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ORIGINAL ARTICLE

Cebus nigrinus impact the seedling assemblage below their main sleeping sites

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Capuchin monkeys (*Cebus nigrinus*) in Argentina prefer particular sleeping trees they maintain over the years. We compared species composition and abundance of seedlings under these sites with that of control sites. Species richness and abundance of seedlings was higher under sleeping trees than in control plots. Moreover, the proportion of dispersed versus non-dispersed species and individuals by capuchins was higher under the most frequently used sleeping trees than in control plots located in other areas of their home range. Thus, the dominance of plant species dispersed by these primates in the seedling assemblages below sleeping trees confirm the strong weight of *C. nigrinus* and their potential influence in the dynamics of the seedling populations in the forest.

Los monos capuchinos (*Cebus nigrinus*) en Argentina prefieren árboles dormideros particulares que mantienen durante varios años. Comparamos la composición y la abundancia de especies de plántulas debajo de estos sitios con la de sitios controles. La riqueza y abundancia de especies de plántulas fue mayor debajo de árboles dormideros que en parcelas controles. Además la proporción de especies e individuos dispersados vs. no dispersados por los capuchinos fue mayor debajo de los árboles dormideros más frecuentemente usados que en parcelas controles ubicadas en otras partes de su área de acción. Así la dominancia de las especies de plantas dispersadas por estos primates en los ensambles de plántulas debajo de los árboles dormideros confirma el fuerte peso de *C. nigrinus* y su influencia potencial en las dinámicas de las poblaciones de plántulas en el bosque.

Keywords: Argentina; *Cebus*; defecation pattern; seedling diversity

Introduction

Models and hypotheses that address the mechanisms underlying the maintenance of high plant species diversity in the tropics consider the diversity of seed dispersal patterns produced by frugivorous vertebrates (Julliot 1997; Bleher & Böhning-Gaese 2001; Fragoso et al. 2003; Wehncke et al. 2003; Russo et al. 2006). Some studies have documented that the continuous use over several years of core areas and sleeping sites by frugivorous mammals within their home-ranges may be reflected in the seedling composition registered at those specific sites (Lieberman et al. 1979; Howe 1980; Chapman 1989; Tutin et al. 1991; Fragoso 1997).

The repeated use of sleeping trees by primate groups may have important implications for forest dynamics and conservation by influencing the nutrient cycle and plant productivity in tropical forest ecosystems (Feeley & Terborgh 2005). Since arboreal primates spend about half of their lives at sleeping trees (Aquino & Encarnación 1986; Chapman 1989; Heymann 1995; Zhang 1995; Di Bitetti et al. 2000),

over time, feces and seeds accumulate under these sites (Tutin et al. 1991; Théry & Larpin 1993; Julliot 1997; Fragoso et al. 2003). In turn, such concentrations of seeds and fecal material may influence the dynamics of tropical and subtropical seedling populations (Julliot 1997; Fragoso et al. 2003; Russo & Augspurger 2004; Culot et al. 2010).

Cebus nigrinus occupies a variety of habitats in tropical and subtropical forests throughout the southern portion of the Atlantic Forest of South America (i.e. the states of Paraná, Santa Catarina and Rio Grande do Sul in Brazil and the province of Misiones in Argentina). It is an omnivorous species with a diet based on fruit and arthropods (Terborgh 1983; Robinson & Janson 1987; Brown & Zunino 1990). Due to the rapid passage of ingested material through their guts (c. 1.5 h), their large home ranges and the long distances traveled daily, *C. nigrinus* deposits a high diversity of seeds in transit, producing a scattered dissemination throughout its home range, moving seeds to appreciable distances away from the parent plant and defecating seeds with small

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quantities of feces (c.5 g) (Wehncke et al. 2003; Wehncke & Dalling 2005; Wehncke & Domínguez 2007). During observations for 17 consecutive months Di Bitetti et al. (2000) registered that a group of *C. nigrinus* in Iguazú National Park, Argentina, used five of 34 sleeping sites within their range much more frequently. These sleeping sites have been repeatedly used by this group several years before and after this study (M. Di Bitetti, pers. obs.). Based on the high diversity of their diet and a cumulative effect of seeds and feces under those sites one may expect that these monkeys could have the potential to exert an influence on the seedling composition under their most used sleeping sites.

Therefore, our objective was to assess if the repeated use of particular sleeping sites by *C. nigrinus* has the potential to modify the seedling composition below the selected sleeping trees in the forest. We evaluated and compared the species composition of seedlings (particularly, the diversity and richness, and the proportion of dispersed and non-dispersed species), under the four most frequently used sleeping trees by our focal group of *C. nigrinus* (see Di Bitetti et al. 2000 for their use and location), with that of control plots located in other areas of their home range in the subtropical forest of the Iguazú National Park, Argentina.

Materials and methods

Study site

The study was conducted in the Iguazú National Park, Argentina (25° 40' S, 54° 30' W), a humid subtropical forest with a marked seasonality in day length and temperature (Crespo 1982). Annual rainfall in the area averages 2000 mm (Brown & Zunino 1990).

We selected four of the five sleeping sites most frequently used by the focal group (see Di Bitetti et al. 2000 for their use and location), that had a DBH larger than 78 cm. One of the sites (site A) consisted of three *Cordia trichotoma* (Boraginaceae) trees close to each other; site B and D were two *Peltophorum dubium* (Fabaceae) trees; and site C was a *Parapiptadenia rigida* (Fabaceae) tree. Of 34 different sleeping sites, the selected sites were used more than 20 times each by the monkeys, and sleeping in these sites corresponded to >50% of the 203 sleeping nights (Di Bitetti et al. 2000).

Seedling surveys

In December 1998, we delimited 12 plots (1 m², three per site) below the crowns of the sleeping trees, and,

for control, 12 plots (1 m², three per site) at four sites (E–H) in the forest with structurally similar vegetation types as the sleeping sites, avoiding tree fall gaps, and at least 200 m away from all known sleeping sites in the area. Sleeping sites and control plots were recorded within the same week. We arbitrarily classified as seedlings all plants that were up to 0.5 m high. Seedlings of all species were surveyed to assess differences in density and species richness between plots. We used the Shannon–Wiener (H') and Fisher (α) indices to describe the species diversity of the plots. We also used the index of evenness (E) within sites to evaluate the uniformity or the pattern of individuals' distribution between the species. We used the program Species Diversity and Richness version 3.02 (Pisces Conservation, UK), which uses a standard bootstrap method for estimating upper and lower 95% confidence intervals. It also allows the comparison of values after a randomization test, resampling it 10,000 times. We compared H' and E between sleeping sites and control sites using the information of individuals and species in all samples (Magurran 1988).

Additionally, to have a more precise idea about the possible influence of *C. nigrinus* on the species assemblage of these sites, we characterized the plant species recorded in all plots by their probability of dispersal by capuchins (Table 1). We categorized species as “dispersed” (species found in more than 30% of feces), “occasionally dispersed” (found in up to 30% of feces), or “not dispersed” by *C. nigrinus* (species never found in feces). This classification was based on a continuous four-year seed dispersal study with this focal group (Wehncke & Domínguez 2007). The categories “dispersed” and “occasionally dispersed” were then pooled together and proportion of species and individuals dispersed were compared with those not dispersed between controls and sleeping sites using the Mann–Whitney–Wilcoxon test.

Results

We registered a total of 74 species and 438 individuals in the 24 plots. Fifty-eight species were found in sites below sleeping trees and 41 species in control sites in the forest (Table 1). Plant diversity was significantly higher in sites A–D than in the control sites ($H' = 3.5$, $\alpha = 23.2$; $H' = 3.1$, $\alpha = 16.9$; $p = 0.002$; for sleeping and control sites, respectively). Evenness was significantly higher in sites A–D than in the control sites ($E = 0.87$; $E = 0.84$; $p = 0.003$; for sleeping and control sites, respectively).

Of the plant species recorded, 62% had fruits that are frequently dispersed by *C. nigrinus*, 14% had occasionally dispersed fruits, whereas 24% had fruits that

Table 1. Spectrum of species and abundance of seedlings recorded in plots below sleeping trees of *C. nigrilus* and in control sites in the same forest at Iguazú NP, Argentina ($n = 24$ plots).

Species	Sleeping sites	Control plots	Probability of dispersal
Acanthaceae	–	2	Not dispersed
<i>Actinostemon concolor</i>	12	21	Not dispersed
<i>Aegiphila mediterranea</i>	1	–	Occasional
<i>Allophylus edulis</i>	14	2	Dispersed
<i>Allophylus guaraniticus</i>	1	–	Occasional
Asclepiadaceae vine	2	–	Dispersed
<i>Aspidosperma australe</i>	1	–	Not dispersed
<i>Banara tomentosa</i>	3	3	Dispersed
<i>Calliandra</i> sp.	–	3	Not dispersed
<i>Campomanesia xanthocarpa</i>	2	–	Dispersed
<i>Chrysophyllum gonocarpum</i>	1	1	Dispersed
<i>Chusquea ramosissima</i>	2	4	Not dispersed
<i>Citrus aurantium</i>	3	–	Occasional
<i>Cordia trichotoma</i>	1	–	Not dispersed
<i>Coussarea contracta</i>	1	–	Dispersed
<i>Dalbergia frutescens</i>	–	4	Not dispersed
<i>Diatenopteryx sorbifolia</i>	–	4	Not dispersed
<i>Erythroxylum</i> sp.	2	–	Not dispersed
<i>Eugenia pyriformis</i>	4	1	Dispersed
<i>Eugenia</i> sp.	3	3	Dispersed
<i>Euterpe edulis</i>	2	3	Occasional
Fern	4	7	Not dispersed
<i>Guarea</i> sp.	1	–	Dispersed
Herbaceous legume	–	2	Occasional
<i>Inga marginata</i>	7	2	Dispersed
<i>Inga uruguënsis</i>	2	–	Dispersed
Large fern	–	2	Not dispersed
Legume	–	1	Occasional
Legume (herbaceous)	–	2	Unknown
<i>Lycianthes australe</i>	1	–	Dispersed
<i>Machaerium stipitetum</i>	–	1	Not dispersed
<i>Miconia discolor</i>	4	–	Dispersed
Myrtaceae sp. 1 (pecosa)	–	1	Dispersed
<i>Nectandra angustifolia</i>	2	–	Dispersed
<i>Nectandra lanceolata</i>	1	–	Dispersed
<i>Nectandra megapotámica</i>	2	–	Dispersed
<i>Ocotea puberula</i>	1	–	Dispersed
<i>Patagonula americana</i>	5	1	Not dispersed
<i>Paullinia elegans</i>	6	–	Dispersed
<i>Pereskia aculeata</i>	4	2	Dispersed
<i>Pilocarpus pennatifolius</i>	1	–	Occasional
<i>Piper</i> sp. 1	7	12	Dispersed
<i>Piper</i> sp. 2	1	–	Dispersed
<i>Piper</i> sp. 3	2	–	Dispersed
<i>Piper tucumanum</i>	5	–	Dispersed
<i>Psychotria</i> sp. 1	10	2	Occasional
<i>Psychotria</i> sp. 2	15	35	Occasional
<i>Rauwolfia sellowii</i>	2	–	Occasional
<i>Ruprechtia</i> sp.	–	1	Not dispersed
Sapindaceae	8	2	Dispersed
<i>Sebastiania</i> sp.	2	–	Not dispersed
<i>Seguieria aculeata</i>	2	–	Not dispersed
<i>Smylax</i> sp.	4	1	Dispersed
<i>Sorocea bonplandii</i>	–	2	Dispersed
<i>Sorocea ilicifolia</i>	18	7	Dispersed
<i>Strychnos brasiliensis</i>	–	1	Not dispersed

(Continued)

Table 1. (Continued).

Species	Sleeping sites	Control plots	Probability of dispersal
<i>Tetracera</i> sp.	2	1	Dispersed
<i>Trichilia catigua</i>	25	10	Dispersed
<i>Trichilia elegans</i>	11	9	Dispersed
<i>Trichilia mollis</i>	1	–	Dispersed
<i>Trichostigma octandrum</i>	5	1	Dispersed
Umbrella fern	–	1	Not dispersed
Vine (leaning)	–	1	Dispersed
Vine (prickly)	1	–	Dispersed
Vine (Sapindaceae)	2	–	Dispersed
Vine sp. 1	25	11	Dispersed
Vine sp. 2	10	4	Dispersed
Vine sp. 3	1	3	Dispersed
Vine sp. 4	1	–	Dispersed
Vine sp. 5	1	–	Dispersed
Vine sp. 6	1	–	Dispersed
Vine sp. 7	1	–	Dispersed
Vine sp. 8	1	–	Dispersed
Vine sp. 9	–	2	Dispersed
Total seedlings	260	178	
Total species	58	41	
% dispersed	71	56	
% occasional	14	12	
% not dispersed	15	32	

are not dispersed by them (Table 1). Proportions of the number of species dispersed and the number of individual seedlings from species dispersed by capuchins were significantly greater in plots under sleeping sites than in control sites (6 versus 2.5 for species, 7.4 versus 2.4 for individuals, $U = 2.16$, $p = 0.03$, Table 2).

Discussion

We detected a significant influence of *C. nigrilus* on the seedling community present below four consistently used sleeping trees at Iguazú NP. We recognize that the seedling spectrum recorded at any site in the forest does not exactly reflect the seed rain produced by *C. nigrilus*; other natural processes such as secondary seed removal and predation have negative effects on the fates of seeds deposited on the forest floor by the monkeys and even on the seedling and sapling stages (Wehncke et al. 2004; Wehncke 2010). Likewise, the treatment of seeds by dispersers, namely diminishing of seed viability through mastication and the passage of seeds through the digestive tracts, are important factors determining the final fate of seeds (Wehncke & Dalling 2005). Furthermore, the seedling spectrum recorded at the plots will not be translated exactly into a future forest due to differential capacities of the plants to establish and to become mature.

Table 2. Comparison of the number of seedling species and individuals dispersed by *C. nigrinus* between sleeping sites (A–D) and control sites (E–H), at Iguazú NP, Argentina ($n = 24$ plots).

Sites	Number of seedling		
	Species dispersed/ not dispersed	Individuals dispersed/ not dispersed	
Sleeping	A	22 /4	66/11
	B	15/3	51/8
	C	12/2	20/3
	D	29/4	92/9
Totals	49/9	229/31	
Control	E	10/6	36/12
	F	13/3	34/13
	G	10/3	18/5
	H	12/6	38/22
Totals	27/13	126/52	

Bearing in mind these caveats, it is nevertheless evident that the number of plant species as well as the number of seeds germinating was higher under sleeping trees than in the rest of the forest. The conclusion that there is a strong influence of *C. nigrinus* on the seedling spectrum below sleeping trees is further confirmed by the dominance of plant species dispersed by these monkeys in the seedling assemblages at those sites.

This effect results from the continuous use of these sites, leading to a specific type of seed rain generated by a group of *C. nigrinus*. So far, seed dispersal mode by *Cebus* monkeys has been characterized as a scattered deposition pattern of seeds in transit with small quantities of feces per defecation (Wehncke et al. 2003, 2004; Wehncke & Dalling 2005; Wehncke & Dominguez 2007; Valenta & Fedigan 2009). Even though we never saw the clumping of feces below their main sleeping sites when measured at small time scales (on a daily basis; E.W., pers. obs.; Wehncke 2004), the accumulation of feces and the seeds therein over several years has a similar effect. Apparently, both modes may be performed by *C. nigrinus* in association with their pattern of diurnal activity, e.g. a scattered deposition would occur during daily activity whereas a clumped deposition is the result of their nightly sleep.

Large frugivorous mammals and particularly primates are known to have an influence on the seed rain and the seedling composition below consistently used sleeping sites (Lieberman et al. 1979; Howe 1980; Chapman 1989; Tutin et al. 1991; Fragoso 1997) and this is also true for *C. nigrinus*. Dependence on animal behavior for seed transport and deposition means that plants are susceptible to dispersal failure

when their seed vectors disappear. As forests continue to be decimated, significant reductions in disperser population densities are likely to have far-reaching consequences for plant populations and communities.

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