken into account because it is very difficult to know how far a bird is calling from the point sampled.

Transect counts (or encounter rates) were calculated by walking along the same eight trails from sunrise to 11.00 h. Each trail was walked twice (sometimes three times) per month depending on the weather conditions. No trail was walked in consecutive days to avoid bias through counting birds in fruiting trees. All study species seen or heard were recorded, with each solitary individual or flock representing a single contact. This method does not take into account the flock size or the distance from the transect, but it has been widely used in other ornithological studies in Brazil (Willis 1979; Willis & Oniki 1981).

FRUIT PRODUCTION

To aid interpretation of the frugivore density data, fruit availability in the harvested and unharvested forest was estimated using fruit traps. In both forest types, 30 fruit traps of 0.25 m² were distributed along forest trails and spaced every 25 m. Each trap consisted of a fibre box with a fine mesh capable of collecting seeds as small as 0.1 mm.

Each month between June 1994 and January 1996 all fruits found in the traps were collected, identified

to the lowest possible taxonomic level and weighed (wet weight). Non-zoochoric fruits were rare, but when present in the traps they were excluded from the sample weighed. *Euterpe edulis* fruits were also weighed separately.

Results

FRUIT PRODUCTION

In both harvested and unharvested forests, overall fruit availability was seasonal (Fig. 1). The total fruit biomass reached 625.2 kg ha⁻¹ and 451.5 kg ha⁻¹ in the unharvested and harvested forest, respectively. *Euterpe edulis* bears ripe fruits during the winter (May to August), and accounted for between 20 and 80% of the biomass of fruits found in the traps during these months in the unharvested forest. The biomass of *Euterpe* fruits in the unharvested forest was 174.3 kg ha⁻¹ and nil in the harvested forest. The difference in the overall fruit biomass was not statistically significant between the harvested and unharvested areas (log-transformed data, $t = 0.994$, d.f. = 19, $P = 0.332$), but there was a statistically significant difference during the fruiting period of *Euterpe* fruits (May to August; $t = 4.91$, d.f. = 7, $P = 0.017$).

CENSUS ESTIMATES

Transect surveys were carried out for 347 h (255.4 km) in the unharvested area and 107 h (58.6 km) in the harvested area. The number of points was also higher in the unharvested area (164 points) than in the harvested area (137 points). This uneven search effort was corrected for in the statistical analysis. The sighting rate of birds in each area is shown in Table 1. The statistical tests were carried out on the frequency data.

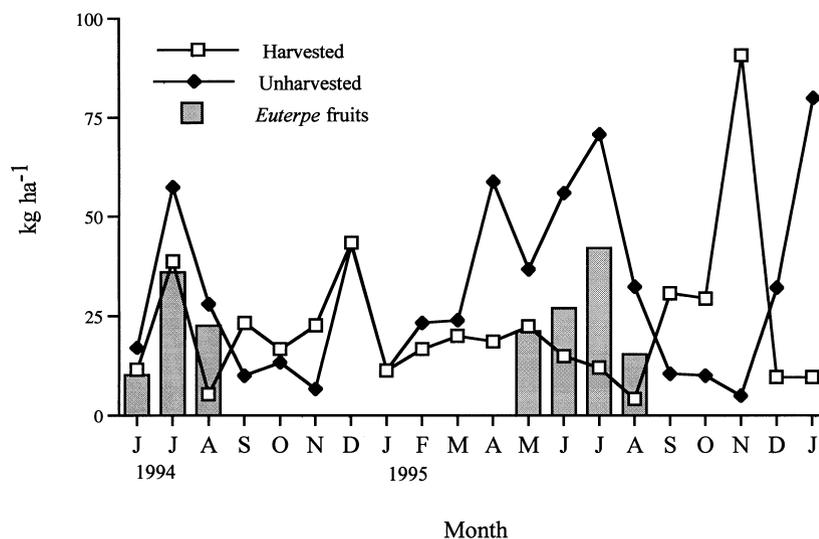


Fig. 1. Fruitfall biomass during a 20-month period in the harvested and unharvested forest (biomass in the unharvested forest include *E. edulis* fruits).

Table 1. Comparative abundance of large avian frugivores that consume *Euterpe edulis* fruits in the unharvested and harvested forests

Species ¹	IPA ²		Transect ³		χ^2 test ⁴ IPA	Transect
	Unharvested 164 points	Harvested 137 points	Unharvested 347 h	Harvested 107 h		
Cracidae						
<i>Penelope obscura</i>	0.03	0.05	0.02	0.08	7.5**	5.59**
<i>Pipile jacutinga</i>	0.01	0.007	0.04	0.02	–	–
Rampastidae						
<i>Bailloni bailloni</i>	0	0.05	0	0.06	–	–
<i>Selenidera maculirostris</i>	0.17	0.16	0.36	0.49	0.04 ^{ns}	3.6 ^{ns}
<i>Rampastos dicolourus</i>	0.1	0.12	0.02	0.06	0.11 ^{ns}	5.01*
<i>Rampastos vitellinus</i>	0.24	0.12	0.45	0.08	5.32*	29.71**
Psittacidae						
<i>Brotogeris tirica</i>	0.92	0.75	2.42	2.31	2.31 ^{ns}	0.49 ^{ns}
<i>Pyrrhura frontalis</i>	0.06	0.07	0.24	0.11	0.03 ^{ns}	5.53*
<i>Triclaria malachitacea</i>	0.22	0.06	0.28	0.23	12.3**	0.64 ^{ns}
Cotingidae						
<i>Carpornis cucullatus</i>	0.01	0.01	0.02	0.04	–	–
<i>Carpornis melanocephalus</i>	0.55	0.15	0.58	0.31	30.4**	10.54**
<i>Lipaugus lanioides</i>	0.006	0.12	0.02	0.12	19.9**	11.61**
<i>Procnias nudicollis</i>	1.00	1.10	0.63	0.59	0.66 ^{ns}	0.21 ^{ns}
<i>Pyroderus scutatus</i>	0.01	0	0.24	0	–	–
Trogonidae						
<i>Trogon viridis</i>	0.86	0.88	1.13	1.09	0.02 ^{ns}	0.1 ^{ns}

* $P < 0.05$; ** $P < 0.01$; ns, not significant; –, not tested for significance.

¹ Nomenclature follows Sick (1993).

² Contacts per point.

³ Contacts per hour.

⁴ The χ^2 test used frequencies corrected for the differences in sampling effort between the two study areas.

COMPARISONS BETWEEN METHODS

The two census methods revealed slightly different results for the effects of palm harvesting on each bird species (Table 1). This includes some discrepancy in the significance of the effects. There is, however, a strong correlation between the results of the point count method and the transect survey method for the unharvested forest ($r = 0.80$, $P < 0.001$) and a modest correlation in the harvested forest ($r = 0.560$, $P < 0.05$). By removing the two outliers (the plain parakeet *Brotogeris tirica* and bare-throated bellbird *Procnias nudicollis*) the methods show an improved correlation ($r = 0.86$, $P < 0.001$ for harvested and $r = 0.97$, $P < 0.001$ for unharvested forest). The abundance of these two species is extremely difficult to estimate. The plain parakeet is extremely mobile and it is likely that the flocks were over-estimated by the transect method. Also, the bare-throated bellbird may have been overestimated by the IPA method, because mostly aural contacts were recorded and this species has a very loud call. It is likely that the same birds were recorded over a distance. Both parakeets (*Brotogeris* and *Pyrrhura*) and the bellbird are difficult to census reliably by the methods used in this study as they clearly violate the assumption of bird censusing that individuals are not counted more than once (Bibby, Burgess & Hill 1992).

The IPA method seems more cautious in detecting

differences between both forested areas (45% of the species were different), while transect counts (encounter rates) showed a slightly higher difference (54% of the species; Table 1). Transect counts detect differences between noisy vagrant species (parakeets and toucans) mainly in the harvested forest, while the IPA method is particularly sensitive to cryptic species that are usually heard, but not seen (blue-bellied parrot *Triclaria malachitacea*, cinnamon-vented piha *Lipaugus lanioides* and the hooded berryeater *Carpornis cucullatus*). As a result of these differences in the census techniques, only those species which were significantly different by both methods were assumed to have different abundances in harvested and unharvested forests (Table 1).

EFFECT ON THE BIRD COMMUNITY

The effect of harvesting can be evaluated at three levels: community, family and species level. As a community the overall abundance of large frugivorous birds was higher in the unharvested forest, but the difference was not statistically significant.

At a species level, two species were significantly rarer in the harvested forest (plus one not present at all), two species were significantly more common in harvested forest (plus one only present in this forest). Four species could not be tested for differences in

abundances in the harvested and unharvested forest due to their rarity in both areas (*P. jacutinga*, *B. bailoni*, *C. cucullatus* and *P. scutatus*). Seven species from 11 tested were either not significantly different or only significant by one method (Table 1).

A month-to-month correlation between the differences in fruitfall and the abundance (transect method) of Cracidae, Cotingidae and Ramphastidae in harvested and unharvested forest, did not show any statistically significant associations in the same month (fruitfall difference \times difference of abundance in Cracidae, $r = 0.09$, $P = 0.68$; Ramphastidae, $r = -0.09$, $P = 0.70$; Cotingidae, $r = -0.354$, $P = 0.125$; Fig. 2) or with the fruitfall of the previous month (Cracidae, $r = -0.11$, $P = 0.62$; Ramphastidae, $r = 0.11$, $P = 0.63$, Cotingidae, $r = 0.26$, $P = 0.26$). These results indicate that the abundance of these three families is not related to fruitfall.

Discussion

ACCURACY OF THE METHODS

Three main methods have been used to detect avian population changes after human disturbance: transect encounter rates (Johns 1986, 1996), mist-netting (Wong 1985) and IPA (this study). As this study focused on large canopy frugivores which are rarely mist-netted, transect encounter rates and IPA were therefore used. The IPA method was found to be more sensitive to elusive cryptic species, such as *Selenidera maculirostris*, *Carpornis* spp., *Triclaria malachitacea*, *Trogon viridis*, *Penelope obscura* and *Lipaugus lanioides*, whereas the transect encounter rate was more sensitive to detection of conspicuous, noisy spec-

ies such as toucans (*Ramphastos*), parakeets (*Brotogetis* and *Pyrrhura*) and jacutinga (*Pipile*).

The two censusing methods showed that between 45 and 50% of species are affected (negatively or positively) by the harvesting process. While some groups showed a tendency to decline, even if not detected by the statistical treatment or sample size, such as the Cotingidae; others are apparently indifferent to harvesting (Psittacidae and Trogonidae). It must also be considered that the unharvested and harvested forest areas studied are close to each other and it is possible that isolated harvested areas may have lower densities of frugivores than that reported here, but in such cases the size of the area *per se* can also affect the frugivore density (Willis 1979).

EFFECTS OF PALM HARVESTING ON THE BIRD COMMUNITY

The effects of palm harvesting on the bird community was not drastic. This could be explained partially because *E. edulis* bears ripe fruits during the peak of overall fruit availability and therefore, other food sources are available to the birds. Moreover, the species are not dependent on *Euterpe* fruits and all species have a flexible diet (Galetti 1996).

Even the so-called *Euterpe*-dependent birds, such as the cinnamon-vented piha *Lipaugus lanioides* (see Collar, Crosby & Stattersfield 1994) were, in fact, more abundant in the palm-harvested forest. *Lipaugus* is the main seed disperser of *E. edulis* in the highlands of Intervales, but its diet is diverse (Laps 1996). Galetti *et al.* (1997) observed that the abundance of jacutinga *Pipile jacutinga* is not related to the *E. edulis* fruit availability.

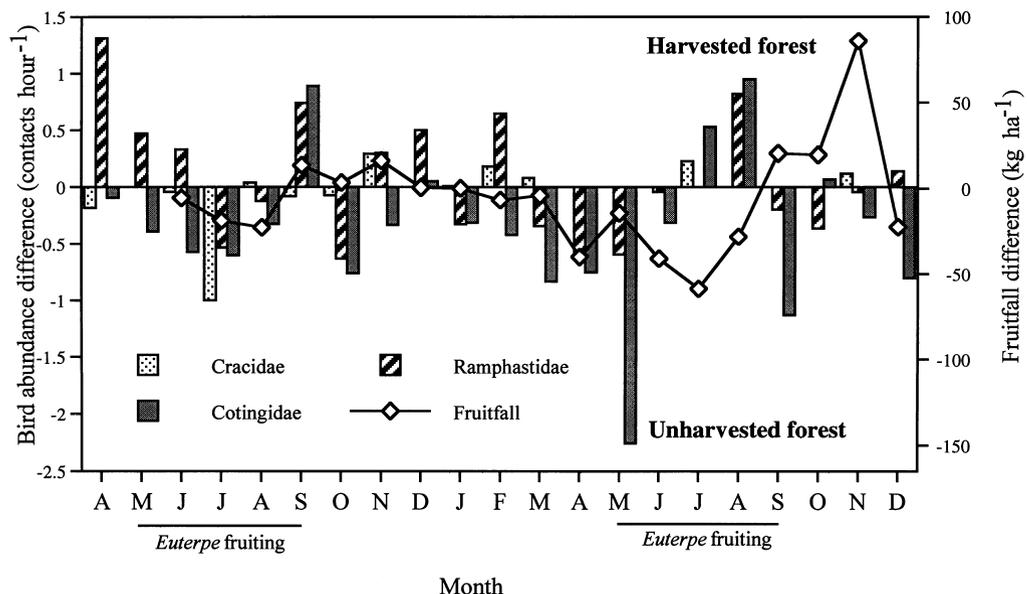


Fig. 2. Differences in bird abundance (encounter rate) and fruitfall biomass (including *E. edulis* fruits) between harvested and unharvested forest in each month.

Toucans (*Ramphastos*, *Selenidera* and *Baillonius*) and cotingas (*Procnias* and *Pyroderus*) are highly fruit dependent, but they may be able to shift to more available fruits (or even insects) in the harvested forest. *E. edulis* has been considered a keystone species because it bears ripe fruits in the winter, a period of overall fruit scarcity in the highlands of Serra do Mar (Laps 1996), but in the lowland forests the winter corresponds to the period of peak fruit production (Galetti 1996). It is hypothesized that Myrtaceae fruits are the main fruit source for birds in the palm harvested forests. Psittacidae (parrots and parakeets), on the other hand, are known to be highly vagrant and their populations showed marked fluctuation over time (Pizo, Simão & Galetti 1995). The psittacid species studied have a generalist diet (Galetti 1996) and the blue-bellied parrot, which is considered *Euterpe*-dependent (Collar *et al.* 1992), showed statistically different abundance only in the IPA method. Trogonidae (e.g. *Trogon viridis*) eat large amounts of insects and complement their opportunistic diet with fruits (Remsen, Hyde & Chapman 1993) and they were not expected to have been affected by *Euterpe* harvesting.

The effects of palm harvesting on the black-headed berry-eater *Carpornis melanocephalus* abundance, may be due to the reduction of understorey fruiting plants, rather than the removal of *Euterpe* palms. This cotinga consumes a wide array of understorey berries, such as Nyctaginaceae, Rubiaceae and Melastomataceae, and only 7.7% of its diet is composed of palm fruits (M. Galetti, unpublished data). The channel billed toucan *Ramphastos vitellinus* is highly vagrant and uses a wide diversity of fruits. Its decline in the harvested forest is not understood, since this species thrives in disturbed habitats (personal observation).

KEYSTONE PLANTS FOR FRUGIVORES RECONSIDERED

Palm fruits are an important food source for several species of mammal and bird (Terborgh 1986a,b; Zona & Henderson 1989) and there has been speculation that the removal of these plants from tropical forests would drastically reduce the diversity and abundance of frugivores (Terborgh 1986a,b).

Gilbert (1980) was the first to mention the importance of 'keystone mutualism' for frugivores and Howe (1984) suggested that the removal of a few 'pivotal' species can cause a 'domino effect' and the whole community would be affected. The hypothesis of keystone plant species gained force after the study of Foster (1982), who described a higher vertebrate mortality in Barro Colorado Island, Panama, after the failure of many fruiting plants caused by El Niño. Based on these ideas, Terborgh (1986a,b) extrapolated the term for tropical forests based on his studies in Peru. He pointed out that 12 plant species (mainly palm fruits and figs) provide the main energy source

to sustain the frugivore community in periods of extensive fruit scarcity.

Recent evidence suggests, however, that the high mortality of mammals in Panama is a seasonal and predictable phenomenon, occurring even in periods without the influence of El Niño (Milton 1990). Catastrophic droughts are, in fact, unpredictable and can affect the population of different groups, including herbivores (folivores), without extinguishing them (Gordon, Brown & Poulsford 1988).

The lack of studies examining the keystone species hypothesis is, probably, because other effects usually work together with the harvesting process (such as logging, hunting and forest fragmentation). Large frugivores (such as guans, ungulates and primates) are the first to disappear in hunted forests, even with low hunting pressure (Silva & Strahl 1991; Peres 1996), and the low abundance of some game species in the harvested area may be due to hunting (e.g. *Pipile jacutinga*, Galetti *et al.* 1997).

Although the results presented here showed that the *Euterpe* palm does not fulfil the role of a keystone species, caution must be observed when applying the conclusions presented here to other areas. Keystone species are site-dependent (Menge *et al.* 1994) and in low-diversity forests or poor fleshy-fruit habitats (such as forest fragments or dry deciduous forests), palm fruits may be more important for frugivores than in the lowland continuous forest. The area studied is extremely rich in fleshy fruits (about 85% of tree species) and showed low seasonality when compared to other tropical forests (Galetti 1996). Also, there is a possible trend suggesting that some groups (toucans and cotingas) may decline in abundance in the harvested forest, but only long-term monitoring can evaluate the responses of these groups. Moreover, the sequence of extinction can be time-lagged, as discussed by Brooks & Balmford (1996) analysing the effects of fragmentation on birds in the Atlantic forest. How fast a population recovers from a severe decline in density depends on species' reproductive rates. Also, long-living species (such as parrots and toucans) will respond slowly to habitat disturbance (Pimm 1991). Information, about reproductive rates of tropical birds is not currently available. Thus, the resilience of each population can be detected in a short-term study, but the effect on the species can be detected only in a long-term study (Pimm 1991; Power *et al.* 1996).

The disturbance caused by the harvesting process of *E. edulis* was evident, since 45–50% of the species were affected, but it is necessary to stress that the high or low consumption of a specific fruit species by the frugivore community does not determine whether a species is 'keystone' or not. It is necessary to evaluate the responses of the community (not single species) to the absence of such a resource over a long time period. If it is impossible or not feasible to have such a natural experiment, then a species cannot be categorized as a

'keystone' species unless theoretical models prove it to be so (see Tanner, Hughes & Connell 1994).

Over the last few years there has been increasing discussion about the keystone species concept. The term 'keystone species' was defined as: '... a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance' (Power & Mills 1995). This definition is a tentative one whose objective is to create a framework for future studies, and it is necessary also to consider species resilience, rate of replacement, and time of the community to re-establish to its climax (Tanner, Hughes & Connell 1994).

Nowadays, there is increasing pressure for implementation of so-called sustainable management in protected reserves in the Atlantic forest. Palm heart exploitation is still very lucrative in the Atlantic forest and several reserves have been harvested illegally (Galetti & Fernandez 1998). We suggest that palm heart management should not be carried out in the highlands, where *E. edulis* is the main food source for birds, nor in small forest fragments. Moreover, long-term monitoring of the bird and mammal populations must be carried out in managed forests.

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